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THE TAXONOMY AND BIOGEOGRAPHY OF THE CICADA GENUS *PAPUAPSALTRIA* GEN. N. (HOMOPTERA, TIBICINIDAE)

Boer, A.J. de, 1995. The taxonomy and biogeography of the cicada genus *Papuapsaltria* gen. n. (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 138: 1-44, figs. 1-190, table 1 [ISSN 0040-7496]. Published 15 June 1995.

The genus *Papuapsaltria* is erected for 18 species, distributed in New Guinea and several nearby islands. Three species (*Thaumastopsaltria nana* (Jacobi, 1903), *Baeturia phyllophora* Blöte, 1960, and *Baeturia ustulata* Blöte, 1960) are transferred to *Papuapsaltria* and redescribed, while 15 species (*P. angulata*, *P. baasi*, *P. bidigitula*, *P. brassi*, *P. dioedes*, *P. dolabrata*, *P. goniodes*, *P. lachlani*, *P. novariae*, *P. plicata*, *P. stoliodes*, *P. spinigera*, *P. toxopei*, *P. ungula*, and *P. woodlarkensis*) are described as new. *Baeturia famulus* Myers is brought into the synonymy of *P. nana* (Jacobi). The phylogeny of *Papuapsaltria* is discussed and some remarks are made on its phylogenetic relationships with some other New Guinean and Australian genera. A very short proximal spine on the fore femur is regarded an autapomorphy for the genus. Several monophyletic subgroups are recognised. Two species (*P. woodlarkensis* and *P. phyllophora*), missing the apomorphy of the genus and not clearly belonging to any of the subgroups, are preliminarily included. A key to the males and maps of distribution are presented.

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Key words. – *Papuapsaltria*, taxonomy, new genus, new species, biogeography, New Guinea.

The great majority of the tibicinid cicadas of New Guinea belong to the '*Baeturia* and related genera complex' as defined earlier (De Boer 1990) by an S-curved aedeagus with winged lateral crests. The genus *Papuapsaltria* is erected for 18 species, clearly belonging to that complex, that could not comfortably be accommodated in any of the existing genera. The species of *Papuapsaltria* are supposed to be closely related, which is corroborated by the distributions of a number of presumed apomorphous characters. Several monophyletic subgroups can be recognized, based upon apparently sound apomorphies. An unambiguous apomorphy for *Papuapsaltria* as a whole could not be found, however. Nevertheless, one character, a very short proximal spine on the fore femur, is shared by most of its species. Furthermore, this character is unique for *Papuapsaltria*.

The phylogenetic position of *P. phyllophora* (Blöte, 1960) and *P. woodlarkensis* sp. n. is very uncertain. These species are included in the genus, since they are more similar to the species of *Papuapsaltria* than to any other species of the '*Baeturia* and related genera complex'.

The phylogenetic relationships of *Papuapsaltria* are discussed; similarities in male operculum suggest a possible sister group relationship with the genus *Guineapsaltria* De Boer.

Papuapsaltria is distributed in New Guinea, including the nearby islands of Yapen, Normanby, and Waigeu, and has an endemic species on Woodlark island. One species, otherwise found in western New Guinea and on Yapen Island, is also recorded from Wetar island near Timor, but not known from any other islands of the Banda area. *Papuapsaltria* has most of its species in Papua New Guinea and seems to be absent from Cendrawasih and the most southern parts of central New Guinea.

MATERIAL AND METHODS

The material examined for this study is deposited in the following collections:

AMNH	American Museum of Natural History, New York
AMSA	Australian Museum, Sydney
BMNH	Natural History Museum [formerly: British Museum (Natural History)], London
BPBM	Bernice P. Bishop Museum, Honolulu
CAS	California Academy of Sciences, San Francisco
ISNB	Institut Royale des Sciences Naturelles de Belgique, Bruxelles

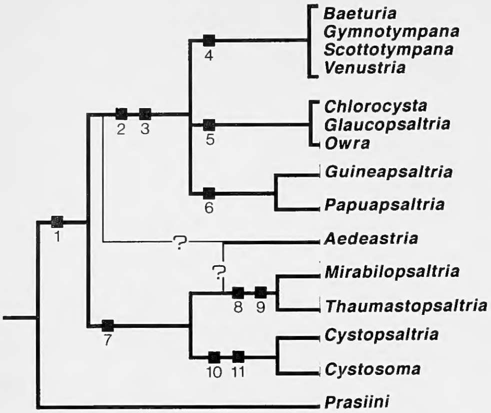


Fig. 1. Phylogenetic relationships of *Papuapsaltria*. Numbers refer to characters discussed in the text.

MCSN	Museo Civico di Storia Naturale 'G. Doria', Genova
Moul	Personal collection Mr M.S. Moulds, Sydney
MVMA	Museum of Victoria, Melbourne
NCSU	North Carolina State University Insect Collection, Raleigh
NMWC	National Museum of Wales, Cardiff
RMNH	Nationaal Natuurhistorisch Museum (formerly: Rijksmuseum van Natuurlijke Historie), Leiden
SMFD	Natur Museum und Forschungs Institut 'Senkenberg' Frankfurt am Main
SMNS	Staatliches Museum für Naturkunde, Stuttgart
SMTD	Staatliches Museum für Tierkunde, Dresden
TMB	Természettudomány Múzeum, Budapest
ZILS	Zoologiska Institutionen Zoologiska Museet, Lund
ZMAN	Instituut voor Systematiek en Populatie Biologie (Zoölogisch Museum), Amsterdam

The following sources have been used for tracing localities: 'Atlas van tropisch Nederland' (1938), 'The Times Atlas of the World Comprehensive Edition' (1968), 'Papua New Guinea a travel survival kit' (Wheeler 1988) and a 'List of New Guinea localities' published by the Bernice P. Bishop Museum (1966).

To examine the male genitalia, the pygofer was pulled out, after overnight softening, with a sharp needle inserted between the pygofer and the 8th abdominal segment. The aedeagus was pulled out at the same time, by inserting the needle between the claspers. Some of the terms used in the descriptions are explained in figs. 12 and 17. Body and tegmen lengths of all specimens were measured, other measurements are based on a maximum of ten specimens, when available.

PHYLOGENY

Papuapsaltria is a fairly heterogeneous genus, which forms part of a larger monophyletic group, defined earlier as the '*Baeturia* and related genera complex' (De Boer 1990). A phylogenetic analysis of this complex, using the computer program PAUP (Swofford 1993) is in preparation. The oriental Prasiini as defined by De Jong (1985), which form the most likely sister group of that complex, will be included as outgroup in this analysis. Preliminary results of the computer analysis indicate that the species of *Papuapsaltria* are closely related, that the genus is probably monophyletic and that it forms the sister group (or groups) of the monophyletic genus *Guineapsaltria* (De Boer 1993a).

The cladograms presented here, showing the phylogenetic position of *Papuapsaltria* within the '*Baeturia* and related genera complex' (fig. 1) and a tentative reconstruction of the relationships of the species of the genus (fig. 2), comply to a large extent with the afore mentioned PAUP analysis. Minor differences are due to the influence of several strongly homoplasious characters, as a result of which the most parsimonious trees do not recognize some of the obvious synapomorphies as such.

The phylogenetic position of *Papuapsaltria*

The presumed apomorphous characters indicated

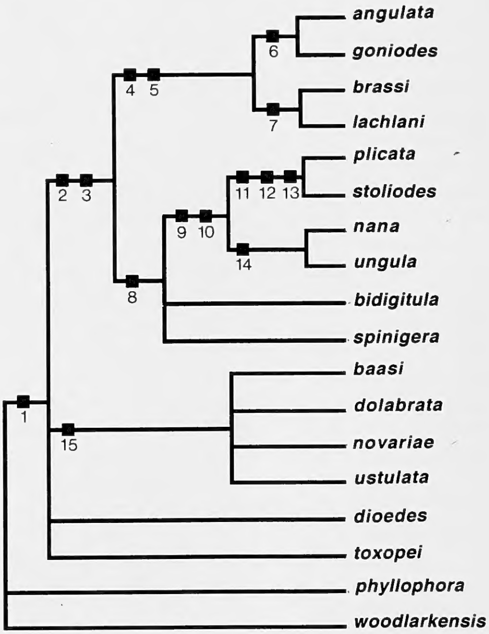


Fig. 2. Phylogenetic reconstruction of *Papuapsaltria*. Numbers refer to characters discussed in the text.

by numbers in the cladogram of fig. 1 are discussed in short. Many of these characters have been discussed earlier (De Boer 1990; 1991; 1992b; 1993a).

1. – Aedeagus S-curved and provided with wing-shaped lateral crests. This is the supposed apomorphy of the '*Beaturia* and related genera complex' (De Boer 1990). The Prasiini have a C-curved aedeagus without lateral crests, which is regarded as plesiomorphous.

2. – Surfaces of head and pronotum fairly smooth; pronotum generally without a distinct medial furrow. This could be two separate characters. Other genera of the complex and the Prasiini have a more wrinkled head and pronotum, while the pronotum generally has a distinct medial furrow, which is regarded as plesiomorphous. This character is not absolutely discriminating; anomalies sporadically occur in both subgroups.

3. – A fairly broad hyaline border along the hind margin of the tegmen. Other genera of the complex and the Prasiini have a very narrow border along the hind margin of the tegmen, which is regarded as plesiomorphous. This character too, is not absolutely discriminating. Furthermore, in *Baeturia* Stål, 1866, this border is quite narrow again, somewhat intermediate relative to the plesiomorphous state.

4. – A large male operculum; the medial margin of the operculum lies medially of the meracanthus. The phylogenetic relationships between the four genera that have this character are discussed in more detail elsewhere (De Boer 1995a). Other genera of the complex and the Prasiini have a generally smaller male operculum, of which the medial margin lies laterally of the meracanthus. Such small opercula are regarded as plesiomorphous. The larger opercula of *P. plicata* and *P. stoliodes* (see below) form two exceptions (see figs 59 & 73) which must be explained by paralellism.

5. – Tegmina with more than 8 apical areas and a more or less continuous band of subapical areas (see plate 22 figs. 2, 3, 6, and 7 in Moulds 1990).

6. – A very small male operculum with a rounded distal part. The distal part is often shorter than the basal part of the operculum. Though this character is not found in all species, it might indicate a sister group relationship between *Papuapsaltria* and *Guineapsaltria*. Such a relationship is in compliance with the most parsimonious computer analyses.

7. – A narrow tymbal cavity. This character is not present in all species of the group it is supposed to define.

8. – The absence of a distinct ridge along the tergite margin bordering the tymbal cavity. This character is also not present in all species of the group it is supposed to define.

9. – A very long first apical area of the tegmen (see figs. 4-5 De Boer 1992b). This character is shared by most species of *Thaumastopsaltria* Kirkaldy, 1900, and some species of *Mirabilopsaltria* De Boer, 1995, and is supposed to be synapomorphous for these two genera together, or for *Thaumastopsaltria* and a part of *Mirabilopsaltria*. In the latter case *Mirabilopsaltria* cannot be regarded as monophyletic (see De Boer 1995b).

10. – Apically pointed tegmina.

11. – Tegmina with reticulate venation (see plate 23 figs. 1-3 Moulds 1990).

The phylogenetic position of *Aedeastria* is ambiguous, as expressed by the question marks in fig. 1. *Aedeastria*, *Mirabilopsaltria*, and *Thaumastopsaltria* share a very similarly shaped angular male operculum and generally very distinct diverging fissures on the vertex. The distinct diverging fissures are possibly synapomorphous for these three genera together. However, nearly all species of *Mirabilopsaltria*, *Cystosoma*, *Cystopsaltria*, and *Thaumastopsaltria* share a strongly bent proximal spine on the fore femur, a character that is also widely distributed in the Prasiini and presumably plesiomorphous. This spine is generally more erect in *Aedeastria* and other genera of the complex, which could be a synapomorphy.

Ingroup phylogeny

A tentative cladogram of *Papuapsaltria* is given in fig. 2. Only characters that are supposed to be apomorphous are discussed here; these are indicated by numbers in the cladogram. The cladogram presented here differs in details from the most parsimonious reconstructions currently calculated by PAUP; differences are caused by a more parsimonious distribution of homoplasious characters. Such homoplasious characters, in which the species of *Papuapsaltria* differ from each other, and which are mentioned in the species descriptions, (e.g., postclypeus shape, number of tymbal ridges, size of auditory capsules, and presence or absence of apical lobes on the aedeagus) are not discussed, since they are presumably of a limited phylogenetic importance. These characters will be included in a final data matrix, which forms the basis for the current computer analysis. The most parsimonious solutions will be published later.

1. – A reduced, knobby, proximal spine on the fore femur (figs. 8-9). This character is regarded as a probable apomorphy for the genus *Papuapsaltria* as a whole, though possibly excluding *P. phyllophora* and *P. woodlarkensis* (see remark below). However, even when these two species are excluded from the genus, this character is not found in all species. *P. bidigitula*, *P. nana*, and to a lesser extent *P. baasi*, *P. dolabrata*, and *P. ustulata*, have a fairly long and generally pointed proximal spine on the fore femur. In these latter species the proximal spine is always distinctly shorter

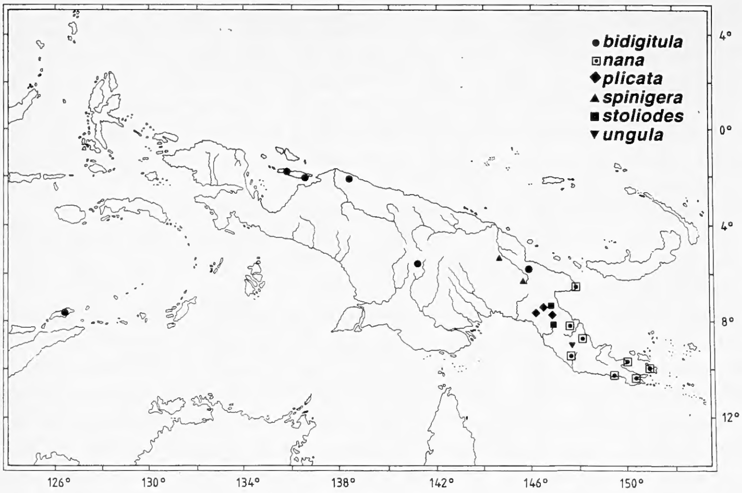


Fig. 3. Localities of *Papuapsaltria bidigitula, P. nana, P. plicata, P. spinigera, P. stoliodes,* and *P. ungula.*

than the distance to the middle spine, however, and it possibly represents just another state of the very same character. Only *P. phyllophora* and *P. woodlarkensis* have a distinctly longer spine; longer than the distance to the middle spine. This latter character is also found in related genera, and therefore presumably plesiomorphous. A reduced spine is unique for *Papuapsaltria.*

2. – A strongly convex distal margin of the pygofer, forming a sometimes weakly incurved distal lobe. The character is less clear in *P. angulata* and considered lost in *P. bidigitula* and *P. nana.* A similar, but smaller and more distinctly incurved, lobe was described for *Scottotympana biardae* De Boer, 1991 and *S. huibregtsae* De Boer, 1991, which must be explained by parallelism. The pygofer of *P. phyllophora* also has a distinctly convex, though much longer, distal margin, and it is not clear whether this fact indicates a close relationship between *P. phyllophora* and the group of 8 species defined by the here discussed apomorphy. The distal margin of the pygofer is only weakly convex in the remaining species of *Papuapsaltria* and in most of the related genera, which is supposedly the plesiomorphous state.

3. – A squarish clasper, without distinct dorsal crest, but with an angular distodorsal corner. This character is not recognized in *P. nana* and *P. ungula,* presumably caused by the development of a globularly rounded dorsodistal protrusion on the clasper (character 14).

4. – A distinct and inwards curving rectangular corner below the lateral protuberance of the pygofer. Due to this incurving corner the ventral part of the pygofer opening is somewhat horseshoe-shaped, with concave margins (fig. 22). The character is unique for four species, but not found in all specimens of one of these four (*P. angulata).*

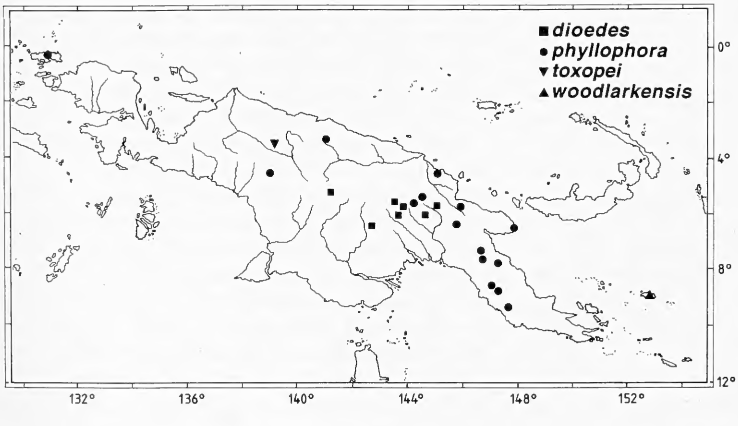


Fig. 4. Localities of *Papuapsaltria dioedes, P. phyllophora, P. toxopei,* and *P. woodlarkensis.*

5. – A square-shaped laminiform clasper, with a single, sharply pointed and outcurving, distoventral protrusion. The character is unique for four species.

6. – A nearly triangular distal part of the male operculum, with a very long and straight medial margin (figs. 17, 29). This operculum shape presumably indicates a sister group relationship between *P. angulata* and *P. goniodes*. Similarly shaped opercula occur in *P. dioedes* (fig. 163), *Guineapsaltria chinai* (Blöte, 1960), *Chlorocysta vitripennis* Westwood, 1851 and *Cystosoma saundersii* Westwood, 1842, which must be explained by parallelisms.

7. – A very long and stout aedeagus. Several other species of this genus (*P. angulata*, *P. baasi*, *P. dolabrata*, *P. novariae*, and *P. spinigera*) have a fairly long aedeagus as well, which stands erect between the claspers and reaches with its curved apical part well beyond the pygofer and anal valves. Similarly exposed aedeagi were also found in several species of *Gymnotympana*. The aedeagi of *P. brassi* and *P. lachlani* are extremely long, however, and presumably indicate the monophyletic origin of these two species.

8. – A thorn-shaped lateral protrusion on the clasper. The bluntly rounded lateral swelling in the clasper of *P. nana* is supposed to be homologous with this protrusion, while a slight swelling on the clasper of *P. woodlarkensis* might also be homologous, and thus indicate a relationship of that species to the species with this apomorphy. The more lobate lateral protrusions described for the claspers of some species of the genus *Thaumastopsaltria* (see De Boer 1992b) are considered to be non-homologous.

9. – A flattened and distinctly posteriorly projecting protuberance on the lateral lobes of the pygofer. The character is presumed to be lost in *P. nana*, though that species still has a fairly stout protuberance, compared to other species of the genus.

10. – The medial part of the clasper forming an almost transparent membrane, arching from the apex to the base of the clasper. This character is presumed lost by a reversal in *P. plicata*.

11. – A fairly large male operculum, with the medial margin of its distal part reaching medially of the meracanthus. Opercula that extend to medially of the meracanthus are synapomorphous for the genera *Baeturia*, *Gymnotympana*, *Scottotympana*, and *Venustria* (see above), but in these genera the distal part of the operculum is generally larger and of a different shape than in the two species of *Papuapsaltria* which share this apomorphy. Similarities with the four genera mentioned above must be explained by parallelism.

12. – A very stout and bicuspidate caudodorsal beak, separated from the pygofer by a distinct fold at its base (figs. 58, 69). A bicuspidate, though differently shaped, caudodorsal beak was found in two species groups of *Baeturia*: the *B. nasuta* group and the *B. viridis* group (De Boer 1982; 1992a), which must be explained by parallelism or convergence. The fold at the base of the beak is unique for these two species of *Papuapsaltria*.

13. – An aedeagus with a pair of distinct and angular dorsal ridges. Less well-developed dorsal ridges, either single or paired, occur in many other species of *Papuapsaltria* and in many related genera.

14. – A globularly rounded dorsodistal protrusion on the clasper (figs. 77, 89). A similar protrusion was found in *Aedeastria hastulata* De Boer, 1993, and several species of *Gymnotympana*, which must be explained by parallelisms.

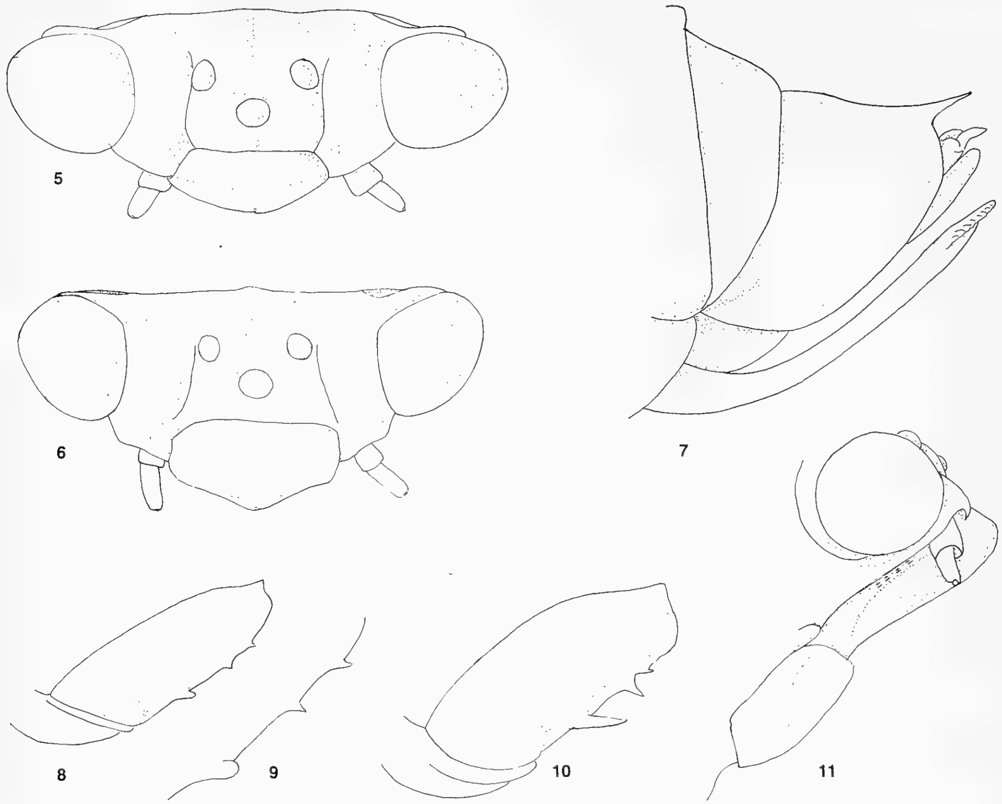
15. – Claspers of which the dorsal crests closely encircle the aedeagus as a short shaft. The claspers of the four species with this character are very similar in other respects, mainly differing in the angle between their apical and basal parts. The character is unique for these four species.

Remark: The phylogenetic positions of *P. phyllophora* and *P. woodlarkensis* are very uncertain. The shape of the head and the operculum of these species suggest that they either belong to *Papuapsaltria* or to *Guineapsaltria*. In spite of the fact that these two species have a fairly long proximal spine on the fore femur, they are preliminary included in *Papuapsaltria*, since their ocelli are more closely together than is common in *Guineapsaltria* and they do not share the distinct subapical lobe on the aedeagus, which is regarded synapomorphous for that genus (De Boer 1993a). The inclusion of these two species in *Papuapsaltria* is supported by the preliminary results of the computer analysis; in several of the most parsimonious reconstructions these species appear at various places between the other species of the genus.

Discussion of other characters of possible phylogenetic relevance

Several other characters, not included in the phylogenetic discussion, are discussed below, since they are supposed to be indicative of a close relationship between species of *Papuapsaltria*:

Cicadas generally have eight apical areas in the tegmen, but several species of *Papuapsaltria* have a different number of apical areas, a number which often even varies between the right and left tegmen of individuals. *P. novariae* has 9 apical areas, this number varies between 8-9 in *P. nana*, between 8-10 in *P. lachlani* and *P. plicata*, and between 9-12 in *P. goniodes*. *P. stoliodes* has generally 8-9 apical areas in the tegmen, but 11-12 in one specimen, and one specimen of *P. baasi* has 7 apical areas in the right tegmen. Such variations only sporadically occur in related genera and the fact that it occurs relatively often in



Figs. 5-11. – 5, head in dorsal view *P. goniodes*, holotype; 6, head in dorsal view *P. nana*, Popondetta; 7, female genital segment in lateral view *P. goniodes*, Daulo; 8, fore femur *P. goniodes*, holotype; 9, detail fore femur *P. goniodes*, holotype; 10, fore femur *P. woodlarkensis*, holotype; 11, head in lateral view *P. goniodes*, holotype.

Papuapsaltria might indicate a close relationship between its species.

Tegmina with a more strongly variable number of apical areas (10-15), are characteristic for *Thaumastopsaltria* (De Boer 1992b), a monophyletic group of four *Gymnotympana* species (De Boer 1995a), a presumed monophyletic group consisting of *Chlorocysta*, *Glaucopsaltria*, and *Owra* (for figs. see Moulds 1990), and for two species of *Mirabilopsaltria* (De Boer 1995b).

Apical and ulnar areas are generally long and slender in *Papuapsaltria* (figs. 21, 65), but distinctly shorter in *P. baasi*, *P. dolabrata*, *P. novariae*, *P. phyllophora* and *P. ustulata* (fig. 137). The tegmina of these five species resemble those of *Guineapsaltria*.

P. dioedes and *P. woodlarkensis* have very similar opercula, which might indicate a close relationship between these species; the lateral margin of the distal part runs almost straight to the distolateral corner of the basal part (figs. 163, 172).

Apart from *P. plicata*, *P. phyllophora*, *P. stoliodes*, *P. toxopei*, *P. woodlarkensis*, and some specimens of *P. bidigitula* the species of *Papuapsaltria* have a very slender caudodorsal beak (compare figs. 12 and 53), often with concave margins in dorsal view (cf. fig. 44). Such an extremely slender caudodorsal beak only sporadically occurs in related genera.

BIOGEOGRAPHY

Papuapsaltria is widely distributed throughout the greater part of New Guinea and further recorded from the islands of Normanby, Roon, Waigeu, Woodlark, and Yapen (figs. 3-4, 32, 129). The genus appears to be absent from Cendrawasih (the Vogelkop peninsula), the southern parts of central New Guinea, and the central mountain ranges of western New Guinea. A record of *P. bidigitula* from Wetar island is considered doubtful, since that species is not known from any of the other Banda islands.

The cicada genera that occur on New Guinea are not evenly distributed over the island. The various genera are generally concentrated with most, and often endemic, species in different parts of the island. Most of these parts, thus recognised as areas of endemism, coincide with fragments of a historic volcanic island arc, known as the Outer Melanesian Arc. Over the last 25 million years or so these fragments have collided at various times and localitions with the northern craton of the Australian continent (for geological information see Pigram & Davies 1987). These facts suggest that the various New Guinean genera evolved on different island arc fragments, prior to the collision of these fragments with Australia. It was inferred (De Boer 1994; 1995a), that the genera *Diceropyga, Gymnotympana*, and *Thaumastopsaltria* probably evolved on the East Papua Composite terrane, which collided about 15 My ago with New Guinea and now forms the greater part of the Papuan peninsula (Pigram & Davies 1987). Similarly *Rhadinopyga* and possibly also *Aedeastria* might originate from any of two microcontinents now forming Cendrawasih, these genera concentrate in western New Guinea (De Boer 1992b; 1993b; 1994). The occurrences of such genera outside their presumed area of origin is supposed to have resulted from dispersal since the time of collision of these areas. Such a hypothesis is corroborated by the fact that those species that do occur outside the areas of presumed origin generally have a relatively wide distribution.

The distribution of the genus *Papuapsaltria* does not readily suggest an origin on any of the arc-fragments or microcontinents that collided with Australia. Certainly, most species of *Papuapsaltria* are found in Papua New Guinea. Of its 18 species, eleven occur in Papua New Guinea, and nine are endemic there. Five of these endemics are restricted to the Papuan peninsula. These numbers of endemics seem to indicate that *Papuapsaltria*, or at least part of that genus, also originates from the East Papua Composite terrane. Several species may have dispersed from the Papuan peninsula to the mountains of western Papua New Guinea. It is remarkable that many species of *Papuapsaltria* were collected from montane altitudes (table 1), so that such a dispersal, from one montane area to another, might have been easily achieved.

However, *Papuapsaltria* has no less than five endemic species in northwestern New Guinea, four of which presumably form a monophyletic group. Furthermore, disregarding the record from Wetar, *P. bidigitula* could also be an endemic of northwestern New Guinea. The distribution of these endemics cannot easily be explained by a dispersal from the Papuan peninsula and a different area of origin, on another fragment of the historic island arc, must certainly be considered for these species. The endemics of northern New Guinea, or at least some of them, could originate either from the Gauttier or Torricelli terranes, or from both. These terranes formed a, probably more or less continuous, part of the Outer Melanesian Arc and collided at about 10 My ago with New Guinea (Pigram & Davies 1987).

As explained above, the monophyly of *Papuapsaltria* is far from certain. The apparent dual origin of the genus, on different parts of the Outer Melanesian Arc, is another factor shedding doubt on its assumed monophyly.

Table 1. Altitudinal ranges of the species of *Papuapsaltria*

P. angulata	700-2070 m
P. baasi	100-750 m
P. bidigitula	0-1350 m
P. brassi	1650-1950 m
P. dioedes	2280-2950 m
P. dolabrata	0-2500 ft
P. goniodes	700-3000 m
P. lachlani	400-1400 m
P. nana	0-150 m
P. novariae	1200-2530 m
P. phyllophora	0-1800 m
P. plicata	2070-2800 m
P. spinigera	700-1550 m
P. stoliodes	1100-2000 m
P. toxopei	1800 m
P. ungula	450 m
P. ustulata	1300-1500 m
P. woodlarkensis	100 m

Taxonomy

Genus ***Papuapsaltria*** gen. n.

Type species. – *P. angulata* sp. n.

Description

The species of *Papuapsaltria* are mostly fairly small. Males generally have a body length shorter than 2 cm and, more often, do not exceed 1.5 cm. Only *P. dioedes* is distinctly larger, with a body length of 20.0-26.5 mm. Body generally ochraceous to reddish brown and often with traces of green, but without special colour markings, though abdomen sometimes with reddish segmental hind margins. Many of the species possibly entirely green when alive. Females of most species, on average, slightly smaller than males but with more robust head and thorax and slightly longer tegmina. Tegmina of males 1.0-1.3 × as long as body length, of females 1.5-1.6 ×. Male abdomen distinctly longer (1.2-2.2 ×) than head and thorax, of females 1.0-1.3 ×. Head fairly broad and short (figs. 5-6), only slightly narrower than anterior part of pronotum, 2.3-2.9 × as wide as long and 1.2-1.5 × as wide as distance between eyes. Postclypeus 2.0-3.3 ×

as wide as long, oblong in dorsal view and weakly protruding, and not swollen ventrally; anterior margin (lateral view) straight or weakly concave (fig. 11). Sides of postclypeus fairly smooth, but often with some weak furrows and with about 6 rows of short parallel ridges in a narrow band along the lorum. Vertex fairly broad and smooth, though with distinct medial fissure. Diverging fissures from center of head to corners of postclypeus generally weakly developed, almost obsolete. Vertex 1.5-2.2× as wide as long; 1.3-2.1× as wide as postclypeus and 1.9-2.5× as wide as eye. Ocelli small and fairly close together. Distance between lateral ocelli 1.2-2.6× the width of frontal ocellus and about as long as (0.8-1.2×) distance between lateral ocellus and eye. Pronotum 2.2-2.9× as wide as long and smoothly vaulted, without distinct medial furrow. Pronotal collar laterally angularly amplified, and slightly curving down at its anterior margin. Tegmina and wings hyaline, venation ochraceous. Tegmina generally with 8, but fairly often more (9-12) apical areas, though rarely with subapical areas. Tegmen with distinct hyaline costal area and generally a broad hyaline border along hind margin. Wings with 6 apical areas, a distinctly broader hyaline border, and large anal fields. Legs ochraceous and unmarked. Fore femur long and slender, with row of 3 erect spines. Proximal spine in most species very short and apically rounded, only slightly longer than middle spine and generally distinctly shorter than distance to middle spine (figs. 8-9). Tymbal with 5-9 parallel sclerotized ridges. Short intercalary ridges can often be discerned, forming a darkened band at half-width across the tymbal. Opercula generally very small. Basal part of operculum slightly vaulted with two rounded elevations, and upcurved at distolateral corner into distinct crest rounding that corner. Lateral part of that crest often short and knobby, distal part generally fairly long and gradually amplifying into distal part of operculum (cf. fig. 17), though in some species shorter and abruptly amplifying into distal part (cf. fig. 29). Distal part of operculum angularly oblong, in most species shorter than basal part. Male operculum not, or only partly, covering tymbal cavity in ventral view, often leaving greater part of folded membrane exposed. Its lateral margin straight and slightly directed mesiad. Operculum shorter than meracanthus and generally not extending medially beyond meracanthus. *P. plicata* and *P. stoliodes* with distinctly larger opercula. Female operculum shorter, but generally of same shape as that of male. Male abdomen very delicate, in the larger sized species distinctly inflated, in small sized species not notably inflated and then of almost the same shape as that of female. First tergite in male fairly short medially, sometimes hidden under metanotum. Medial part of second tergite less than 1.5× as long as lateral parts, proximal margin of second tergite weakly convex, sometimes slightly concave medially (figs. 68, 177) and almost straight between auditory capsules and sternite 2, forming a distinct ridge along tymbal cavity (cf. fig. 17). Lateral parts of 2nd tergite weakly swollen at anterior margins and almost adjacent to tymbals, leaving a narrow gap between tymbal and 2nd tergite. First sternite swollen and bluntly rounded posteriorly. Female abdomen more robust than that of male, with slender pygofer. Ovipositor sheaths reaching beyond apex of bluntly rounded caudodorsal beak. Male pygofer globularly rounded, convexly rounded dorsally, and often with distinctly convex distal margins. Caudodorsal beak short and straight, not curved over basal part of claspers or anal valves (much larger and strongly bent in *P. plicata* and *P. stoliodes*). Claspers fairly short and directed downwards, fused, or nearly fused, at base, forming a ring-shaped collar around base of anal valves. Clasper generally sharply pointed at apex, and sometimes with sharply pointed lateral protrusion. Apical part of clasper generally with slender and sharply edged clasper hollow. Aedeagus S-curved with winged lateral crests, often with 1 or 2 dorsal ridges, and sometimes with small subapical lobe (aedeagus of *P. phyllophora* strongly deviating). Aedeagal pore round.

Gender: Feminine.

Key to the males

1. Clasper distinctly bicuspidate, with sharply pointed apical protrusion and distinct, pointed or rounded, lateral protrusion. (cf. fig. 56) 2

– Clasper not bicuspidate, with only one pointed and generally apical protrusion 7

2. Opercula reaching medially of meracanthus (figs. 59, 73). Pygofer with sharp fold at base of caudodorsal beak (figs. 54, 66). Caudodorsal beak bicuspidate (figs. 58, 69); broad in lateral view. Aedeagus with short and broad lateral crests and distinct dorsal ridges (figs. 62, 71) 3

– Opercula not reaching medially of meracanthus (cf. fig. 82). Pygofer without sharp fold at base of caudodorsal beak. Caudodorsal beak not bicuspidate; slender in lateral view (cf. figs. 78-79). Aedeagus with long and slender lateral crests and either without, or with weak, dorsal ridges 4

3. Operculum reaching beyond apex of meracanthus (fig. 73). Claspers very broad towards apex, ending in two short thorn-shaped protuberances; medial part of clasper not membranous (fig. 72). Auditory capsules weakly swollen. Body length under 19.5 mm .... *P. plicata*

– Operculum not reaching beyond apex of meracanthus (fig. 59). Claspers with very long and slender apical protrusion and shorter lateral protrusion; medial part of clasper membranous (fig.

56). Auditory capsules distinctly swollen. Body length over 19.5 mm .... *P. stoliodes*

4. Clasper with globularly swollen dorsodistal protrusion and a very long spiny apical protrusion; medial part of clasper membranous (figs. 77, 89 arrow). Tegmen with fairly narrow hyaline border along hind margin 5
– Clasper without globularly swollen dorsodistal protrusion and a fairly short apical protrusion; medial part of clasper not membranous (figs. 100, 104). Tegmen with broad hyaline border along hind margin 6
5. Caudodorsal beak very long and slender in lateral view, more than 3× as long as broad (fig. 78). Distal margin of pygofer strongly convex. Lateral lobe of pygofer with long, slender, and distinctly posteriorly projecting protuberance. Clasper with sharply pointed lateral spine (fig. 77). Folded membrane visible in ventral view. Tymbal with 8 ridges. Auditory capsules distinctly swollen. Anterior margin of postclypeus almost continuous with anterior margins of vertex lobes. Body length under 15 mm .... *P. ungula*
– Caudodorsal beak fairly short, about 2× as long as broad (fig. 84). Distal margin of pygofer weakly convex. Lateral lobe of pygofer with broadly rounded, hardly protruding protuberance. Clasper with bluntly rounded lateral protrusion (fig. 89). Folded membrane not visible in ventral view. Tymbal with 5 ridges. Auditory capsules hardly swollen. Anterior margin of postclypeus angularly curving back at lateral corners, forming a right angle with anterior margins of vertex lobes. Body length over 15 mm .... *P. nana*
6. Clasper base forming broad ring-shaped collar with two finger-shaped dorsomedial protrusions around base of anal valves (fig. 100). Lateral protrusion of clasper shorter, or as long as, apical protrusion. Tymbal with 6 ridges. Folded membrane visible in ventral view. Caudodorsal beak pointed at apex. Lateral protuberance on pygofer lobe broad; pygofer forming a distinct angular corner under lateral protuberance (fig. 93) .... *P. bidigitula*
– Clasper base not forming a distinct collar around base of anal valves (fig. 104). Lateral protrusion of clasper distinctly longer than apical protrusion. Tymbal with 8 ridges. Folded membrane not visible in ventral view. Caudodorsal beak rounded at apex. Lateral protuberance on pygofer lobe narrow; pygofer forming a very small angular corner under lateral protuberance (fig. 105) ....*P. spinigera*
7. Claspers parallel, only weakly diverging near apices (cf. fig. 162) 8
– Claspers strongly diverging towards apices (cf. fig. 15) 12
8. Tymbal with 6 ridges. Caudodorsal beak slender in lateral view (cf. fig. 157) 9
– Tymbal with 7 or 9 ridges. Caudodorsal beak fairly broad in lateral view (cf. fig. 183) 11
9. Body length over 19.5 mm. Distal part of operculum fairly long, longer than basal part, and with long medial margin (fig. 163). Pygofer with narrow protuberance on lateral lobe (fig. 157). Auditory capsules hardly swollen. Aedeagus not incised at apex (fig. 158). Tegmina with long and slender apical and ulnar areas and a broad hyaline border along hind margin (cf. fig. 21) .... *P. dioedes*
– Body length under 16.5 mm. Distal part of operculum shorter than basal part, and with short medial margin (fig. 136). Pygofer with broad protuberance on lateral lobe (cf. fig. 134). Auditory capsules distinctly swollen. Aedeagus weakly incised at apex (cf fig. 131). Tegmina with short apical and ulnar areas and a fairly narrow hyaline border along hind margin (cf. fig 137) 10
10. Tegmina with 9 apical areas. Sternites 1 and 2 not adjacent (fig. 136). Dorsal margin of clasper in lateral view forming a right angle with ring-shaped clasper base .... *P. novariae*
– Tegmina with 8 apical areas. Sternites 1 and 2 almost adjacent (fig. 145). Dorsal margin of clasper in lateral view almost continuous with ring-shaped clasper base .... *P. dolabrata*
11. Body length under 15 mm. Tegmina with short apical and ulnar areas (cf. fig. 137), costa distinctly swollen at pentagonal first ulnar area (fig. 176). Anterior margin of postclypeus almost continuous with anterior margins of vertex lobes. Proximal spine of fore femur fairly long, as long as, or longer than distance to middle spine. Tymbal with 9 ridges. Folded membrane between abdomen and operculum not visible in ventral view. Aedeagus very broad in lateral view and pick-shaped, with long and slender downwards directed apical part, square-shaped membranous dorsal part, and short and broad lateral crests (fig. 186). Clasper with straight and rounded apical part, and forming incurving dorsodistal protuberance over aedeagus (fig. 185) ....*P. phyllophora*
– Body length over 19 mm. Tegmina with long and slender apical and ulnar areas (cf. fig. 21), costa not swollen at quadrangular first ulnar area (cf. fig. 175). Anterior margin of postclypeus angularly curving back at lateral corners, forming a right angle with anterior margins of vertex lobes. Proximal spine of fore femur very short, distinctly shorter than distance to middle spine. Tymbal with 7 ridges. Folded membrane between abdomen and operculum visible in ventral view.

Aedeagus slender S-curved with long and slender lateral crests. Clasper with recurving and pointed apical part, not forming dorsodistal protuberance over aedeagus (fig. 152) .... *P. toxopei*

12. Distal margin of pygofer weakly convex between base of caudodorsal beak and lateral protuberance. Angular corner under lateral protuberance of pygofer not curved inwards or absent, or strongly folded inwards and then thorn-shaped; ventral half of pygofer opening generally not horseshoe-shaped (cf. fig. 167) 13

– Distal margin of pygofer strongly convex between base of caudodorsal beak and lateral protuberance. Angular corner under lateral protuberance of pygofer strongly curved inwards; ventral half of pygofer opening somewhat horseshoe-shaped (fig. 22) 16

13. Body length over 17 mm. Folded membrane between operculum and abdomen visible in ventral view. Tegmina with long and slender apical and ulnar areas, and a broad hyaline border along hind margin.(cf. fig. 21) 14

– Body length under 15 mm. Folded membrane between operculum and abdomen not visible in ventral view. Tegmina with short apical and ulnar areas, and a fairly narrow hyaline border along hind margin. (cf. fig. 137) 15

14. Clasper squarish, laminiform, with thorn-shaped outcurving protrusion on ventral margin (fig. 15). Pygofer with distinct rectangular corner under lateral lobe (fig. 12). Distal part of operculum almost triangular, with very long medial margin; lateral margin concave to distolateral corner of operculum base (fig. 17). Proximal spine of fore femur short, much shorter than distance to middle spine. Auditory capsules distinctly swollen. Caudodorsal beak slender in lateral view (fig. 12) ... *P. angulata*

– Clasper hook-shaped, with sharply pointed downwards directed apical part (fig. 171). Pygofer with thorn-shaped, inwards curving, protuberance under lateral lobe (fig. 167). Distal part of operculum oblong, with short medial margin; lateral margin almost straight to distolateral corner of operculum base (fig. 172). Proximal spine of fore femur fairly long, longer than distance to middle spine. Auditory capsules weakly swollen. Caudodorsal beak broad in lateral view (fig. 166) .... *P. woodlarkensis*

15. Pygofer with distinct rectangular corner under lateral lobe. Tymbal with 7-8 ridges. Anterior margin of postclypeus almost continuous with anterior margins of vertex lobes. Sternites 1 and 2 adjacent. Aedeagus with small subapical lobe (fig. 114) .... *P. ustulata*

– Pygofer without rectangular corner under lateral lobe. Tymbal with 6 ridges. Anterior margin of postclypeus angularly curving back at lateral corners, forming a right angle with anterior margins of vertex lobes. Sternites 1 and 2 not adjacent. Aedeagus without subapical lobe (fig. 124) .... *P. baasi*

16. Body length over 18 mm. Distal part of operculum fairly long, longer than basal part. Sternites 1 and 2 widely separated. Aedeagus reaching not, or only just, beyond apex of anal valves (fig. 24) *P. goniodes*

– Body length under 16 mm. Distal part of operculum shorter than basal part. Sternites 1 and 2 almost adjacent. Aedeagus reaching far beyond apex of anal valves (cf. fig. 34) 17

17. Pygofer lobe with broad laminiform lateral protuberance (fig. 34). Clasper with concave distal margin (fig.42). Claspers strongly diverging towards apices (fig. 38). Clsaper base forming a low collar around base of anal valves .... *P. lachlani*

– Pygofer lobe with narrow lobate lateral protuberance (fig. 45). Clasper with convex distal margin (fig. 47). Claspers weakly diverging towards apices (fig. 46). Clasper base forming a broad collar around base of anal valves .... *P. brassi*

Papuapsaltria angulata sp. n.
(figs. 12-20, 32)

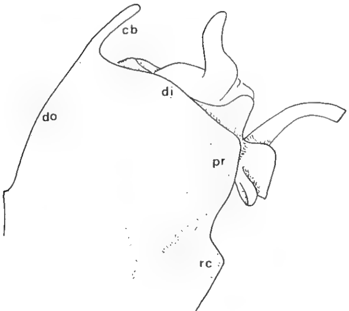
Type material. – Holotype ♂: 'N Guinea: NE Bulldog Rd. 2070 m 60 km S. Wau' [print]; '22-

Figs. 12-20. *Papuapsaltria angulata* sp. n. – 12, pygofer in lateral view, paratype; 13, male caudodorsal beak in dorsal view, paratype; 14, pygofer from aslant, paratype; 15, claspers, paratype; 16, female operculum, Nami Creek; 17, male operculum, paratype; 18, detail aedeagus apex, holotype; 19, aedeagus in lateral view, holotype; 20, female caudodorsal beak in dorsal view, Nami Creek.

Lettering: bp = basal part of operculum; c = crest around distolateral corner of basal part of operculum; cb = caudodorsal beak; di = distal margin of pygofer; dm = distomedial margin of operculum; do = dorsal margin of pygofer; dp = distal part of operculum; fm = folded membrane; lm = lateral margin of operculum; m = medial margin of operculum; me = meracanthus; pr = protuberance on lateral lobe of pygofer; rc = rectangular corner below lateral protuberance of pygofer; ve = ventral margin of pygofer.

Figs. 22-31. *Papuapsaltria goniodes* sp. n. – 22, pygofer from behind, Ayura; 23, pygofer from aslant, Ayura; 24, pygofer in lateral view, Daulo, arrow indicating distal lobe; 25, male caudodorsal beak in dorsal view, Daulo; 26, claspers, Daulo; 27, aedeagal apex, holotype; 28, aedeagus in lateral view, holotype; 29, male operculum, Daulo; 30, female caudodorsal beak in dorsal view, Daulo; 31, female operculum, Daulo.

Lettering: st 1 = sternite 1; st 2 = sternite 2.



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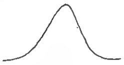

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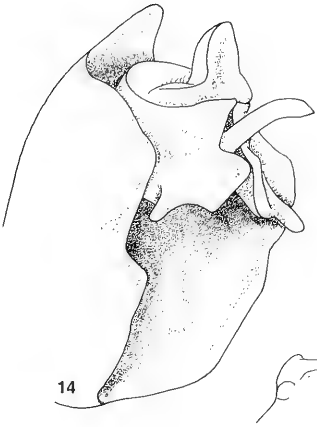

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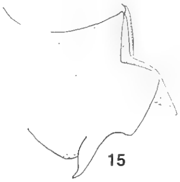

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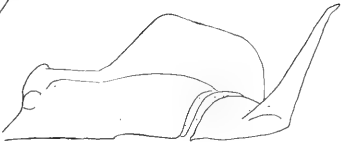

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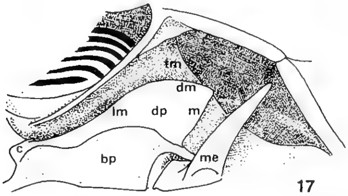

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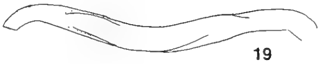

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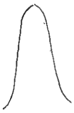

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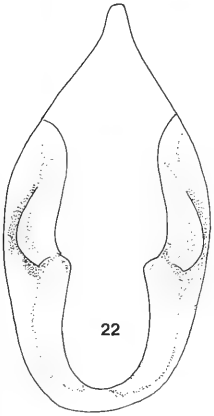

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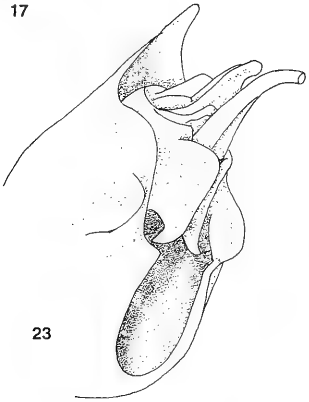

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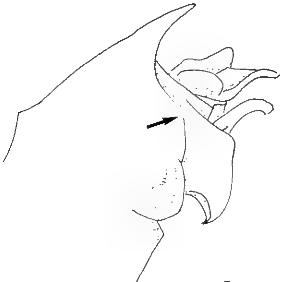

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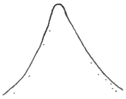

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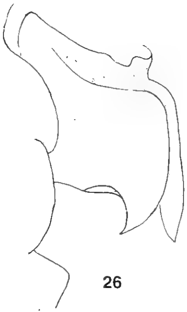

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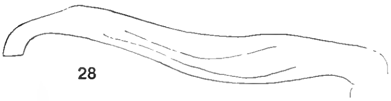

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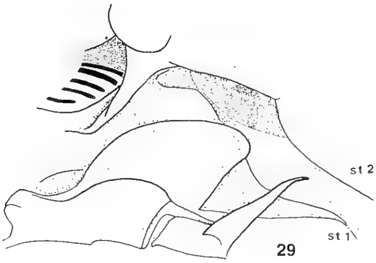

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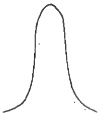

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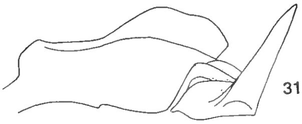

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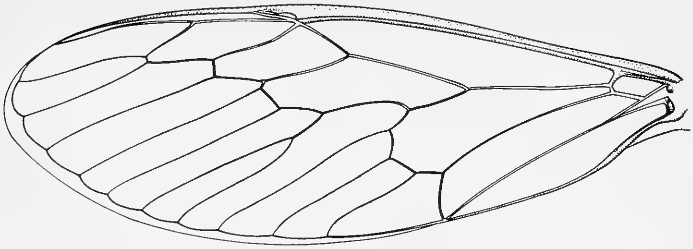


Fig. 21. *Papuapsaltria goniodes* sp. n. Left tegmen, male Mt. Otto.

31.v.1969' [print]; 'J. Sedlacek Collector Bishop Mus.' [print], BPBM. – Paratypes: PAPUA NEW GUINEA: same data as holotype, 1♀, BPBM; Nami Ck., Wau, 1700-1800 m, 17.ix.1965, J. Sedlacek, 1♂, ZMAN; Nami Ck., 6 km W. Wau, 1700 m, 12.vi.1962, J. Sedlacek, 1♀, BPBM.

P. angulata is the type species of *Papuapsaltria*. Males are easily recognized by the broad and rectangular clasper, with slender, sharply pointed, and laterally bending ventral protrusion.

Description

Body light brown and unmarked. Females slightly larger than males, with distinctly longer tegmina. Tegmina of males 1.1× as long as body length, of females 1.4×. Male abdomen 1.7-1.8× as long as head and thorax, of females 1.2×.

Head: Ochraceous brown, without setae. Postclypeus angularly protruding, anterior margin angularly bent medially, and almost continuous with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) weakly concave. Distance between lateral ocelli 0.9-1.0× as long as distance between lateral ocellus and eye, and 1.9-2.3× as wide as frontal ocellus.

Tegmina: Hyaline, with 8 long and slender apical areas, a broad hyaline costal area and a very broad hyaline border along hind margin.

Legs: Fore femur with three very short, about equally long, erect spines. Proximal spine finger-shaped and distinctly shorter than distance to middle spine.

Tymbal: Five parallel transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin and a 6th, most proximal, ridge almost reaching ventral margin. Intercalary ridges can hardly be discerned.

Opercula: Male operculum (fig. 17) not covering tymbal cavity in ventral view, leaving a wide gap between operculum and abdomen; folded membrane clearly visible in ventral view. Distal part of operculum longer than basal part and almost triangle-shaped, medially elongate. Lateral margin bending convexly into straight distal margin and concavely into crest of basal part. The lateral part of this crest short and knobby. Distomedial corner rectangular. Medial margin long and straight. Meracanthus longer than operculum, but not reaching to abdomen. Female operculum (fig. 16) much shorter than that of male, with oblong shaped distal part.

Abdomen: Male abdomen inflated. First tergite short, partly hidden under metanotum. Medial part of 2nd tergite less than 2× as long as lateral part. Anterior margin of 2nd tergite distinctly concave medially. First and 2nd sternite adjacent. Auditory capsules weakly developed, not visible in dorsal view. Female abdomen very slender. Female caudodorsal beak (fig. 20) slender, pointed at apex. Ovipositor sheaths just reaching to apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 12. Dorsal margin weakly convex, continuous with short and very slender caudodorsal beak. Distal margin weakly convex between caudodorsal beak and lateral protuberance, forming a weakly developed distal lobe. Caudodorsal beak in dorsal view (fig. 13) short and slender, triangle-shaped and rounded at apex. Lateral lobe of pygofer curving outwards towards ventral margin, forming a weakly developed, but broad and rectangular laminiform protuberance. Pygofer forming a very distinct rectangular and slightly incurving corner just below this protuberance (figs. 12, 14). Ventral margin of pygofer angularly convex. Ventral half of pygofer opening in holotype horseshoe-shaped (seen from behind cf. fig. 22), with broad, rounded, basal margin and concave lateral margins, incurving towards rectangular corners, but narrower, V-shaped with converging margins, in paratype. Clasper (fig. 15) laminiform, with almost rectangular dorsodistal corner and straight distal margin, and with a sharply pointed thorn-shaped protrusion at half-length of ventral margin. Protrusion of clasper bending strongly outwards and reaching laterally beyond pygofer margin. Rectangular dorsodistal corner of clasper bending mesiad, distally of aedeagus and supporting aedeagus in upright position. Claspers strongly diverging towards ventrodistal corners. Clasper base forming a smoothly rounded, though discontinuous ring around base of anal valves; with dorsal parts of clasper bases curving mesiad, proximally of aedeagus, and almost touching each other. Aedeagus standing erect between claspers, fairly close to anal valves, but with apical part curving away, reaching beyond distal margins of claspers. Aedeagus (fig. 19) long and slender, weakly S-curved, with long slender lateral crests and a pair of weakly developed dorsal crests, restricted to its distal half. Aedeagus strongly curved near apex. Aedeagal pore round (fig. 18).

Measurements: Body length ♂: 17.5 & 18.6 mm, ♀ 19.5 mm; tegmen length ♂: 21.2 mm, ♀: 28.1 mm; head length ♂: 1.2 mm, ♀: 1.2 & 1.5 mm; pronotum length ♂: 1.7 mm, ♀: 2.0 mm; mesonotum length ♂: 3.5 mm, ♀: 5.7 mm; head width ♂: 3.1 & 3.3 mm, ♀: 3.9 mm; width of pronotal collar ♂: 4.3 & 4.8 mm, ♀: 6.2 mm.

Distribution (fig. 32). – Central Papua New Guinea, the most western part of the Papuan peninsula.

Etymology. – Angulatus (Latin) means angular and refers to the angular claspers.

Papuapsaltria goniodes sp. n.
(figs. 5, 7-9, 11, 21-32)

Type material. – Holotype ♂: 'NEW GUINEA (NE) Mt. Otto, 2200 m, June 24, 1955' [print]; 'J.L. Gressitt collector' [print], BPBM. – Paratypes: PAPUA NEW GUINEA: Aiyura, nr Kainantu, 1700-2200 m, 6.i.1965, J.L. Gressitt, 1♂, ZMAN; Daulo Pass, 2400 m, 15.v.1963, J. Sedlacek, 1♂, BPBM; Daulo Pass, Asaro-Chiambu Div., 3000 m, 13.vi.1955, J.L. Gressitt, 1♂, BPBM; same data but 8500 ft, J.J.M. Scent-Ivany, 1♀, MVMA; Mt. Hagen, 1959, E. Reiner, 1♂, SMFD; Mt. Piora, 6°45' S 146°00' E, 2100 m, 12.vi.1966, G.A. Samuelson, 1♀, BPBM.

P. goniodes is slightly larger than *P. angulata*. These two species share a similar, almost triangularly elongate operculum but the male genitalia differ considerably. *P. goniodes* can be recognized by its variable tegmen venation and its deviating shape of the head, with the lateral ocelli somewhat wider apart than in other species of *Papuapsaltria*.

Description

Body light brown to dark reddish brown, unmarked. Females slightly smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.2-1.3× as long as body length, of females 1.4-1.5×. Male abdomen 1.5-1.9× as long as head and thorax, of females 1.2-1.3×.

Head (fig. 5): Reddish brown, without setae. Postclypeus much broader than in *P. angulata* and bluntly rounded, anterior margin weakly convex, almost continuous with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) straight or weakly concave (fig. 11). Distance between lateral ocelli distinctly longer (1.1-1.2) than distance between lateral ocellus and eye, and 2.0-2.6× the width of frontal ocellus.

Tegmina: Hyaline. Venation variable (fig. 21), often differing between left and right tegmen of individuals, with 9-12 apical areas and, rarely, a subapical area between ulnar and apical areas. Only 9-10 apical areas reach the ulnar or basal areas, others are formed by a more distal splitting of veins. Tegmen generally with a very broad hyaline costal area and a very broad hyaline border along hind margin.

Legs: Fore femur with three very short, about equally long, erect spines. Proximal spine finger-shaped and distinctly shorter than distance to middle spine (figs. 8-9).

Tymbal: Five parallel transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin, a 6th ridge almost reaching ventral margin and a 7th, most proximal, ridge only partly separated from proximal tymbal margin, reaching to about half the tymbal width. Six short intercalary ridges clearly visible.

Opercula: Male operculum (fig. 29) not covering tymbal cavity in ventral view, leaving a wide gap between operculum and abdomen; folded membrane

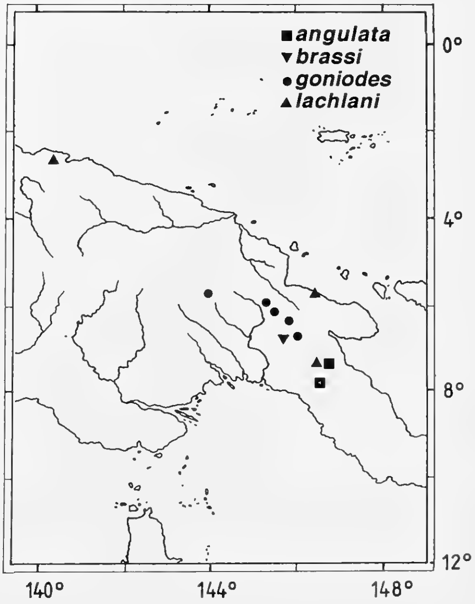


Fig. 32. Localities of *Papuapsaltria angulata*, *P. brassi*, *P. goniodes*, and *P. lachlani*.

clearly visible in ventral view. Distal part of operculum longer than basal part and medially elongate, almost triangle-shaped, as in *P. angulata*, but with lateral margin often bending more angularly from crest of basal part. Lateral margin convexly bent into almost straight distal margin. Distomedial corner of operculum almost rectangular, medial margin long and straight. Meracanthus slightly longer than operculum, but not reaching abdomen. Female operculum (fig. 31) much shorter than that of males. Distal part shorter than basal part, oblong. Distal margin straight, in one specimen slightly convex at half-length, distomedial corner rectangular, medial margin short and straight.

Abdomen: Male abdomen inflated. First tergite short, partly hidden under metanotum. Medial part of 2nd tergite less than 1.5× as long as lateral part. Anterior margin of 2nd tergite very weakly concave medially. First and 2nd sternite generally adjacent, but sometimes separated. Auditory capsules well developed, protruding and visible in dorsal view. Female abdomen slender. Female caudodorsal beak (fig. 30) slender and sharply pointed at apex. Ovipositor sheaths not reaching to apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 24. Dorsal margin weakly convex, continuous with short caudodorsal beak. Distal margin distinctly convex between caudodorsal beak and lateral protuberance, forming a weakly protruding lobe on pygofer (fig. 24 arrow). Caudodorsal beak fairly slender in lateral view, but broader at its base than in *P. angulata*, triangular with concave margins and pointed at apex (fig. 25). Lateral lobe of pygofer with narrow, rounded, and outcurving lobate protuberance. Pygofer forming a distinct rectangular and slightly incurving corner just below this protuberance (figs. 23-24). Ventral margin of pygofer angularly convex. Ventral half of pygofer opening horseshoe-shaped (fig. 22), with broad, rounded basal margin and concave lateral margins; in curving towards rectangular corners. Clasper (fig. 26) very broad and short, square-shaped in lateral view. Rectangular distodorsal corner of clasper bending mesiad, distally of aedeagus and supporting aedeagus in upright position. Distal margin of clasper straight, but slightly recurving to sharply pointed, downwards directed, thorn-shaped apex. Claspers slightly diverging towards apices. Clasper base forming a low ring-shaped collar around base of anal valves. This collar is medially indented around aedeagus, and less distinct than in foregoing species. Aedeagus standing erect between claspers, close to anal valves, but with apical part curving away, reaching well beyond distal margins of claspers. Aedeagus (fig. 28) weakly S-curved, most strongly curved and distinctly narrowing near apex, its most apical part almost rectangularly bent. Aedeagus with long and distinct lateral crests, a rounded middorsal ridge and a pair of weakly developed dorsal crests near apical bending point. Apex of aedeagus with slight medial incision (fig. 27).

Measurements: Body length ♂: 18.9-20.5 mm ($\bar{x}$ 19.9 mm), ♀: 17.8 & 18.0 mm; tegmen length ♂: 23.0-25.3 mm ($\bar{x}$ 24.0 mm), ♀: 26.0 & 27.1 mm; head length ♂: 1.2-1.5 mm, ♀: 1.5 mm; pronotum length ♂: 1.9-2.0 mm, ♀: 2.1 & 2.2 mm; mesonotum length ♂: 4.0-4.7 mm, ♀: 4.7 & 4.8 mm; head width ♂: 3.6-3.9 mm, ♀: 4.0 mm; width of pronotal collar ♂: 4.7-5.5 mm, ♀: 5.6 & 5.7 mm.

Distribution (fig. 32). – *P. goniodes* is distributed in central northern Papua New Guinea, just west of the Huon peninsula.

Etymology. – Goniodes (Greek) means angular and refers to the angular claspers.

Papuapsaltria lachlani sp. n.
(figs. 32-42)

Type material. – Holotype ♂: 'PAPUA NEW GUINEA Wau 28 Dec 1970 R.B. Lachlan' [print]; AMSA. – Paratypes: IRIAN JAYA: Ifar, Cyclops Mts., 400-800 m, 7-9.ix.1962, J. Sedlacek, 1♂, BPBM; PAPUA NEW GUINEA: Kiambavi vill., Saidor, Finisterre Range, 1-28.viii.1958. W.W. Brandt, 1♂, ZMAN; Wau, Big Wau Creek, 1200 m, Thomas W. Davies, 1♀, CAS; Wau, Morobe Distr., 20.x.1969, James E. Tobler, 1♀, CAS; Wau, Morobe Distr., Mt. Missim, 2080 m, 17.iii.1966, Gressitt, 1♂, BPBM.

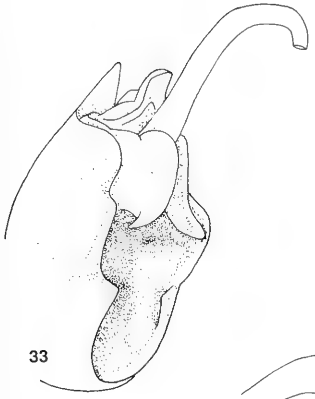
P. lachlani closely resembles *P. goniodes* in shape of male genitalia, but is distinctly smaller and has almost oblong-shaped opercula. Some specimens have an aberrant tegmen venation.

Description

Body red-brown to greenish. Females slightly smal-

Figs. 33-42. *Papuapsaltria lachlani* sp. n. – 33, pygofer from aslant, holotype; 34, pygofer in lateral view, holotype; 35, male caudodorsal beak in dorsal view, holotype; 36, pygofer in lateral view, Ifar; 37, aedeagal apex, holotype; 38, claspers from behind, holotype; 39, male operculum, holotype; 40, female operculum, Big Wau Creek; 41, female caudodorsal beak in dorsal view, Big Wau Creek; 42, claspers, holotype.

Figs. 43-52. *Papuapsaltria brassi* sp. n. – 43, pygofer from aslant, paratype; 44, male caudodorsal beak in dorsal view, holotype; 45, pygofer in lateral view, paratype; 46, claspers from behind, holotype; 47, claspers, holotype; 48, aedeagus in lateral view, paratype; 49, aedeagal apex, paratype; 50, male operculum, holotype; 51, female operculum, Purosa Camp; 52, female caudodorsal beak in dorsal view, Purosa Camp.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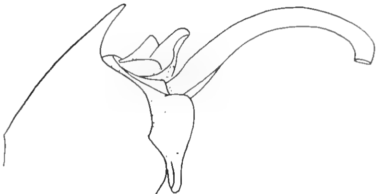
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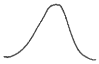
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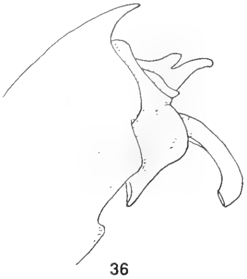
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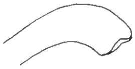
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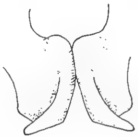
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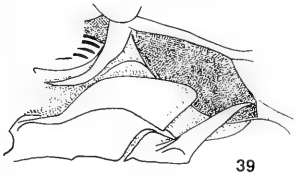
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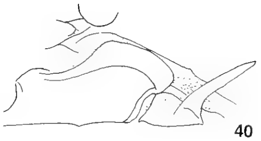
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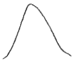
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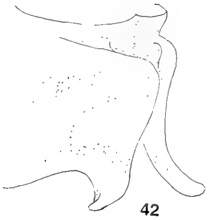
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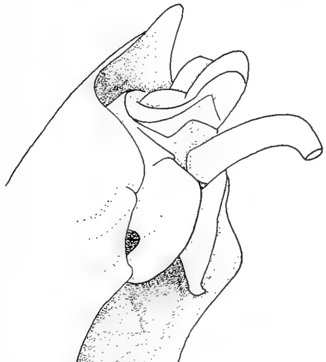
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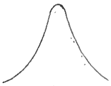
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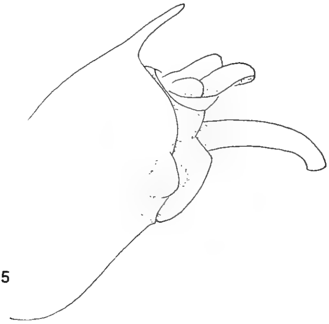
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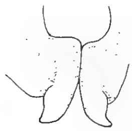
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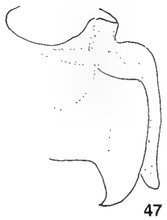
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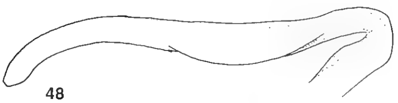
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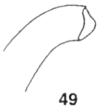
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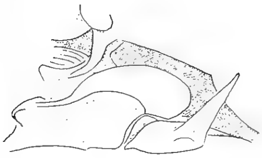
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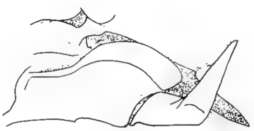
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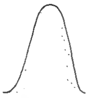
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ler than males, but with more robust head and thorax. Tegmina of males 1.1-1.3× as long as body length, of females 1.3-1.4×. Male abdomen 1.4-1.7× as long as head and thorax, of females 0.9-1.2×.

Head: Reddish brown, often with some short red-brown setae on postclypeus and anterior parts of vertex. Diverging fissures on vertex fairly distinct in holotype, almost obsolete in paratypes. Postclypeus of holotype and females oblong and angularly protruding beyond vertex lobes, with almost straight anterior margin, angularly bending back at lateral corners and forming an almost right angle with anterior margins of vertex lobes. Postclypeus of other material with weakly convex anterior margin, almost continuous with anterior margins of vertex lobes. Postclypeus slightly swollen; anterior margin (lateral view) weakly convex. Distance between lateral ocelli in males as long as, in females slightly longer than distance between lateral ocellus and eye, and 2.0-2.3× the width of frontal ocellus.

Thorax: Pronotum with weak medial furrow.

Tegmina: Hyaline, venation sometimes variable, forming 8-10 long and slender apical areas and a very distinct hyaline costal area. Tegmen with a broad hyaline border along hind margin.

Legs: Fore femur with three very short, about equally long, erect spines. Proximal spine often extremely short and finger-shaped, though fairly long and pointed in specimen from Saidor, and always shorter than distance to middle spine.

Tymbal: Six parallel transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin and a 7th, most proximal, ridge almost reaching ventral margin. Six short intercalary ridges can hardly be discerned.

Opercula: Male operculum (fig. 39) very short, not covering tymbal cavity in ventral view; leaving a wide gap between operculum and abdomen; folded membrane partly visible in ventral view. Distal part of operculum distinctly shorter than basal part and angular, almost oblong-shaped. Lateral margin almost straight, bending gradually into crest of basal part and angularly into long and straight distal margin. Distal margin forming a sharp angle with short and straight medial margin. Meracanthus reaching well beyond operculum, but not reaching abdomen. Female operculum (fig. 40) as in male, but shorter.

Abdomen: Male abdomen not inflated. First tergite short, partly, or completely, hidden under metanotum. Medial part of 2nd tergite less than 1.5× as long as lateral part. Anterior margin of 2nd tergite weakly convex medially. First and 2nd sternite not adjacent. Auditory capsules swollen and clearly visible in dorsal view. Female caudodorsal beak (fig. 41) triangular, almost pointed at apex. Ovipositor sheaths reaching just beyond apex of caudodorsal beak.

Male genitalia: Very similar to *P. goniodes.* Pygofer in lateral view as in fig. 34. Dorsal margin weakly convex, continuous with short and slender caudodorsal beak. Distal margin strongly convex between caudodorsal beak and lateral protuberance, forming an almost rectangular and incurving lobe. Caudodorsal beak in dorsal view broad, almost rectangularly protruding in Saidor specimen, but narrower and apically rounded in others (fig. 35). Lateral lobe of pygofer with distinct, angularly rounded, lobate, outcurving laminiform protuberance. Pygofer forming a distinct rectangular and slightly incurving corner just below this protuberance (fig. 33). Ventral margin of pygofer straight. Ventral half of pygofer opening horseshoe-shaped (cf. fig. 22), with broad, rounded basal margin and concave lateral margins; incurving towards rectangular corners. Claspers (fig. 42) as in *P. goniodes*, very broad and short, square-shaped in lateral view. Dorsal margin of clasper straight or weakly convex. Rectangular distodorsal corner of clasper bending mesiad, distally of aedeagus and supporting aedeagus in upright position. Distal margin of clasper straight, but slightly concave to sharply pointed, downwards directed, thorn-shaped apex. Claspers strongly diverging towards apices (fig. 38). Clasper base forming a low ring-shaped collar around base of anal valves. This collar medially indented around aedeagus. Aedeagus standing erect between claspers, close to anal valves, with its apical part curving away, reaching well beyond distal margins of claspers. Aedeagus of holotype very long, reaching far beyond apex of caudodorsal beak (fig. 34), in other specimens much shorter, curved directly above dorsal margins of claspers (fig. 36). Aedeagus weakly S-curved, angularly but slightly bent at about 3/4 its length (fig. 33) and strongly curved near apex, with short straight subapical part. Lateral crests long and distinct. Apex of aedeagus slightly dilated, with round pore (fig. 37).

Measurements: Body length ♂: 13.7-14.0 mm, ♀: 13.3 & 13.7 mm; tegmen length ♂: 16.6-20.1 mm, ♀: 18.2 & 18.4 mm; head length ♂: 1.3-1.4 mm, ♀: 1.4 mm; pronotum length ♂: 1.4-1.7 mm, ♀: 1.6 & 1.7 mm; mesonotum length ♂: 2.3-3.1 mm, ♀: 3.1 mm; head width ♂: 3.1-3.3 mm, ♀: 3.3 mm; width of pronotal collar ♂: 3.7-4.1 mm, ♀: 4.2 & 4.3 mm.

Distribution (fig. 32). – *P. lachlani* is widely distributed in northern New Guinea and the western part of the Papuan peninsula.

Etymology. – This species is named in honour of Mr R.B. Lachlan who collected the holotype.

Papuapsaltria brassi sp. n.
(figs. 32, 43-52)

Type material. – Holotype ♂: 'No 10, Purosa

Camp, Okapa area, 1950 m, ix-25-1959' [print]; 'Eastern Highlands District L.J. Brass coll' [print]; 'sixth Archbold Exped. to Papua New Guinea' [print]; 'AMNH New York' [print], AMNH. – Paratypes: PAPUA NEW GUINEA: same data as holotype but 29.ix.1959, 1♂, 1♀, AMNH; Okapa, 13 km SE, 1650-1870 m, 26.-viii.1964, J. & M. Sedlacek, 1♂, BPBM; Okapa, 1900 m, 3.vi.1967, G.A. Samuelson, 1♀, BPBM.

P. brassi strongly resembles *P. lachlani*, but is slightly larger and has slightly shorter and less strongly diverging claspers. *P. brassi* is most easily separated from *P. lachlani* by a more oval-shaped male operculum, a narrower gap between operculum and abdomen and smaller protrusions on the lateral lobes of pygofer.

Description

Body yellow-brown or olive green. Females larger than males. Tegmina of males 1.3× as long as body length, of females 1.4×. Male abdomen 1.4-1.6× as long as head and thorax, of females 1.2-1.3×.

Head: Reddish brown, with some short red-brown setae on postclypeus and vertex. Postclypeus hardly protruding, anterior margin weakly convex, almost continuous with anterior margins of vertex lobes, and not swollen; anterior margin (lateral view) weakly concave. Distance between lateral ocelli 1.0-1.2× as long as distance between lateral ocellus and eye and 1.9-2.3× the width of frontal ocellus.

Legs: Fore femur with row of three erect spines. Most proximal spine very short, hardly longer than middle spine and much shorter than distance to middle spine.

Tegmina: Hyaline, with 8 apical areas, a narrow but distinct costal area and a fairly narrow hyaline border along hind margin.

Tymbal: Six parallel transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin and a 7th, most proximal, ridge almost reaching ventral margin. Six short intercalary ridges can hardly be discerned.

Opercula: Male operculum (fig. 50) very short, not covering tymbal cavity in ventral view, but leaving only a narrow gap between operculum and abdomen; folded membrane not visible in ventral view. Distal part of operculum distinctly shorter than basal part and oval-shaped. Lateral margin very short, bending gradually into crest of basal part and convexly curving into long and weakly convex distal margin. Distomedial corner broadly rounded, medial margin weakly convex. Meracanthus reaching well beyond operculum and beyond anterior margin of abdominal segment 2. Female operculum (fig. 51) much shorter than that of males. Distal part much shorter than basal part, nearly oblong, with weakly convex distal margin. Distolateral corner rounded, distomedial corner almost rectangular. Medial margin short and straight.

Abdomen: Male abdomen not inflated. First tergite short, either partly, or completely, hidden under metanotum. Medial part of 2nd tergite hardly longer than lateral parts. Anterior margin of 2nd tergite weakly convex medially. First and 2nd sternite not adjacent. Auditory capsules swollen and clearly visible in dorsal view. Female abdomen of same shape as in male. Female caudodorsal beak in dorsal view (fig. 52) slender triangular, narrowly rounded at apex. Ovipositor sheaths just reaching beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view (fig. 45) closely resembling that of *P. lachlani*. Caudodorsal beak very slender and straight, dorsally not continuously rounded with convex dorsal margin of pygofer. Distal margin of pygofer strongly convex between caudodorsal beak and lateral protuberance, forming a fairly distinct inwards curving lobe. Caudodorsal beak narrowly triangular with concave margins, and apically rounded (fig. 44). Lateral lobe of pygofer with distinct, narrowly rounded lobate outcurving protuberance. Pygofer forming a rectangular and slightly incurving corner just below this protuberance, which is smaller than in *P. lachlani* and hardly visible in lateral view (figs. 43, 45). Ventral margin of pygofer straight. Ventral half of pygofer opening horseshoe-shaped (cf. fig. 22), with broad, rounded basal margin and concave lateral margins; incurving towards rectangular corners. Claspers (fig. 47) as in *P. lachlani*, but reaching less far beyond pygofer margin. Dorsal margin of clasper straight. Rectangular distodorsal corner of clasper bending mesiad, distally of aedeagus and supporting aedeagus in upright position. Distal margin of clasper weakly convex towards thorn-shaped apex. Claspers weakly diverging towards apices (fig. 46). Clasper base forming a very distinct ring-shaped collar around base of anal valves. This collar is medially indented around aedeagus. Aedeagus standing erect between claspers, close to anal valves, but with apical part curving away, reaching well beyond distal margins of claspers. Aedeagus (fig. 48) weakly S-curved, with short, but distinct, lateral crests restricted to its proximal half, and a distinct and slender dorsal crest. Aedeagal pore almost round (fig. 49).

Measurements: Body length ♂: 14.6-15.5 mm, ♀: 15.6 & 16.1 mm; tegmen length ♂: 19.1-19.6 mm, ♀: 22.3 & 22.4 mm; head length ♂: 1.1-1.2 mm, ♀: 1.3 mm; pronotum length ♂: 1.6 mm, ♀: 1.8 mm; mesonotum length ♂: 3.1-3.5 mm, ♀: 3.5 & 4.2 mm; head width ♂: 3.1-3.2 mm, ♀: 3.3 & 3.4 mm; width of pronotal collar ♂: 3.9-4.3 mm, ♀: 4.2 & 4.9 mm.

Distribution (fig. 32). – All specimens come from Okapa, in the Eastern Highlands of Papua New Guinea.

Etomology. – This species is named in honour of Mr L.J. Brass who collected the holotype, and many other specimens on which the current revision of the '*Baeturia* and related genera complex' is based.

Papuapsaltria stoliodes sp. n.
(figs. 3, 53-64)

Type material. – Holotype ♂: 'NEW GUINEA: PAPUA / Owen Stanley Range / Goilala: Bome, 1950 m / iv.16-30.1958' [print]; 'W.W. Brandt / Collector / BISHOP' [print], BPBM. – Paratype: PAPUA NEW GUINEA: Wau, 1100-1300 m, 2.i.1966, L. & M. Sedlacek, 1♂, BPBM.

Other material: PAPUA NEW GUINEA: Mt. Kaindi, 30.iv.1962. J.L. Gressitt, 1♀, BPBM; Edi Creek, 2000 m, 31.v.1962, J. Sedlacek, 1♂, BPBM; Mt Missim, 2100 m, 21.iii.1968, J.H. Sedlacek, 1♀, BPBM; Wau, 9-12.i.1962, J., J.H., & M. Sedlacek, G. Monteith & native collectors, 1♀, BPBM.

Males of *P. stoliodes* are easily recognized by the folded pygofer and the long and slender clasper, with a thorn-shaped lateral protuberance. Three females from the same area presumably belong to this species but are not included in the type series.

Description

Body light brown. Females smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.2-1.3× as long as body length, of female 1.6×. Male abdomen 1.5-1.9× as long as head and thorax, of females 1.1-1.3×.

Head: Postclypeus angularly protruding, smoothly rounded anteriorly, its anterior margin weakly convex, almost continuous with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave (fig. 53). Distance between lateral ocelli 0.8-0.9× as long as distance between lateral ocellus and eye and 1.5-2.2× the width of frontal ocellus.

Legs: Fore femur (fig. 57) with row of three erect spines. Most proximal spine very short, hardly longer than middle spine and much shorter than distance to middle spine.

Tegmina: Hyaline, venation in holotype with 11-12, in other material with 8, long and slender apical areas. Tegmen with a distinct costal area and a broad hyaline border along hind margin.

Tymbals: Six slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin, and a 7th, most proximal, ridge spanning only about 3/4 of tymbal width. Lateral band of seven intercalary ridges weakly developed.

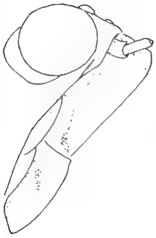
Opercula: Male operculum (fig. 59) quite large, covering greater part of tymbal cavity; folded membrane not visible in ventral view. Distal part of operculum angularly oval-shaped, medially distinctly reaching beyond meracanthus. Lateral margin short and straight, angularly bending into long and angularly convex distal margin and angularly bending into crest of basal part. Medial margin angularly bent at half-length. Meracanthus reaching beyond operculum, and just beyond anterior margin of abdominal segment 2. Distal part of female operculum (fig. 63) shorter than basal part and angularly rounded, sickle-shaped.

Abdomen: Male abdomen distinctly inflated. First tergite very short and medially hidden under metanotum. Medial part of 2nd tergite fairly long, about twice as long as lateral parts. Anterior margin of 2nd tergite weakly concave medially. Auditory capsules distinctly swollen. First and 2nd sternites adjacent. Female caudodorsal beak in dorsal view (fig. 64) broad, triangular, and bluntly rounded at apex. Ovipositor sheaths reaching just beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view (fig. 54) with sharp fold at base of caudodorsal beak. Dorsal margin of pygofer convex, though weakly concave towards proximal end, and continuously curved with broad and stout caudodorsal beak. Distal margin forming an obtuse angle with margin of beak, and an angularly rounded, inwardly curved lobe just above lateral protuberance. Ventral margin straight, but angularly bent near lateral protuberance, though not forming a distinct or protruding corner (figs. 54-55). Ventral margins weakly converging to base of pygofer; basal part of pygofer opening broad, U-shaped. Caudodorsal beak in dorsal view (fig. 58) very broad and stout, bicuspidate; medially incised at distal margin. Lateral lobe of pygofer strongly curving inwards towards end of distal margin, forming a short, dorsoventrally flattened, and distinctly posteriorly project-

Figs. 53-64. *Papuapsaltria stoliodes* sp. n. – 53, postclypeus in lateral view, holotype; 54, pygofer in lateral view, holotype; 55, pygofer from aslant, holotype; 56, claspers, holotype; 57, male fore femur, Wau; 58, male caudodorsal beak in dorsal view, holotype; 59, male operculum, holotype; 60, aedeagus in dorsal view, holotype; 61, aedeagal apex in lateral view, holotype; 62, aedeagus in lateral view, holotype; 63, female operculum, Wau; 64, female caudodorsal beak in dorsal view, Wau.

Figs. 66-75. *Papuapsaltria plicata* sp. n. – 66, pygofer from aslant, Mt. Missim; 67, pygofer in lateral view, Mt. Missim; 68, male first and second tergites in dorsal view, Mt. Missim; 69, male caudodorsal beak in dorsal view, Mt. Missim; 70, aedeagal apex, Bulldog Road; 71, aedeagus in lateral view, Bulldog Road; 72, claspers, Mt. Missim; 73, male operculum, Mt. Missim; 74, female operculum, Mt. Missim; 75, female caudodorsal beak in dorsal view, Mt. Missim.



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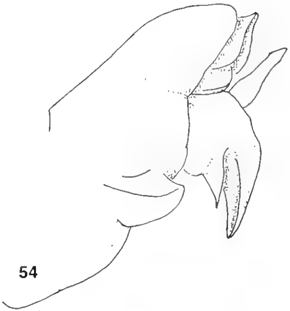

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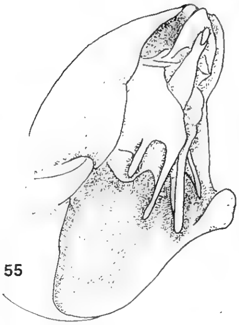

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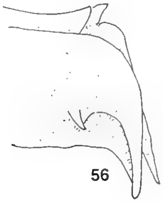

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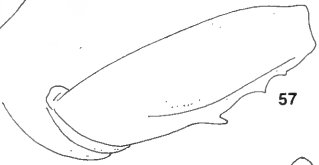

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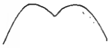

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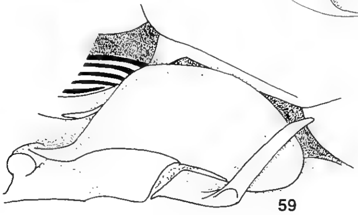

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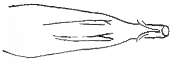

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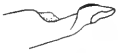

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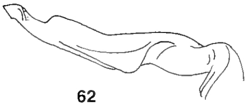

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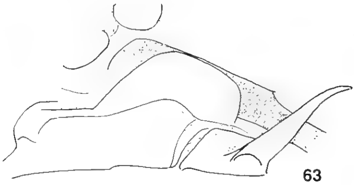

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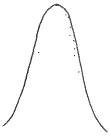

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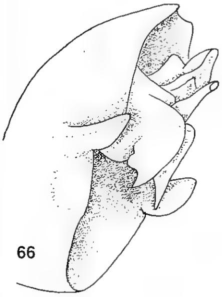

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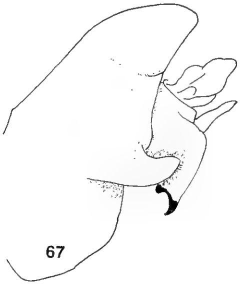

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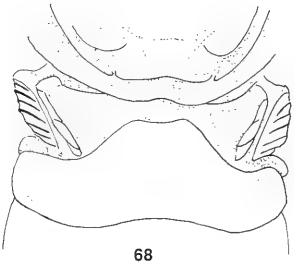

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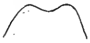

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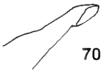

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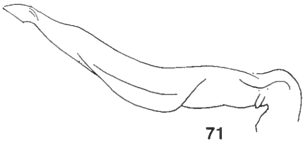

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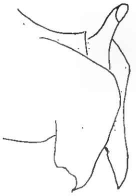

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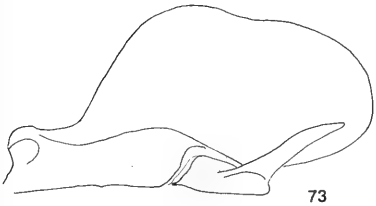

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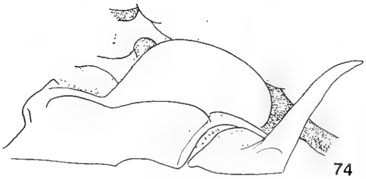

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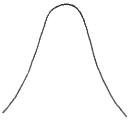

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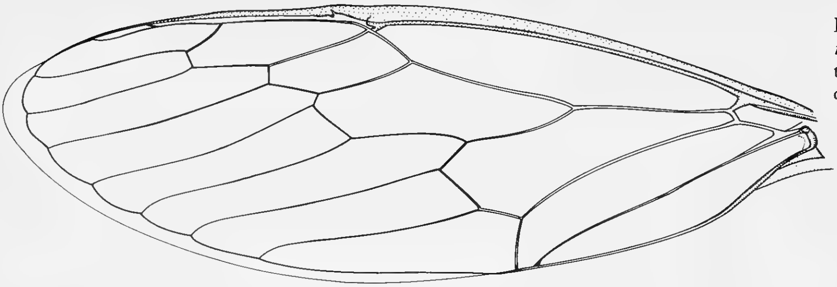


Fig. 65. *Papuapsaltria plicata* sp. n. Left tegmen, male Bulldog Road.

ing protuberance. Claspers (fig. 56) very slender, laminiform and slightly diverging towards apices. Dorsal margin straight, curving down at rounded distodorsal corner. Clasper slightly bending inwards distally of aedeagus. Apical part very long and slender, with almost membranous and transparent medial part, arching between apex and base of clasper. Clasper forming a short, sharply pointed thorn-shaped lateral protrusion at its base, in paratype distinctly longer than in holotype. Aedeagus (fig. 62) short and almost straight, most strongly curved near apex. Lateral crests broadening, almost angularly amplified, towards proximal ends and curving upwards at distal ends, fusing to a small ridge at apical bending point of aedeagus. Pair of distinct dorsal ridges (fig. 60) abruptly ending at angularly protruding distal corners. Aedeagal pore almost round (fig. 61).

Remark: The male from Edi Creek lacks the greater part of its abdomen.

Measurements: Body length ♂: 18.6 & 19.1 mm, ♀: 17.6-18.7 mm; tegmen length ♂: 20.0-25.0 mm, ♀: 28.8 mm; head length ♂: 1.2-1.3 mm, ♀: 1.5-1.6 mm; pronotum length ♂: 1.8-2.0 mm, ♀: 2.0-2.4 mm; mesonotum length ♂: 3.8-4.1 mm, ♀: 4.6-5.0 mm; head width ♂: 3.1-3.4 mm, ♀: 3.7-3.9 mm; width of pronotal collar ♂: 5.0-5.2 mm, ♀: 5.7-5.8 mm.

Distribution (fig. 3). – *P. stoliodes* is endemic to the central western part of the Papuan peninsula.

Etymology. – Stoliodes (Greek) means folded and refers to the peculiarly folded pygofer.

Papuapsaltria plicata sp. n.

(figs. 3, 65-75)

Type material. – Holotype ♂: ' NEW GUINEA (NE) / Mt. Kaindi, 16 km / SW of Wau, 2200 m / 8-9.vi.1962' [print]; 'Light Trap / J. Sedlacek / BISHOP' [print], BPBM. – Paratypes: PAPUA NEW GUINEA: same data as holotype 1♂, BPBM; Bulldog Rd., c 14 km S. Edie Creek, 2450 m, 4-10.vii.1966, G.A. Samuelson, 1♂, BPBM; Mt. Kaindi, 2400 m, 27.i.1963, J. Sedlacek, 1♂, BPBM; Mt. Kaindi, 2350 m, 26.v.1967, J.L. Gressitt, 1♂, BPBM; Mt. Kaindi, 9.vi.1962, J. & M. Sedlacek, 1♀, BPBM; Mt. Missim, 2400-2800 m, 22-30.v.1968, J.L. Gressitt, R.C.A. Rice & J. Sedlacek, 1♂, BPBM; Mt. Missim, 2400 m, 21.iv.1968, J. & M. Sedlacek, 1♂, ZMAN; Mt. Missim, Morobe Prov., 2400 m, 23.iv.1968, J. Sedlacek, 1♂, BPBM; same data 1♂, ZMAN; Mt. Missim, Wau, Morobe Distr., 1200-1800 m, 8.xii.1963, H. Clissold, 1♀, ZMAN; Mt Strong, 2600-3000 m, 8-10.i.1968, J. & M. Sedlacek, 1 ♂, BPBM.

P. plicata closely resembles *P. stoliodes*, sharing a very similarly folded pygofer, but is distinctly larger. Males have a larger operculum and a shorter, bicuspidate, clasper.

Description

Body light brown. Females smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.2-1.3× as long as body length, of females 1.6×. Male abdomen 1.7-2.2× as long as head and thorax, of females 1.1-1.3×.

Head: Postclypeus fairly narrow, angularly protruding, anterior margin weakly convex, almost continuous with anterior margins of vertex lobes. Postclypeus weakly swollen; anterior margin (lateral view) almost straight. Ocelli large and fairly close together; distance between lateral ocelli 0.6-0.9× as long as distance between lateral ocellus and eye and 1.2-2.0× the width of frontal ocellus.

Legs: Fore femur with row of three erect spines. Most proximal spine very short, though longer than middle spine, much shorter than distance to middle spine.

Tegmina: Hyaline, venation variable, generally with 8, but sometimes with 9-10 long and slender apical areas (fig. 65); additional areas often caused by splitting of the 8th apical area. Tegmen with distinct costal area and fairly broad hyaline border along hind margin.

Tymbals: Six slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin, and a 7th, most proximal, ridge spanning only about 3/4 of tymbal width. Lateral band of seven intercalary ridges weakly developed.

Opercula: Male operculum (fig. 73) larger than in *P. stoliodes*, almost completely covering tymbal cavity; folded membrane not visible in ventral view. Distal part of operculum angular and oblong, medially distinctly reaching beyond meracanthus. Lateral margin long and straight, forming a distinct and obtuse angle with crest of basal part and with distal margin. Distal margin long and straight, sometimes weakly concave at about half-length. Medial margin angularly convex. Meracanthus not reaching distal margin of operculum. Distal part of female operculum (fig. 74) about as long as basal part and oblong-shaped, with convex distal margin and rounded corners.

Abdomen: Male abdomen distinctly inflated. Medial part of 2nd tergite fairly long, about twice as long as lateral parts (fig. 68). Anterior margin of 2nd tergite weakly concave medially. First and second sternites adjacent. Auditory capsules weakly inflated. Female caudodorsal beak in dorsal view (fig. 75) narrow triangular and bluntly rounded at apex. Ovipositor sheaths not reaching beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view (fig. 67) with sharp fold at base of caudodorsal beak. Dorsal margin almost straight, convexly bent into stout caudodorsal beak. Distal margin making an obtuse angle with margin of beak, and forming an angularly rounded, inwardly curved lobe just above lateral protuberance. Ventral margin angularly bent at half-length. Pygofer from behind with almost parallel ventral margins; basal part of pygofer opening broad, U-shaped (fig. 66). Caudodorsal beak in dorsal view (fig. 69) very broad and stout, bicuspidate; medially incised at distal margin. Lateral lobe of pygofer strongly curving inwards towards end of distal margin, forming a long and slender, dorsoventrally flattened and upwards curving, but distinctly posteriorly projecting, almost laminiform protuberance. Claspers (fig. 72) very slender, almost laminiform, slightly diverging towards apices. Dorsal margin straight, curving down at rounded distodorsal corner and slightly bending inwards distally of aedeagus. Apical part shorter and broader than in *P. stoliodes*, and bicuspidate; ending in two, often darkly sclerotized, small thorns. Aedeagus (fig. 71) angularly upcurved at half-length, but weakly recurving near apex. Lateral crests slightly broadening towards proximal ends. A small, weakly developed collar at apical bending point of aedeagus, not clearly connected to lateral crests. Distinct dorsal ridge, abruptly ending in angularly protruding distal corner. Aedeagal pore oval (fig. 70).

Measurements: Body length ♂: 20.0-22.5 mm ($\bar{x}$ 21.2 mm), ♀: 16.4-19.1 mm; tegmen length ♂: 24.3-29.3 mm ($\bar{x}$ 26.0 mm), ♀: 28.8-30.8 mm; head length ♂: 1.3-1.5 mm, ♀: 1.5-1.6 mm; pronotum length ♂: 1.9-2.2 mm, ♀: 2.0-2.5 mm; mesonotum length ♂: 3.7-4.7 mm, ♀: 4.8-5.2 mm; head width ♂: 3.3-3.7 mm, ♀: 3.7-4.1 mm; width of pronotal collar ♂: 5.0-6.0 mm, ♀: 5.8-6.2 mm.

Distribution (fig. 3). – This species appears restricted to the western part of the Papuan peninsula, all specimens were collected in the viscinity of the town of Wau.

Etymology. – Plicata (Latin) means folded and refers to the peculiarly folded pygofer.

Papuapsaltria ungula sp. n.
(figs. 3, 76-82)

Type material. – Holotype ♂: 'NEW GUINEA: PAPUA Kokoda-Pitoki 450 m, iii-24-1956' [print]; 'J. L. Gressitt Collector' [print], BPBM. – Paratype: PAPUA NEW GUINEA: British New Guinea, 1921, R. Neil (Rothschild Bequest BM 1939 1), ♂, BMNH.

Only two males are available of this species. *P. ungula* is presumably closely related to *P. stoliodes*, as is suggested by the shared transparent medial part of the clasper. The species can be recognized by its claw-shaped clasper, with a very long and spiny apical part and a sharp lateral protrusion. *P. ungula* can further be recognized by its long and curved caudodorsal beak.

Description

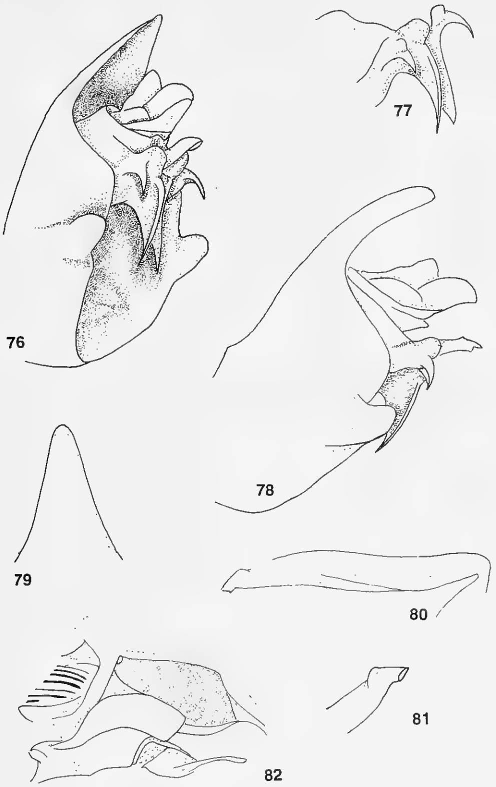
Body greenish brown. Tegmina 1.1× as long as body length. Abdomen 1.5-1.6× as long as head and thorax.

Head: Vertex and postclypeus with short red-brown setae. Postclypeus angularly protruding, anterior margin almost continuous with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave. Ocelli large and fairly close together. Distance between lateral ocelli 0.7-0.8× as long as distance between lateral ocellus and eye and 1.4-1.7× the width of frontal ocellus.

Legs: Fore femur with row of three erect spines. Most proximal spine fairly short, hardly longer than middle spine and much shorter than distance to middle spine.

Tegmina: Hyaline, with 8 apical areas, a narrow but distinct costal area and a fairly narrow hyaline border along hind margin.

Tymbals: Seven slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin, and an 8th, most proximal, ridge spanning only about 3/4 of tymbal width. Lateral band of seven intercalary ridges weakly developed.



Figs. 76-82. *Papuapsaltria ungula* sp. n., holotype: 76, pygofer from aslant; 77, claspers; 78, pygofer in lateral view; 79, caudodorsal beak in dorsal view; 80, aedeagus in lateral view; 81, aedeagal apex; 82, operculum.

Operculum (fig. 82): Very small, not covering tymbal cavity; folded membrane hardly visible in ventral view. Distal part of operculum shorter than basal part, angularly oblong, and erect, not reaching medially of meracanthus. Lateral margin short and straight, concavely curving into crest of basal part and forming an obtuse angle with long and straight distal margin. Medial margin straight, distomedial corner almost rectangular. Meracanthus just reaching anterior margin of abdomen.

Abdomen: Not inflated. First tergite short, not hidden under metanotum. Medial part of 2nd tergite only slightly longer than lateral parts. Anterior margin of 2nd tergite convex dorsally, but weakly concave medially. First and 2nd sternites almost adjacent. Auditory capsules strongly inflated.

Genitalia: Pygofer in lateral view as in fig. 78. Dorsal margin straight at base, but broadly convex, continuous with long and slender, convexly bent caudodorsal beak. Distal margin angularly convex, forming a distinct and angular distal lobe on pygofer, and forming an almost right angle with weakly concave margin of beak. Ventral margin almost straight. Ventral margins weakly converging towards base of pygofer; basal part of pygofer opening broad, V-shaped (fig. 76). Caudodorsal beak in dorsal view (fig. 79) long, triangular, and rounded at apex. Lateral lobe of pygofer weakly curving inwards towards end of distal margin, forming a short and conically shaped, dorsoventrally flattened, and distinctly posteriorly projecting protuberance. Claspers (fig. 77) distinctly bifurcate, claw-shaped, and slightly diverging towards apices. Dorsal part of clasper forming a globularly rounded protuberance adjacent to aedeagus and supporting aedeagus in upright position. Apical part of clasper very long and slender, strongly curved down and sharply pointed. Medial part of clasper membranous as in *P. stoliodes* and *P. nana*, and almost transparent between apex and base. Clasper forming a short, thorn-shaped, sharply pointed and downwards curving lateral protuberance at the base of its globular dorsal protuberance. This lateral protuberance shorter than the apical part of clasper. Aedeagus (fig. 80) shorter than in most foregoing species, just reaching beyond clasper, and angularly upcurved at half-length, but weakly recurving near apex. Lateral crests very slender, slightly broadening towards their proximal ends and upcurving at their distal ends. Crests fused to a small collar around apical bending point of aedeagus (fig. 81), though connection between collar and crests very vague. Aedeagus with rounded dorsal ridge and distinct ventral crest. Aedeagal pore oval-shaped.

Measurements: Body length: 13.2 & 14.8 mm; tegmen length: 15.0 & 16.8 mm; head length: 1.0 & 1.1 mm; pronotum length: 1.5 mm; mesonotum length: 2.7 & 2.9 mm; head width: 2.8 & 2.9 mm; width of pronotal collar: 3.5 & 3.7 mm.

Distribution (fig. 3). – *P. ungula* is probably endemic to the Papuan peninsula.

Etymology. – The name ungula (Latin claw) refers to the claw-shaped clasper.

Papuapsaltria nana (Jacobi, 1903) n. comb.
(figs. 3, 6, 83-91)

Baeturia beccarii. – Distant 1892: Tab xiv figs. 27, 27a-b only (non Distant, 1888).

Acrilla nana Jacobi, 1903: 13, fig. 5.

Baeturia famulus Distant, 1906: 157. – Kato 1931: 74; Kato 1932: 184; Blöte 1958: 266; Metcalf 1963: 245-250; Duffels & Van der Laan 1985: 252; De Boer 1986: 176; De Boer 1993a: 16. (**syn. n.**).

Thaumastopsaltria nana. – Distant 1906: 160; Metcalf 1963: 259; De Boer 1992b: 17-18.

The following references to *famulus* refer to other species: *Baeturia famulus* Stål MS; Distant 1892: 149 in synonymy of *Baeturia beccarii* is *Muda virguncula*, *Baeturia famulus*; Myers 1928: fig. 18 is *Aedeastria latifrons* (Blöte, 1960), and *Baeturia famulus*; Lallemand 1931: 78, the specimen indicated is a female belonging to *Baeturia macgillavryi* De Boer, 1989.

Lectotype designation. – The type series of *Acrilla nana* comes from Milne Bay, but the number of type specimens is not known (Jacobi 1903). In the Dresden museum I found 3♂ and 5♀ from Milne Bay from the collection of A. Jacobi; 1♂ and 1♀ are labelled 'typus' and one ♀ 'cotypus'. One male in the BMNH from the same locality and from the Distant collection, is also labelled 'typus'. All these specimens belong to the same species. The male with the 'typus' label from the Dresden collection is hereby designated lectotype, the other specimens with typus/cotypus labels are regarded as paralectotypes, but the remaining 2♂ and 3♀ should possibly also be regarded as paralectotypes.

Nomenclature and synonymy. – *Baeturia famulus* is a manuscript name of Stål which was regarded as a synonym of *Baeturia beccarii* Distant, 1888, when it was mentioned in Distant's 'Monograph of Oriental Cicadidae' (1892). Some years later *Baeturia beccarii* was transferred to the genus *Muda* Distant, 1897 (Distant 1906), and brought into the synonymy of *Muda virguncula* (Walker, 1857) by Moulton (1923). Distant's type of *Baeturia beccarii* in the BMNH certainly belongs to the genus *Muda*. The specimen depicted by Distant (1892) as *Baeturia beccarii* (table xiv figs 27, 27 a-b) is not a *Muda* however. Distant realized this and in his 'Synonymic Catalogue of Homoptera' (1906) he presents *Baeturia famulus* separately from *Muda beccarii*. Distant does not give a description of *B. famulus*, he merely refers to Stål MS and *Baeturia beccarii* (fig only) in his monograph of 1892.

From that moment the name *Baeturia famulus* Distant became valid, with as its description the figure published in 1892 and the depicted specimen as its holotype, *B. famulus* Stål never having been published than as a junior synonym (see Int. code art. 11 e). This depicted specimen was identified by Blöte as one from Bujakori, S New Guinea, and is now in the BMNH. Though the specimen does not bear any identification labels of Distant, it can be recognized by the 9 apical areas in its left tegmen. As Blöte realized, this specimen could not be the one indicated as *famulus* Stål MS, since it was collected in 1890 and Stål died in 1878. Apart from some doubt it sheds on the correctness of Blöte's identification of the Bujakori specimen as the one depicted in 1892, this is of no further consequence.

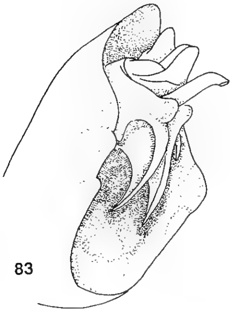
I here follow Blöte and regard the Bujakori specimen as the holotype of *Baeturia famulus* Distant, 1906. Comparison of types revealed that *B. famulus* Dist. is a junior synonym of *Thaumastopsaltria nana* (Jacobi, 1903), originally described as *Acrilla nana*.

Both Metcalf (1963) and Duffels & Van der Laan (1985) incorrectly regarded Myers as the author of *B. famulus*, originating from an incorrect interpretation of Distant, 1906. Metcalf falsely stated that Distant (1906) regarded *B. famulus* to be a synonym of *Baeturia beccarii*.

Myers (1928) mentioned 'an undoubtedly distinct species *B. famulus* Dist.' and depicted its aedeagus. Depicted however, is not the holotype of *B. famulus* Distant, but a specimen of an altogether different species. This specimen could be traced in the BMNH and is labeled 'Aru; Wallace; 67/66' and has on a separate pin, labeled '*famulus*' in pencil in Myers' hand, a preparation of part of its abdomen and pygofer glued on yellow mika. Though these parts are heavily crushed, the aedeagus is in good condition and matches Myers' drawing. The specimen belongs to *Aedeastria latifrons* (Blöte, 1960) which will remain its valid name, the name *B. famulus* Myers being a homonym.

Material examined. – Neu Guinea, Staudinger, 1♀ det. *Acrilla nana*, SMFD; PAPUA NEW GUINEA: Bujakori, viii.1890, L. Loria, 1♂ det. *beccarii*, 3♂, 1♀, MCSN; same data 1♂ holotype *Baeturia famulus* Distant, 2♀, BMNH; Finschhafen, 250 ft, 9.ix.1944, H. Hoogstraal, 2♂, NCSU; Menapi, Cape Vogel peninsula, 0-30 m, 25.iv.1953, G.H.H. Tate, 1♂, AMNH; same data but Geoffrey M. Tate, 2♂, AMNH; Milne Bay, ♂ typus *Acrilla nana* paralectotype, BMNH; Milne Bay, Coll. A. Jacobi 1911-5, 1♂ Typus *Acrilla nana* lectotype, 1♀ typus *Acrilla nana* paralectotype, 1♀ cotypus *Acrilla nana* paralectotype, SMTD; Milne Bay, 2♂, 3♀, (paralectotypes?) SMTD; Milne Bay, 1♀, ZILS; Peria Creek, Kwagira riv., 50 m, 14.viii-6.ix.1953, Geoffrey M. Tate, 5♂, 1♀, AMNH; same data 1♂, ZMAN; Popondetta, 25 m, v.1966, Shanahan-Lippert, 8♂, 1♀, BPBM; same data but vi.1966, 5♂, 3♀, BPBM; same data 2♂, 1♀, ZMAN; Popondetta, 60 m, 1-4.ix.1963, J. Sedlacek, 9♂, 3♀, BPBM; same data 2♂, 1♀, ZMAN; Popondetta, Buka-Bara, 23.ix.1963, P. Shanahan, 1♂, BPBM; Pt. Glasgow, Mamai Plnt., 150 m, 6.ii.1965, R. Straatman, 1♂, BPBM; without locality label: Sayer, 1♂, 1♀ det. *famulus* MS Stål, 1♀, BMNH: D'ENTRECASTEAUX ISLANDS: Normanby I., Wakaiuna, Sewa Bay, 15-30.x.1956, W.W. Brandt, 1♂, BPBM; same data but 21-30.xi.1956, 1♀; 11-20.xii.1956, 1♀, both BPBM.

P. nana lacks the distinctly convex distal margin of the pygofer, shared by many of the foregoing species. The clasper of *P. nana*, however, strongly suggests a close relationship with *P. ungula*. The claspers of these species share a similar apex and a similarly transparent medial part. However, the clasper of *P. nana* has a larger dorsal protrusion and a much smaller lat-



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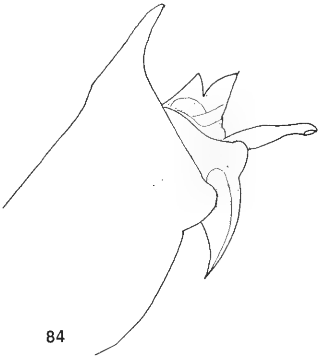

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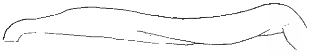

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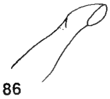

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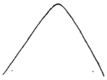

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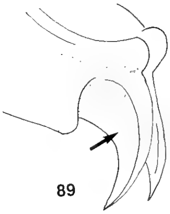

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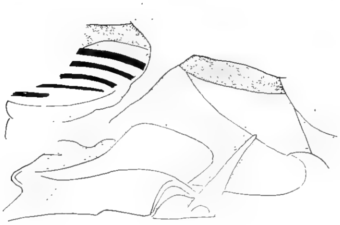

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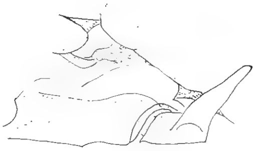

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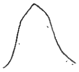

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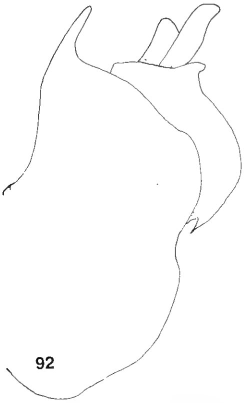

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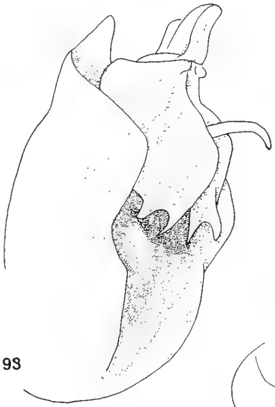

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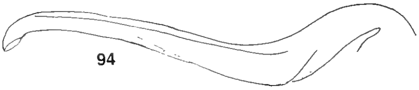

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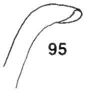

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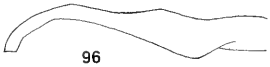

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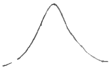

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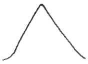

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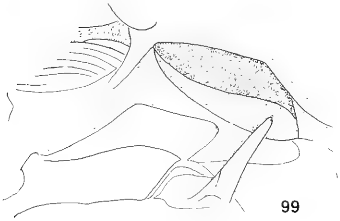

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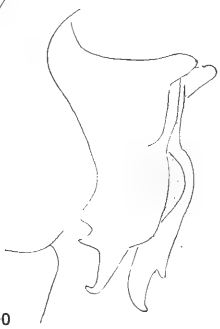

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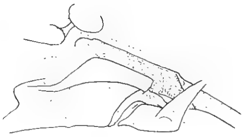

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eral protrusion, the latter forming a bluntly rounded lobe.

Description

Body yellowish brown or olive green. Females smaller than males, but with more robust head and thorax and longer tegmina. Tegmina of males 1.0-1.2× as long as body length, of females 1.2-1.3×. Male abdomen 1.4-1.8× as long as head and thorax, of females 1.1-1.4×.

Head (fig. 6): Vertex and postclypeus practically bald. Postclypeus broad and sharply edged, distinctly protruding beyond vertex lobes, forming an obtuse angle anteriorly. Anterior margin of postclypeus sharply curving back at lateral corners, forming almost right angles with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave. Vertex with weak furrows between ocelli. Distance between lateral ocelli fairly variable, 0.9-1.3× as long as distance between lateral ocellus and eye and 1.6-3.2× the width of frontal ocellus.

Thorax: Pronotum often with distinct medial furrow.

Legs: Fore femur with row of three erect spines. Most proximal spine generally distinctly longer than middle spine, but much shorter than distance to middle spine.

Tegmina: Generally with 8, occasionally with 9-10, apical areas, a distinct costal area and a broad hyaline border along hind margin.

Tymbals: Four slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin, and a 5th, most proximal, ridge almost reaching ventral margin. Lateral band of four intercalary ridges weakly developed.

Opercula: Male operculum (fig. 87) very small, not covering tymbal cavity, leaving a wide gap between operculum and abdomen; folded membrane completely visible in ventral view. Distal part of operculum shorter than basal part, angularly oblong, and erect, not reaching medially of meracanthus. Lateral margin short and straight, concavely curving into crest of basal part and forming an obtuse angle with long and straight distal margin. Medial margin straight, distomedial corner almost rectangular. Meracanthus reaching beyond operculum and just beyond edge of folded membrane. Female operculum (fig. 90) very similar to that of males, with angularly oblong distal part.

Abdomen: Male abdomen distinctly inflated. First tergite short, not hidden under metanotum. Medial part of 2nd tergite nearly twice as long as lateral parts. Anterior margin of 2nd tergite concave medially. Auditory capsules weakly inflated. First and 2nd sternites not adjacent. Female caudodorsal beak in dorsal view (fig. 91) narrow triangular and rounded, almost pointed at apex. Ovipositor sheaths reaching just beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 84. Dorsal margin straight, though concave at base of caudodorsal beak and angularly bent into short and straight beak. Distal margin weakly convex, not forming a lobe on pygofer, and concavely bent into margin of beak. Ventral margin almost straight. Pygofer from behind with almost parallel ventral margins; basal part of pygofer opening broad U-shaped (fig. 83). Caudodorsal beak in dorsal view (fig. 88) short triangular, and rounded or truncate at apex. Lateral lobe of pygofer gradually curving inwards towards end of distal margin, forming a fairly large, distinctly swollen and bluntly rounded lateral protuberance. Claspers (fig. 89) closely resembling those of *P. ungula*, with dorsal part forming a globularly rounded, but larger, protuberance adjacent to aedeagus, and supporting aedeagus in upright position. Apical parts of claspers strongly curved down and slightly diverging towards apices, forming a long, slender, and sharply pointed ridge along their convex distal margins. This ridge arches into a small, lobate lateral protuberance at the base of clasper. Medial part of clasper membranous and almost transparent between apex and base. Aedeagus (fig. 85) weakly upcurved, abruptly narrowing and strongly curved down near apex. Aedeagus with very slender lateral crests and a distinct pair of dorsal ridges. Aedeagal pore round (fig. 86).

Measurements: Body length ♂: 15.5-21.0 mm ($\bar{x}$ 17.5 mm ± 1.1), ♀: 14.9-17.0 mm ($\bar{x}$ 15.9 mm ± 0.7); tegmen length ♂: 16.5-21.0 mm ($\bar{x}$ 18.8 mm ± 1.0), ♀: 18.7-21.0 mm ($\bar{x}$ 19.8 mm ± 0.7); head length ♂: 1.5-1.9 mm ($\bar{x}$ 1.6 mm), ♀: 1.5-1.8 mm ($\bar{x}$ 1.7 mm); pronotum length ♂: 1.6-2.2 mm ($\bar{x}$ 1.8 mm), ♀: 1.8-2.2 mm ($\bar{x}$ 1.9 mm); mesonotum length ♂: 3.1-4.1 mm ($\bar{x}$ 3.4 mm), ♀: 3.2-3.9 mm ($\bar{x}$ 3.4 mm); head width ♂: 3.0-3.9 mm ($\bar{x}$ 3.4 mm), ♀: 3.5-4.0 mm ($\bar{x}$ 3.8 mm); width of pronotal collar ♂: 4.0-5.4 mm ($\bar{x}$ 4.4 mm), ♀: 4.5-5.0 mm ($\bar{x}$ 4.8 mm).

Figs. 83-91. *Papuapsaltria nana* (Jacobi, 1903): 83, pygofer from aslant, Peria Creek; 84, pygofer in lateral view, Peria Creek; 85, aedeagus in lateral view, Popondetta; 86, aedeagal apex, Popondetta; 87, male operculum Popondetta; 88, male caudodorsal beak in dorsal view, Popondetta; 89, claspers, Peria Creek, arrow indicating membranous medial part; 90, female operculum, Kwagira River; 91, female caudodorsal beak, Kwagira River.

Figs. 92-101. *Papuapsaltria bidigitula* sp. n.: 92, pygofer in lateral view, holotype; 93, pygofer from aslant, Feramin; 94, aedeagus in lateral view, holotype; 95, aedeagal apex in lateral view, holotype; 96, aedeagus in lateral view, Wetar; 97, male caudodorsal beak in dorsal view, holotype; 98, female caudodorsal beak in dorsal view, Wetar; 99, male operculum, holotype; 100, claspers, Wetar; 101, female operculum, Wetar.

Distribution (fig. 3). – *P. nana* is recorded from the Huon- and Papuan peninsulas of New Guinea, and from Normanby Island of the D'Entrecasteaux Islands.

Papuapsaltria bidigitula sp. n.
(figs. 3, 92-101)

Type material. – Holotype ♂: 'NEW GUINEA: (NE) / Feramin, 150-120 m / June 15-18, 1959' [print], 'W. W. Brandt / Collector / BISHOP' [print], BPBM. – Paratypes: IRIAN JAYA: Ansus, A.B. Mayer, 1893, 1♂, BMNH; Jobie, R.H.F. Rippon, N.M.W., 1918.93. 1♂, NMWC; PAPUA NEW GUINEA: same data as holotype 1♀; same data but 23-31.v.1959, 1♀; 1-6.vi.1959, 2♀; 7-14.vi.1959, 1♂; all BPBM; Damanti, Finisterre Mts., Morobe Dist., 2-11.x.1964, M.E. Bacchus, 1♂, 4♀, BMNH; Eliptamin Valley, 1200-1350 m, 16-30.viii.1959, W.W. Brandt, 1♂, ZMAN; same data but 19-30.viii.1959, 1♀, BPBM; WETAR ISLAND: Wetter near Timor, W. Doherty, 1903.31, 1♂, 1♀, BMNH.

P. bidigitula shares a bifurcate clasper with *P. plicata*, *P. stoliodes*, and *P. ungula*. The species is easily recognized by the shape of its clasper base, forming a broad, ring-shaped collar, often with two distinct paramedian protrusions at the base of the anal valves. The shapes of the clasper and, especially, of the aedeagus are variable, suggesting that the material might belong to several species.

Description

Body reddish brown. Females smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.2-1.3× as long as body length, of females 1.3-1.5×. Male abdomen 1.2-1.7× as long as head and thorax, of females 1.1-1.3×.

Head: Vertex and postclypeus with short red-brown setae. Postclypeus broad, distinctly protruding beyond vertex lobes and smoothly rounded anteriorly. Anterior margin of postclypeus weakly convex, but sharply curving back at lateral corners, forming almost right angles with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave. Distance between lateral ocelli 1.0-1.4× as long as distance between lateral ocellus and eye and 1.8-3.0× the width of frontal ocellus.

Legs: Fore femur with row of three spines. Most proximal spine generally very short and strongly bent, almost adjacent to femur, but longer and more erect in specimens from Wetar and Ansus. Proximal spine much shorter than distance to middle spine.

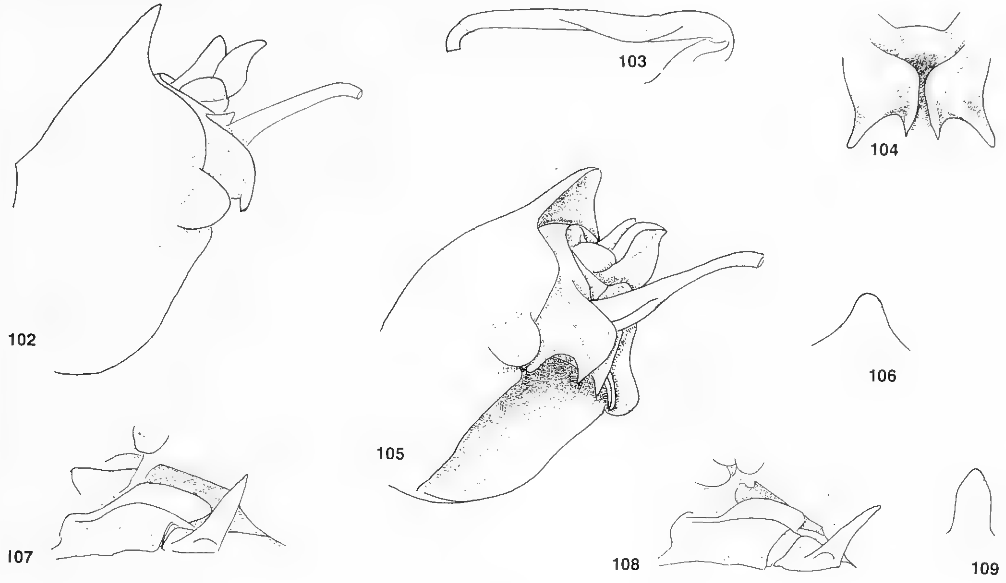
Tegmina: Hyaline, with 8 apical areas, a distinct costal area and a fairly broad hyaline border along hind margin.

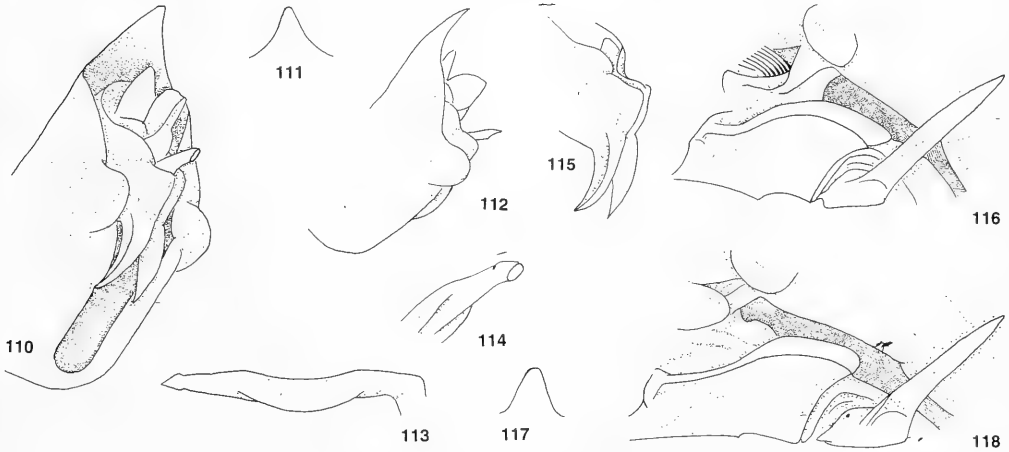
Tymbals: Six slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin. Lateral band of seven intercalary ridges weakly developed.

Opercula: Male operculum (fig. 99) very small, not covering tymbal cavity in ventral view and generally leaving folded membrane exposed, but covering most of folded membrane in specimen from Ansus. Distal part of operculum shorter than basal part, angularly oblong and erect, not reaching medially of meracanthus. Lateral margin long and straight, concavely curving into crest of basal part and forming an obtuse angle with long and straight distal margin. Medial margin short and straight, distomedial corner almost rectangular. Meracanthus reaching beyond operculum, but not reaching to margin of abdominal segment 2. Female operculum (fig. 101) very similar to that of male, with angularly oblong distal part.

Abdomen: Male abdomen hardly inflated. First tergite short, almost completely hidden under metanotum middorsally. Medial part of 2nd tergite slightly less than 2× as long as lateral parts. Anterior margin of 2nd tergite weakly concave medially. First and 2nd sternites generally not adjacent, but adjacent in specimen from Ansus. Auditory capsules distinctly inflated. Female caudodorsal beak in dorsal view (fig. 98) triangular and pointed at apex. Ovipositor sheaths reaching just beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 92. Dorsal margin almost straight and angularly concave at base of caudodorsal beak. Distal margin weakly convex, forming an obtuse angle with margin of beak. Ventral part of pygofer lobe forming an angular corner under lateral protuberance. Ventral margin straight. Ventral margins converging to base of pygofer; basal part of pygofer opening broad, V-shaped (fig. 93). Caudodorsal beak in dorsal view (fig. 97) short triangular, almost pointed at apex. Lateral lobe of pygofer weakly curving inwards towards end of distal margin, but recurving near ventral margin, forming a broad, rectangular and weakly swollen laminiform protuberance. Claspers (fig. 100) distinctly bifurcate, very short and broad, angular in lateral view, and slightly diverging towards apices. Dorsal margin straight, curving down at rounded distodorsal corner. Clasper weakly inflated around aedeagus, and forming a thorn-shaped and sharply pointed apical protrusion and a generally more rounded lateral protrusion. In some specimens the lateral protrusion is the longest, in others the apical protrusion. Basal parts of claspers fuse to a broad and smoothly rounded collar around base of anal valves. This collar generally with two, almost finger-shaped, paramedian pro-





Figs. 102-109. *Papuapsaltria spinigera* sp. n. – 102, pygofer in lateral view, Korop; 103, aedeagus in lateral view, paratype; 104, claspers, holotype; 105, pygofer from aslant, holotype; 106, male caudodorsal beak in dorsal view, holotype; 107, male operculum, holotype; 108, female operculum, Okapa; 109, female caudodorsal beak in dorsal view, Okapa.
Figs. 110-118. *Papuapsaltria ustulata* (Blöte, 1960). – 110, pygofer from aslant, holotype; 111, male caudodorsal beak in dorsal view, holotype; 112, pygofer in lateral view, holotype; 113, aedeagus in lateral view, Kutsime; 114, aedeagal apex, Kutsime; 115, claspers, holotype; 116, male operculum, holotype; 117, female caudodorsal beak in dorsal view, Kutsime; 118, female operculum, Kutsime.

trusions at its dorsal margin, which are only weakly developed in the specimens from Damanti and Feramin, and absent in the specimen from Eliptamin. Aedeagus quite long, slender, and S-curved, with broad and angular lateral crests and a distinct dorsal crest. Aedeagus in the western part of the distribution area (Ansus, Jobi and Wetar) with slender dorsal crest and gradually curving down to apex (fig. 96), but in all other specimens, with more angular dorsal crest and more angularly bent near apex (fig. 94). Aedeagal pore weakly incised, almost round (fig. 95).

Measurements: Body length ♂: 13.1-16.2 mm ($\bar{x}$ 14.7 mm ± 1.1), ♀: 11.6-15.6 mm ($\bar{x}$ 14.2 mm ± 1.3); tegmen length ♂: 15.7-20.4 mm ($\bar{x}$ 19.0 mm ±

1.9), ♀: 15.5-22.4 mm (x̄ 20.6 mm ± 2.3); head length ♂: 1.1-1.4 mm (x̄ 1.2 mm), ♀: 1.1-1.4 mm (x̄ 1.3 mm); pronotum length ♂: 1.4-1.7 mm (x̄ 1.6 mm), ♀: 1.5-2.0 mm (x̄ 1.8 mm); mesonotum length ♂: 2.7-3.8 mm (x̄ 3.2 mm), ♀: 3.0-3.5 mm (x̄ 3.2 mm); head width ♂: 3.2-3.4 mm (x̄ 3.3 mm), ♀: 3.0-3.8 mm (x̄ 3.5 mm); width of pronotal collar ♂: 3.6-4.4 mm (x̄ 4.0 mm), ♀: 3.7-4.9 mm (x̄ 4.5 mm).

Distribution (fig. 3). – *P. bidigitula* has a very peculiar distribution. The species is recorded from northern and central Irian Jaya, Yapen Island, and from Wetar Island. Since the species has not been recorded from any of the intermedate Banda islands, the record from Wetar is considered dubious.

Etymology. – Digitulus is the diminutive form of digita (Latin) finger; the name refers to the two small finger-shaped protuberances on the ring-shaped dorsal parts of the claspers.

Papuapsaltria spinigera sp. n.
(figs. 3, 102-109)

Type material. – Holotype ♂: 'E Highlands Dist., Okapa c 5000 ft. 20.xii.1964 R.H. Hornbrook' [-print]; 'M.E. Bacchus BM 1965-120' [print]; 'British Museum' [print], BMNH. – Paratypes: PAPUA NEW GUINEA: same data as holotype 1♂, 1♀, BMNH; Korop Upper Jimi R. 1300 m, 12.vii.1955, J.L. Gressitt, 1♂, BPBM.

P. spinigera is presumably closely related to the five foregoing species, sharing a similarly bifurcate clasper. *P. spinigera* is distinctly smaller than these species and is easily recognized by the long lateral protrusion of its clasper, which is longer than the apical part of clasper.

Description

Body greenish brown. Female smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.2-1.3 × as long as body length, of female 1.5 ×. Male abdomen 1.2-1.4 × as long as head and thorax, of female 1.0 ×.

Head: Vertex and postclypeus with short red-brown setae. Postclypeus broad,

distinctly protruding beyond vertex lobes and smoothly rounded anteriorly. Anterior margin of postclypeus almost straight, but sharply curving back at lateral corners, forming almost right angles with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave. Diverging fissures on vertex weakly developed. Distance between lateral ocelli in males 1.0 x, in females 1.2 x, as long as distance between lateral ocellus and eye and 1.6-1.8 × the width of frontal ocellus.

Legs: Fore femur with row of three erect spines. Most proximal spine very short, hardly longer than middle spine and much shorter than distance to middle spine.

Tegmina: Hyaline, with 8 long and slender apical areas, a distinct costal area, and a fairly broad hyaline border along hind margin.

Tymbals: Seven slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin, and an 8th, most proximal, ridge spanning only about 3/4 of tymbal width. Lateral band of seven intercalary ridges weakly developed.

Opercula: Male operculum (fig. 107) very small, not covering tymbal cavity, but leaving only a narrow gap between operculum and abdomen; folded membrane not visible in ventral view. Distal part of operculum shorter than basal part, angularly oblong, and erect, not reaching medially of meracanthus. Lateral margin short and straight, concavely curving into crest of basal part and forming an obtuse angle with long and straight distal margin. Medial margin straight, distomedial corner almost rectangular. Meracanthus reaching beyond anterior margin of abdominal segment 2. Female operculum (fig. 108) very similar to that of males, with angularly oblong distal part.

Abdomen: Male abdomen not inflated. First tergite very short. Medial part of 2nd tergite only slightly longer than lateral parts. Anterior margin of 2nd tergite straight medially. First and 2nd sternites adjacent. Auditory capsules strongly inflated. Abdomen of the only female specimen available dried in and twisted. Female caudodorsal beak in dorsal view (fig. 109) narrow, triangular, and bluntly rounded at apex. Ovipositor sheaths reaching distinctly beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 102. Dorsal margin almost straight and almost continuous with straight margin of short and stout caudodorsal beak. Distal margin angularly convex, forming a distinct distal lobe on pygofer, and concavely bending into margin of beak. Ventral margin straight. Pygofer from behind with almost parallel ventral margins; basal part of pygofer opening broad, U-shaped (fig. 105). Caudodorsal beak in dorsal view (fig. 106) short triangular, with concave margins and rounded apex. Lateral lobe of pygofer weakly curving inwards towards end of distal margin, forming a small, lobate, almost laminiform protuberance, projecting beyond pygofer margin. Claspers (fig. 104) distinctly bifurcate, very short and broad, angular in lateral view, and slightly diverging towards apices. Dorsal margin straight, curving down at rounded distodorsal corner and slightly bending inwards distally of aedeagus. Apical part of clasper short, thorn-shaped, directed downwards, with a small inwards directed clasper hollow. Clasper forming a long, spiny, but apically rounded lateral protuberance near its base. This lateral protuberance is longer than the apical part of clasper. Clasper base not forming a distinct collar around base of anal valves. Aedeagus (fig. 103) very long, reaching far beyond apex of caudodorsal beak, weakly S-curved, narrowing and strongly curving down near apex. Lateral crests short and restricted to proximal half of aedeagus. Aedeagal pore round.

Measurements: Body length ♂: 11.8-12.7 mm, ♀: 11.5 mm; tegmen length ♂: 14.3-16.2 mm, ♀: 16.7 mm; head length ♂: 1.0-1.1 mm, ♀: 1.1 mm; pronotum length ♂: 1.4-1.5 mm, ♀: 1.5 mm; mesonotum length ♂: 2.6-3.0 mm, ♀: 3.0 mm; head width ♂: 2.7-3.0 mm, ♀: 3.1 mm; width of pronotal collar ♂: 3.3-3.8 mm, ♀: 4.0 mm.

Distribution (fig. 3). – *P. spinigera* is probably restricted to northeastern Papua New Guinea.

Etymology. – Spinigera (Latin) means spiny and refers to the lateral spine on the clasper.

Papuapsaltria ustulata (Blöte, 1960) comb. n. (figs. 110-118, 129)

Baeturia ustulata Blöte, 1960: 75, fig. 32; Duffels & Van der Laan 1985: 255; De Boer 1993a: 16.

P. ustulata is a small species with sharply pointed pick-shaped claspers, males can further be recognized by a very short distal part of the operculum and an extremely long meracanthus.

Description

Body bicolorate: head and thorax ochraceous, tinged with green, abdomen more reddish brown. Females larger than males. Tegmina of males 1.1-1.2× as long as body length, of females 1.2×. Male abdomen 1.4-1.5× as long as head and thorax, of females 1.1-1.4×.

Head: Ochraceous. Postclypeus and anterior part of vertex lobes with some short red-brown setae. Postclypeus slightly protruding, almost oblong-shaped and smoothly rounded anteriorly. Anterior margin of postclypeus weakly convex, almost continuous with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave, strongly concave in holotype. Lateral parts of postclypeus very smooth, with some weak furrows, but almost without rows of parallel ridges. Ocelli fairly close together. Distance between lateral ocelli 1.5-1.8× as long as distance between lateral ocellus and eye and 0.8-1.1× the width of frontal ocellus.

Thorax: Pronotum with weak medial furrow. Mesonotum greenish, cruciform elevation ochraceous.

Legs: Femora ochraceous, tibiae and tarsi reddish. Fore femur with row of three erect spines. Proximal spine fairly long in holotype, longer than middle spine and almost as long as distance to middle spine, but in other specimens only slightly longer than middle spine and distinctly shorter than distance to middle spine.

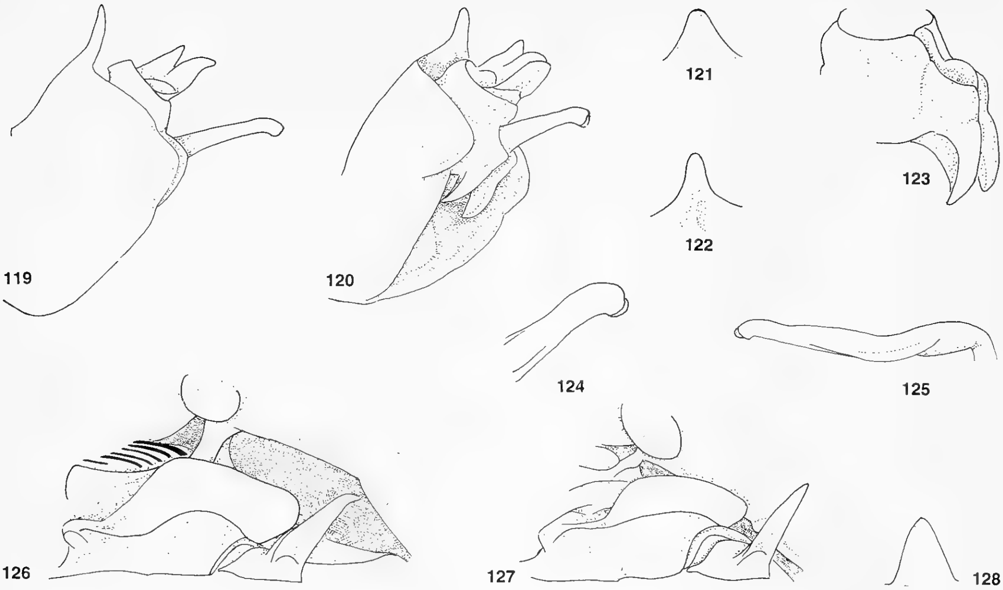
Tegmina: Hyaline, with 8 apical areas and a distinct hyaline costal area. Hyaline border along hind margin of tegmen fairly narrow in holotype, distinctly broader in other specimens.

Tymbals: Holotype with seven transverse sclerotized ridges from dorsal to ventral margin and an 8th, most proximal, ridge almost reaching ventral margin. Other specimens with one complete ridge less.

Opercula: Male operculum (fig. 116) very short, but partly covering tymbal cavity in ventral view, leaving a narrow gap between operculum and abdomen; folded membrane hardly visible in ventral view. Distal part of operculum very short and erect, hardly more than a continuation of the crest along distolateral corner of basal part, only slightly amplifying mesiad to less than 1/3 as long as basal part. Lateral margin convexly bent into straight distal margin. Distal margin forming a sharp angle with short medial margin. Meracanthus very long and slender, reaching beyond anterior margin of abdominal segment 3. Female operculum (fig. 118) as in male.

Abdomen: Red-brown, distal part green in holotype. One specimen with row of dark ventrolateral spots on segments 3-7. Male abdomen very slender, not inflated. First tergite very short and middorsally almost completely hidden under metanotum. Medial part of 2nd tergite slightly longer than lateral parts. Anterior margin of 2nd tergite straight medially. First and 2nd sternites adjacent. Auditory capsules very large, bulgy, clearly visible in dorsal view. Female abdomen even more slender than in male. Female caudodorsal beak in dorsal view (fig. 117) triangular, rounded at apex. Ovipositor sheaths just reaching beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 112. Dorsal margin weakly concave, convexly bent into straight and slender caudodorsal beak. Distal margin weakly convex between caudodorsal beak and lateral protuberance, concavely bent into margin of beak, not forming a distal lobe on pygofer. Caudodorsal beak in dorsal view (fig. 111) very slender, with concave margins, rounded or pointed at apex. Lateral lobe of pygofer sharply bent inwards, especially in holotype, forming a large angular, slightly posteriorly protruding and distinctly swollen protuberance. Pygofer forming an angular, in holotype more rounded, corner just below this protuberance. Ventral margin of pygofer weakly convex. Ventral half of pygofer opening narrow U-shaped (fig. 110),



Figs. 119-128. *Papuapsaltria baasi* sp. n.: 119, pygofer in lateral view, Mokai; 120, pygofer from aslant, Mokai; 121, male caudodorsal beak in dorsal view, Tor River; 122, male caudodorsal beak in dorsal view, Mokai; 123, claspers, Mokai; 124, aedeagal apex, Mokai; 125, aedeagus in lateral view, Bodem; 126, male operculum, Mokai; 127, female operculum, Bodem; 128, female caudodorsal beak in dorsal view, Bodem.

with weakly concave basal margin; ventral margins almost parallel. Claspers (fig.115) very short, hardly reaching beyond pygofer margin, and weakly diverging towards apices; pick-shaped, with rectangular square-shaped dorsal part and slender, slightly recurving, sharply pointed, and downwards directed apical part. Dorsal part of clasper curving mesiad, as a shaft encircling aedeagus, and supporting aedeagus in upright position. Apical part of clasper with large and sharply edged clasper hollow. Basal parts of claspers curving inwards, but not fusing, forming an almost continuous collar around base of anal valves. Aedeagus standing erect between claspers, adjacent to anal valves. Aedeagus (fig. 113) weakly S-curved, almost straight, but angularly bent near apex, with distinct lateral crests and a weak dorsal ridge. Apical part of aedeagus abruptly broadening, and forming a small and angular protrusion at apical bending point. Aedeagal pore oval, almost round (fig. 114).

Measurements: Body length ♂: 13.2-13.7 mm, ♀: 14.5 & 16.4 mm; tegmen length ♂: 15.1-16.4 mm, ♀: 19.9 mm; head length ♂: 1.0-1.2 mm, ♀: 1.3 & 1.5 mm; pronotum length ♂: 1.5-1.6 mm, ♀: 1.9 mm; mesonotum length ♂: 2.8-3.0 mm, ♀: 3.4 & 3.6 mm; head width ♂: 2.9-3.3 mm, ♀: 3.4 & 3.7 mm; width of pronotal collar ♂: 3.6-3.9 mm, ♀: 4.7 & 4.8 mm.

Material examined. – IRIAN JAYA: Bernhard Camp, 100 m, 10.iv.1939, Neth Ind. – American New Guinea Expedit., L.J. Toxopeus, ♂ holotype *Baeturia ustulata*, RMNH; Karubaka, Swart vall., 1300 m, 1.xi.1958, J.L.

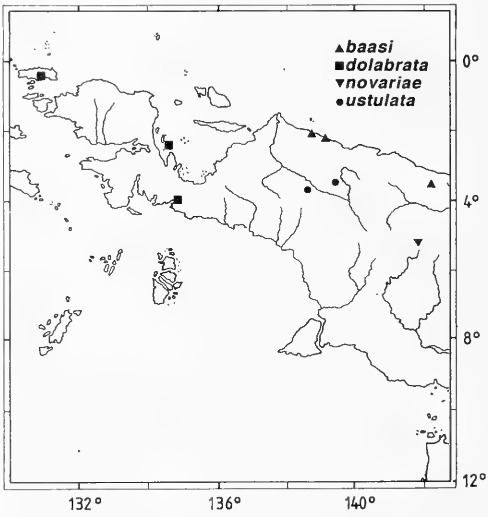


Fig. 129. Localities of *Papuapsaltria baasi, P. dolabrata, P. novariae*, and *P. ustulata*.

Gressitt, 2♂, BPBM; Kutsime, West of Swart vall., 1500 m, 14.xi.1958, J.L. Gressitt, 2♀, BPBM.

Distribution (fig. 129). – *P. ustulata* is endemic to central western New Guinea, north of the central mountain ranges.

Papuapsaltria baasi sp. n.
(figs. 119-129)

Type material. – Holotype ♂: 'NEW GUINEA NETH. / Bodem, 100 m, 11 km / SE Oerberfaren / July 7-17, 1959' [print]; 'T.C. Maa / Collector / Bishop' [print], BPBM. – Paratypes: IRIAN JAYA: same data as holotype 1♂, 4♀, BPBM; same data 1♂, 1♀, ZMAN; Tor river (mouth), 4 km E of Hol Maffen, 1.vii.1959, T.C. Maa, 1♂, BPBM.

Other material. – PAPUA NEW GUINEA: Mokai vill., Torricelli Mts., 700 m, 16-31.xii.1958, W.W. Brandt, 1♂, BPBM; same data but 750 m, 1-23.i.1959, 1♂, BPBM.

P. baasi closely resembles *P. ustulata* and is of about the same size, but has distinctly larger opercula. Males can be easily separated from *P. ustulata* by the claspers, which are fused to a high and smoothly rounded collar around the base of anal valves. A similar collar is found in *P. novariae* and *P. dolabrata*, which are described below.

Description

Body reddish brown. Females of about the same size as males, with relatively slightly longer tegmina and a more robust head and thorax. Tegmina of males 1.1-1.3× as long as body length, of females 1.2-1.3×. Male abdomen 1.2-1.5× as long as head and thorax, of females 1.1-1.4×.

Head: Reddish brown, with short red-brown setae. Postclypeus oblong, distinctly protruding beyond vertex lobes and smoothly rounded anteriorly. Anterior margin of postclypeus weakly convex, but sharply curving back at lateral corners, forming almost right angles with anterior margins of vertex lobes. Dorsal surface of postclypeus weakly undulated; laterally slightly indented. Postclypeus not swollen; anterior margin (lateral view) concave. Lateral parts of postclypeus very smooth, with some weak furrows, but almost without rows of parallel ridges along lorum. Distance between lateral ocelli 1.0-1.2× as long as distance between lateral ocellus and eye and 2.1-2.8× the width of frontal ocellus.

Thorax: Pronotum with weak medial furrow. Mesonotum greenish, cruciform elevation ochraceous.

Legs: Femora ochraceous, tibiae and tarsi reddish. Fore femur with row of three erect spines. Proximal spine fairly long, often slightly longer than middle spine, but much shorter than distance to middle spine.

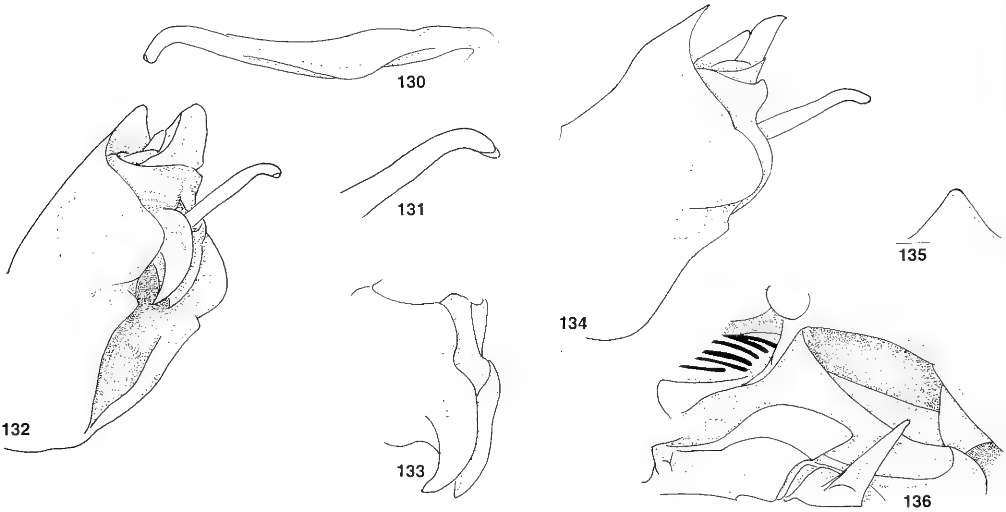
Tegmina: Hyaline, with 8 apical areas and a very narrow costal area; specimen from Tor River with 7 apical areas in right tegmen. Hyaline border along hind margin of tegmen fairly narrow as in holotype of *P. ustulata*, but distinctly broader in one female.

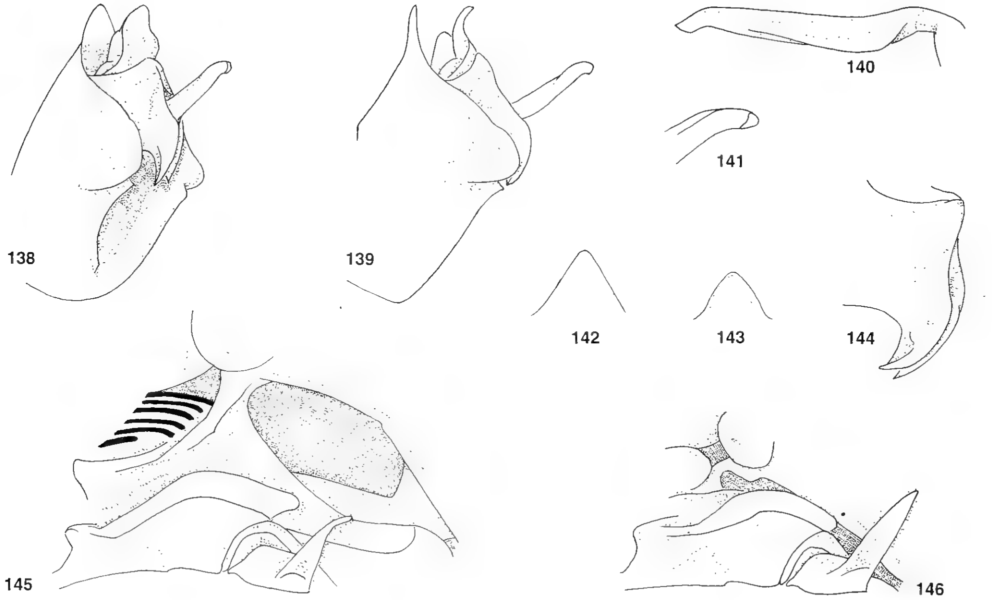
Tymbals: Five transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin and a 6th, most proximal, ridge almost reaching ventral margin. Intercalary ridges weakly developed.

Opercula: Male operculum (fig. 126) small, but distinctly longer than in *P. ustulata*, only partly covering tymbal cavity in ventral view, leaving a narrow gap between operculum and abdomen; folded membrane hardly visible in ventral view. Distal part of operculum almost as long as basal part. Lateral margin long and straight, forming an obtuse angle with crest of basal part and with straight distal margin. Medial margin weakly convex; distomedial corner rounded. Meracanthus not reaching to anterior margin of abdomen. Female operculum (fig. 127) as in male, but with shorter distal part.

Abdomen: Red-brown. Male abdomen very slender, not inflated. First tergite very short, almost completely hidden under metanotum middorsally. Medial part of 2nd tergite less than 1.5× as long as lateral parts. Anterior margin of 2nd tergite weakly concave medially. First and 2nd sternites adjacent. Auditory capsules very large, bulgy, clearly visible in dorsal view. Female abdomen even more slender than in male. Female caudodorsal beak in dorsal view (fig. 128) triangular and pointed at apex. Ovipositor sheaths just reaching beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 119. Dorsal margin weakly concave to base and angularly bent into slender caudodorsal beak. Caudodorsal beak straight in type specimens, but recurved in Mokai specimens. Distal margin weakly convex between caudodorsal beak and lateral protuberance, but not forming a distal lobe on pygofer; and concavely, in Mokai specimens angularly, bent into margin of beak. Caudodorsal beak in dorsal view apically rounded, broadly triangular in type specimens (fig. 121), very slender and with a sharp medial ridge at its base in Mokai specimens (fig. 122). Lateral lobe of pygofer slightly curved inwards, but recurved towards ventral margin, forming a broad, rounded, laminiform protuberance. Pygofer of specimen from Tor River forming an angular corner just below this protuberance, such a corner is absent in other specimens. Ventral margin of pygofer almost straight. Ventral half of pygofer opening narrow V-shaped (fig. 120); ventral margins converging to a sharp angle at the





Figs. 130-136. *Papuapsaltria novariae* sp. n. – 130, aedeagus in lateral view, holotype; 131, aedeagal apex, holotype; 132, pygofer from aslant, holotype; 133, claspers, holotype; 134, pygofer in lateral view, holotype; 135, caudodorsal beak in dorsal view, holotype; 136, operculum, paratype.

Figs. 138-146. *Papuapsaltria dolabrata* sp. n. – 138, pygofer from aslant, holotype; 139, pygofer in lateral view, holotype; 140, aedeagus in lateral view, Etna Bay; 141, aedeagal apex, Etna Bay; 142, male caudodorsal beak in dorsal view, holotype; 143, female caudodorsal beak in dorsal view, Roon; 144, claspers, holotype; 145, male operculum, paratype Waigeu; 146, female operculum, Roon.

base of pygofer opening. Claspers (fig. 123) very short as in *P. ustulata*, hardly reaching beyond pygofer margin, and slightly diverging towards apices; pick-shaped, with rectangular square-shaped dorsal part and slender, downwards directed, slightly recurving and sharply pointed apical part. Dorsal part of clasp-

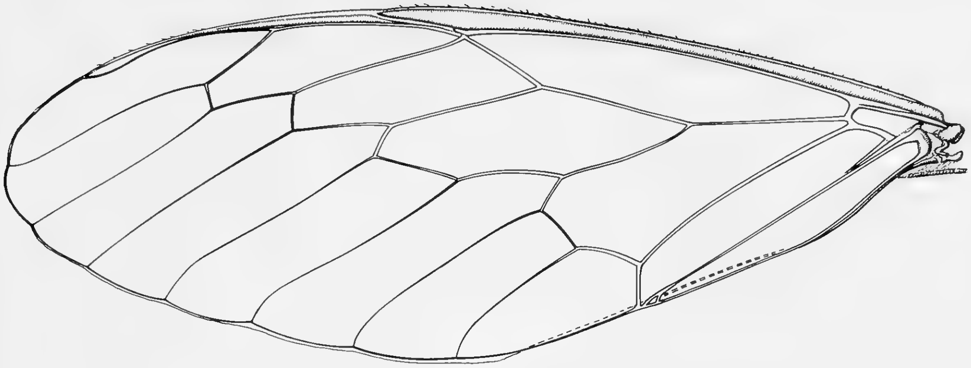


Fig. 137. *Papuapsaltria dolabrata* sp. n.: left tegmen, male, Waigeu .

er curving mesiad, as a shaft encircling aedeagus, and supporting aedeagus in upright position. Apical part of clasper broader than in *P. ustulata*, with large and sharply edged clasper hollow. Basal parts of claspers fused at distinct medial ridge, forming a high and smoothly rounded continuous collar around base of anal valves. Aedeagus standing erect between claspers, adjacent to anal valves. Aedeagus (fig. 125) almost straight, but strongly curved down, and abruptly narrowing near slightly incised apex (fig. 124), with slender lateral crests and a weak dorsal ridge. Aedeagus in one specimen from Mokai distinctly broader than in other specimens.

Measurements: Body length ♂: 11.7-14.5 mm (x̄ 13.0 mm ± 0.9), ♀: 12.1-13.7 mm (x̄ 12.9 mm ± 0.5); tegmen length ♂: 13.7-17.5 mm (x̄ 15.5 mm ± 1.4), ♀: 15.6-16.9 mm (x̄ 16.3 mm ± 0.6); head length ♂: 1.1-1.3 mm (x̄ 1.2 mm), ♀: 1.2-1.5 mm (x̄ 1.4 mm); pronotum length ♂: 1.4-1.6 mm (x̄ 1.5 mm), ♀: 1.5-1.7 mm (x̄ 1.6 mm); mesonotum length ♂: 2.3-3.2 mm (x̄ 2.8 mm), ♀: 2.6-3.0 mm (x̄ 2.8 mm); head width ♂: 2.8-3.3 mm (x̄ 3.0 mm), ♀: 3.0-3.3 mm (x̄ 3.2 mm); width of pronotal collar ♂: 3.4-4.1 mm (x̄ 3.7 mm), ♀: 3.5-4.1 mm (x̄ 3.8 mm).

Distribution (fig. 129). – *P. baasi* is endemic to the mountain ranges of northern New Guinea.

Etymology. – This species is named in honour of Hendrik Baas in acknowledgement of our long discussions on the paleogeography of New Guinea.

Papuapsaltria novariae sp. n.
(figs. 129-136)

Type material. – Holotype ♂: 'NEW GUINEA NE / Eliptamin Valley / 1200-1350 m / July 16-31, 1959' [print]; 'W.W. Brandt / Collector / Bishop' [print], BPBM. – Paratype: IRIAN JAYA: same data as holotype but 1665-2530 m, 9.vi.1959, 1♂, BPBM.

Only two males are known of this species. *P. novariae* closely resembles *P. baasi* in the shape of the genitalia: its clasper base forming a similarly high collar around the base of the anal valves. The dorsal corner of the *P. novariae* clasper is more rounded, however. *P. novariae* is distinctly larger than the two foregoing species and shows a much wider gap between operculum and abdomen. The species shares the latter character with *P. dolabrata* described next. *P. novariae* can further be recognized by its 9 apical areas in the tegmina.

Description

Body reddish brown. Tegmina 1.2-1.3× as long as body length. Abdomen 1.4-1.6× as long as head and thorax.

Head: Reddish brown, with short red-brown setae. Postclypeus oblong, slightly protruding beyond vertex lobes and smoothly rounded anteriorly. Anterior margin of postclypeus weakly convex, but sharply curving back at lateral corners, forming almost right angles with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) straight. Lateral parts of postclypeus very smooth, with some weak furrows, but almost without rows of parallel ridges along lorum. Distance between lateral ocelli slightly longer than distance between lateral ocellus and eye and 1.7-1.9× the width of frontal ocellus.

Legs: Femora ochraceous, tibiae and tarsi reddish. Fore femur with row of three erect spines. Proximal spine very short, slightly longer than middle spine, but much shorter than distance to middle spine.

Tegmina: Hyaline, with 9 apical areas, a distinct and hyaline costal area, and a fairly narrow hyaline border along hind margin.

Tymbals: Five transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin and a 6th, most proximal, ridge almost reaching ventral margin. Intercalary ridges hardly visible.

Operculum (fig. 136): Very short. Distal part more than half as long as basal part, not covering tymbal cavity, and leaving a very wide gap between operculum and abdomen; folded membrane clearly visible in ventral view. Lateral margin long and straight, forming an obtuse angle with crest of basal part and angularly or convexly bending into straight distal margin. Medial margin straight, forming a sharp angle with distal margin. Meracanthus reaching to about halfway the gap between operculum and abdomen.

Abdomen: Red-brown, more inflated than in the two foregoing species. First tergite very short, almost completely hidden under metanotum middorsally. Medial part of 2nd tergite almost 2 × as long as lateral parts. Anterior margin of 2nd tergite distinctly concave medially. First and 2nd sternites not adjacent. Auditory capsules weakly swollen and not visible in dorsal view.

Genitalia: Pygofer in lateral view as in fig. 134. Dorsal margin concave, but convexly, almost angularly, bent into straight and slender caudodorsal beak. Distal margin weakly convex between caudodorsal beak and lateral protuberance, but not forming a distal lobe on pygofer, and concavely bent into margin of beak. Caudodorsal beak in dorsal view (fig. 135) broadly triangular and bluntly rounded at apex. Lateral lobe of pygofer slightly curved inwards, but recurved towards ventral margin, forming a broad, rounded, and laminiform protuberance. Pygofer forming a small rectangular corner just below this protuberance. Ventral margin of pygofer almost straight. Ventral half of pygofer opening narrow V-shaped (fig. 132); ventral margins converge to a sharp angle at base of pygofer opening. Claspers (fig. 133) closely resembling those of *P. baasi*, but almost parallel, only slightly diverging near apices. Claspers hardly reaching beyond pygofer margin, their basal parts fused at distinct medial ridge, forming a high and smoothly rounded continuous collar around base of anal valves. Dorsal part of clasper more rounded than in *P. baasi*, curving mesiad, as a shaft encircling aedeagus. Apical part of clasper recurving, directed downwards and sharply pointed, with a large and sharply edged clasper hollow. Aedeagus standing erect between claspers, adjacent to anal valves, in holotype reaching far above claspers, in paratype just reaching above dorsal margin of clasper. Aedeagus (fig. 130) almost straight, but strongly, almost angularly, curved down towards its distinctly incised apex (fig. 131). Aedeagus with slender lateral crests and a weak dorsal ridge.

Measurements: Body length: 16.0 & 16.4 mm; tegmen length: 19.3 & 21.1 mm; head length: 1.2 mm; pronotum length: 1.7 & 1.8 mm; mesonotum length: 3.4 & 3.8 mm; head width: 3.3 & 3.5 mm; width of pronotal collar: 4.3 & 4.4 mm.

Distribution (fig. 129). – *P. novariae* is only known from Eliptamin valley, in the central mountain ranges of western Papua New Guinea.

Etymology. – The name *novariae* is derived from the latin words novem (nine) and ariae (areas) and refers to the nine apical areas of tegmen.

Papuapsaltria dolabrata sp. n.
(figs. 129, 137-146)

Type material. – Holotype ♂: 'INDONESIA / Irian Jaya / A.J. de Boer / A.L.M. Rutten & / R. de Vos' [print]; ' Roon Island / YENDE / 60 m. at light / 7.xi.1993' [print], ZMAN. – Paratypes: IRIAN JAYA: same data as holotype 2♂, ZMAN; Etna baai, 25.xi.1939, Nieuw Guinea Exp., KNAG 1939, 2♂, RMNH; Roon, Fruhstorfer, 1♂, 1♀, BMNH; Waigeu, Camp Nok, 2500 ft., iv.1938, L.E. Cheesman, 3♂, 5♀, BMNH; same data 1♂, 1♀, ZMAN; same data but v.1938, 3♀.

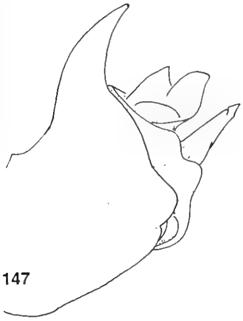
P. dolabrata closely resembles *P. baasi* in size and shape of body, but shares a wide gap between operculum and abdomen with *P. novariae*. *P. dolabrata* is easily separated from these two species by its sharply downwards directed dorsal margin of the claspers; the distal margin of the clasper is almost continuous with the ring-shaped clasper base (lateral view). *P. dolabrata* has an extremely narrow hind margin of tegmen.

Description

Body olive green to light brown. Females smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.1-1.2 × as long as body length, of females 1.3-1.4 ×. Male ab-

Figs. 147-155. *Papuapsaltria toxopei* sp. n.: 147, pygofer in lateral view; 148, pygofer from aslant; 149, aedeagus in lateral view; 150, aedeagal apex; 151, male caudodorsal beak in dorsal view; 152, claspers; 153, male operculum; 154, female operculum; 155, female caudodorsal beak in dorsal view.

Figs. 156-164. *Papuapsaltria dioedes* sp. n.: 156, pygofer from aslant, holotype; 157, pygofer in lateral view, holotype; 158, aedeagus in lateral view, holotype; 159, male fore femur, Pengagl; 160, male caudodorsal beak in dorsal view, holotype; 161, female caudodorsal beak in dorsal view, Pengagl; 162, claspers, holotype; 163, male operculum, holotype; 164, female operculum, Pengagl.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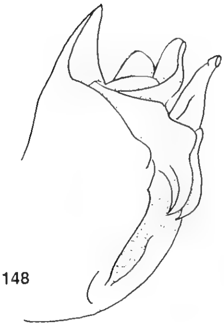
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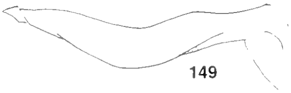
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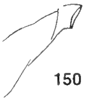
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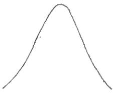
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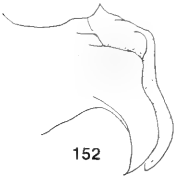
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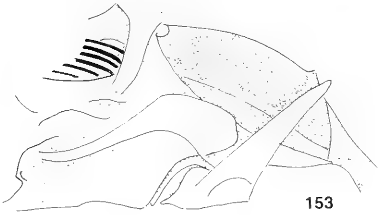
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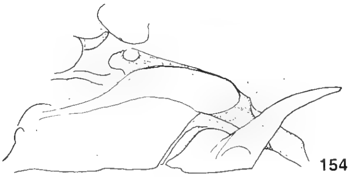
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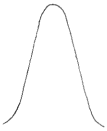
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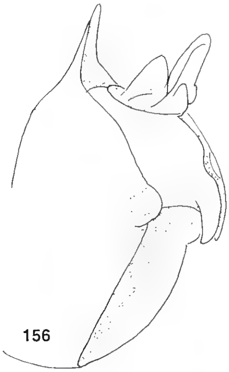
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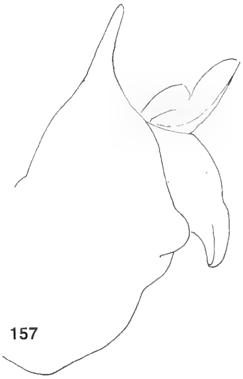
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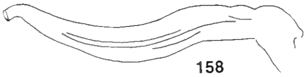
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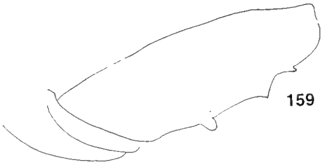
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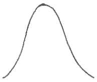
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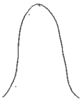
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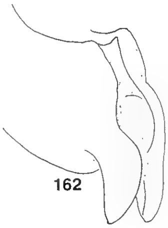
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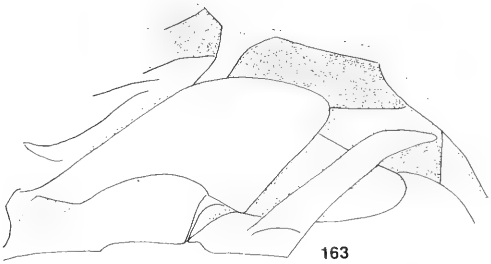
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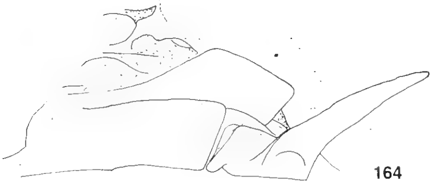
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domen 1.4-1.7× as long as head and thorax, of females 1.1-1.5×.

Head: Olive green, with short red-brown setae. Postclypeus oblong, distinctly protruding beyond vertex lobes and smoothly rounded anteriorly. Anterior margin of postclypeus weakly convex, but sharply curving back at lateral corners, forming almost right angles with anterior margins of vertex lobes. Dorsal surface of postclypeus weakly undulated; laterally slightly indented. Postclypeus not swollen; anterior margin (lateral view) concave. Lateral parts of postclypeus very smooth, with some weak furrows, but almost without rows of parallel ridges along lorum. Distance between lateral ocelli 1.0-1.2× as long as distance between lateral ocellus and eye and 1.7-2.6× the width of frontal ocellus.

Legs: Femora ochraceous, tibiae and tarsi reddish. Fore femur with row of three erect spines. Proximal spine fairly long, slightly longer than middle spine, but much shorter than distance to middle spine.

Tegmina: Hyaline, with 8 apical areas and distinct and hyaline costal area. Venation often dark red-brown. Hyaline border along hind margin of tegmen extremely narrow, hardly visible.

Tymbals: Five transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin and a 6th, most proximal, ridge almost reaching ventral margin. Intercalary ridges weakly developed.

Operculum: Male operculum (fig. 145) not covering tymbal cavity, leaving a very wide gap between operculum and abdomen; folded membane clearly visible in ventral view. Distal part of operculum short, less than half as long as basal part. Lateral margin straight, forming an obtuse angle with crest of basal part and angularly or convexly bent into straight distal margin. Medial margin straight, forming a narrowly rounded corner with distal margin. Meracanthus not reaching beyond folded membrane. Female operculum (fig. 146) as in male, but much shorter. Distal part as in *P. ustulata*, erect and hardly more than a continuation of the crest along distolateral corner of basal part, and only slightly amplifying mesiad to less than 1/5× as long as basal part.

Abdomen: Male abdomen hardly inflated. First tergite very short, almost completely hidden under metanotum middorsally. Medial part of 2nd tergite about 2× as long as lateral parts. Anterior margin of 2nd tergite weakly concave medially. First and 2nd sternites not adjacent. Auditory capsules weakly swollen, and hardly or not visible in dorsal view. Female caudodorsal beak in dorsal view (fig. 143) broadly triangular and rounded, almost pointed, at apex. Ovipositor sheaths almost reaching to apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 139. Dorsal margin straight, continuous with, or concavely bent into, slender caudodorsal beak. Distal margin weakly convex between caudodorsal beak and lateral protuberance, and concavely bent into margin of beak. Caudodorsal beak in dorsal view (fig. 142) broad and triangular, almost rectangular at apex. Lateral lobe of pygofer slightly curved inwards, but recurving towards ventral margin, forming a very large, weakly indented, and lobate laminiform protuberance, almost triangular in lateral view. Pygofer forming a small but distinct rectangular corner just below this protuberance. Ventral margin of pygofer straight. Ventral half of pygofer opening narrow V-shaped (fig. 138), ventral margins converging to a sharp angle at base of pygofer opening. Claspers quite different from the three foregoing species. Whereas in these three species the dorsal margin of the clasper part, which bends around aedeagus, ends in almost right angle on the fused ring-shaped clasper base (see fig. 144), in *P. dolabrata* this margin merges with the basal ring under a very slight angle (fig. 152). Moreover, the apical part of clasper is less strongly bent down than in the three foregoing species. Claspers pick axe-shaped almost parallel, only slightly diverging near apices. Apical part of clasper recurved and sharply pointed, with a large and sharply edged clasper hollow. Claspers closely encircling aedeagus at their bending point. Aedeagus, unlike the three foregoing species, not erect between claspers, but slightly directed posteriad. Aedeagus (fig. 149) weakly S-curved, with slender lateral crests and a very distinct, rounded dorsal ridge. Aedeagus weakly incised at apex; aedeagal pore almost round (fig. 150).

Measurements: Body length ♂: 14.1-14.9 mm (x̄ 14.4 mm ± 0.3), ♀: 12.1-14.1 mm (x̄ 12.8 mm ± 0.6); tegmen length ♂: 16.1-17.2 mm (x̄ 16.8 mm ± 0.5), ♀: 16.0-18.6 mm (x̄ 17.1 mm ± 0.8); head length ♂: 1.2-1.5 mm (x̄ 1.3 mm), ♀: 1.2-1.6 mm (x̄ 1.4 mm); pronotum length ♂: 1.5-1.7 mm (x̄ 1.6 mm), ♀: 1.4-1.8 mm (x̄ 1.7 mm); mesonotum length ♂: 2.7-3.1 mm (x̄ 2.9 mm), ♀: 2.7-3.2 mm (x̄ 2.9 mm); head width ♂: 3.1-3.3 mm (x̄ 3.2 mm), ♀: 3.1-3.5 mm (x̄ 3.3 mm); width of pronotal collar ♂: 3.7-4.1 mm (x̄ 3.9 mm), ♀: 3.8-4.4 mm (x̄ 4.1 mm).

Distribution (fig. 129). – *P. dolabrata* is distributed in western New Guinea, recorded from Etna Bay, Roon Island, and Waigeu Island, but not from the intermediate Birds Head peninsula.

Etymology. – Dolabrata means shaped as a dolabra (Latin) pickaxe. The name refers to the shape of the claspers.

Papuapsaltria toxopei sp. n.
(figs. 4, 147-155)

Type material. – Holotype: 'Neth. Ind.-American /

New Guinea Exped. / Mist Camp 1800 m / 23.i.1939 L.J. Toxopeus' [print]; 'Paratype' [print, orange label]; '*Baeturia / toxopeusi*' [written]; 'Mus. Leiden' [print], ♂, RMNH. Paratype: IRIAN JAYA: same data as holotype but 19.i.1939 and without identification label, 1 ♀ paratype *B. toxopeusi*, RMNH.

P. toxopei presumably belongs to this genus, as is indicated by the small male opercula and short femoral spines, but its phylogenetic position within the genus is not clear. *P. toxopei* is very similar, and presumably closely related, to the four foregoing species. The hook-shaped and sharply pointed claspers of *P. toxopei* somewhat resemble those of *P. woodlarkensis*, but similar claspers occur in several related genera.

Description

Body reddish brown, mesonotum greenish. Female smaller than male, but with more robust head and thorax, and longer tegmina. Tegmina of male 1.3× as long as body length, of female 1.5×. Male abdomen 1.5× as long as head and thorax, of female 1.2×.

Head: Vertex and postclypeus with short red setae. Postclypeus angularly protruding. Anterior margin of postclypeus almost continuous with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave. Vertex with fairly distinct diverging fissures. Distance between lateral ocelli 0.9-1.0× as long as distance between lateral ocellus and eye and 1.5-1.9× the width of frontal ocellus.

Legs: Fore femur with row of three erect spines. Most proximal spine very short, slightly longer than middle spine, but much shorter than distance to middle spine.

Tegmina: Hyaline, with 8 long and slender apical areas, a distinct hyaline costal area, and a broad hyaline border along hind margin.

Tymbals: Six slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin, and a 7th, most proximal, ridge almost reaching ventral margin. Lateral band of seven intercalary ridges weakly developed.

Opercula: Male operculum (fig. 153) very small, not covering tymbal cavity in ventral view, leaving a wide gap between operculum and abdomen; folded membrane exposed in ventral view. Distal part of operculum narrow, and angularly oblong, shorter than basal part. Operculum not reaching medially of meracanthus. Lateral margin very long and straight, gradually curving into crest of basal part and forming an obtuse angle with short and straight distal margin. Medial margin straight, distomedial corner angularly rounded. Meracanthus very long, reaching beyond anterior margin of abdomen. Female operculum (fig. 154) very similar to that of male, but with shorter and broader distal part.

Abdomen: Male abdomen long and slender, weakly inflated. First tergite not hidden under metanotum. Medial part of 2nd tergite less than 2× as long as lateral parts. Anterior margin of 2nd tergite straight medially. First and 2nd sternites not adjacent. Auditory capsules strongly inflated and protruding, visible in dorsal view. Female caudodorsal beak in dorsal view (fig. 155) long and slender, rounded at apex. Ovipositor sheaths not reaching to apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 147. Dorsal margin convex, concave near base, and continuous with convexly bent caudodorsal beak. Distal margin weakly convex, forming an obtuse angle with concave margin of beak. Ventral margin straight. Ventral margins weakly converging to base of pygofer; basal part of pygofer opening V-shaped (fig. 148). Caudodorsal beak in dorsal view (fig. 151) slender, triangular, narrowly rounded at apex. Lateral lobe of pygofer strongly curving inwards towards end of distal margin, forming a bluntly rounded and distinctly swollen protuberance. Claspers (fig. 152) hook-shaped and parallel, only slightly diverging near sharply pointed apices. Dorsal part of clasper forming an angularly protruding corner, bending around aedeagus. Apical part of clasper smoothly rounded, lobate, with large and sharply edged clasper hollow. Aedeagus (fig. 149) weakly S-curved, strongly curved down near apex, with long and slender lateral crests and distinct dorsal ridge. Lateral crests curving upwards at their distal ends and fusing to a very small collar at apical bending point of aedeagus. Aedeagal pore round.

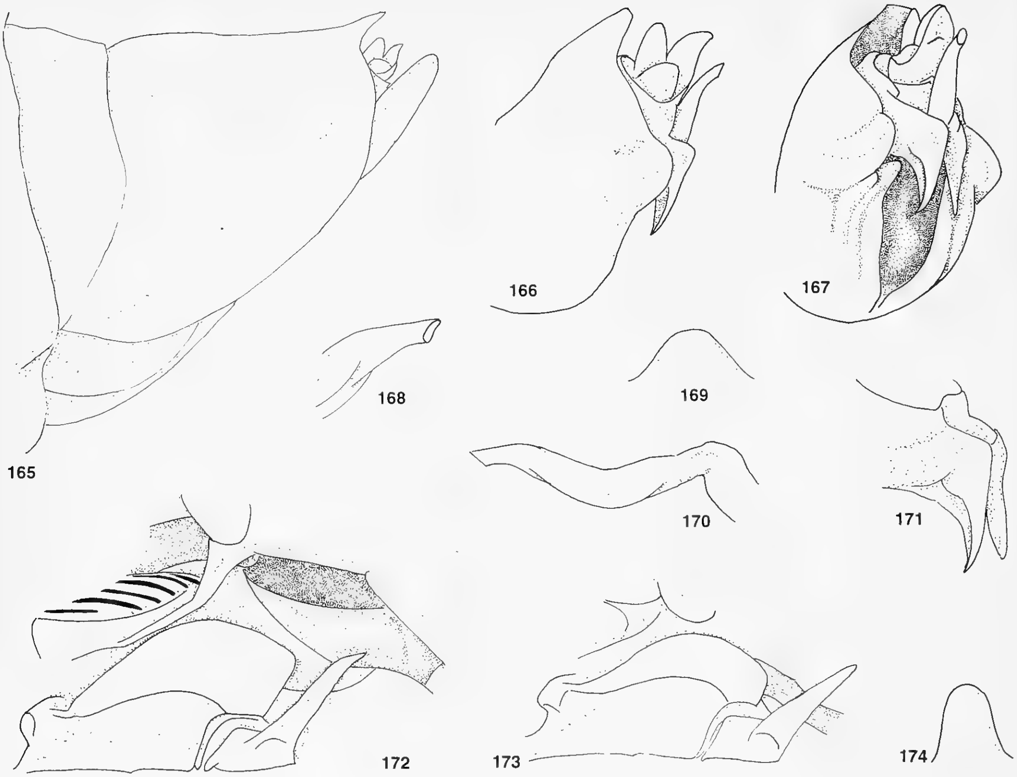
Measurements: Body length ♂: 19.4 mm, ♀: 17.2 mm; tegmen length ♂: 23.5 mm, ♀: 25.0 mm; pronotum length ♂: 1.7 mm, ♀: 2.1 mm; mesonotum length ♂: 3.8 mm, ♀: 3.0 mm; head length ♂: 1.2 mm, ♀: 1.5 mm; head width ♂: 3.4 mm, ♀: 3.9 mm; width of pronotal collar ♂: 4.8 mm, ♀: 5.7 mm.

Distribution (fig. 4). – *P. toxopei* is known from only one locality in northern Irian Jaya.

Etymology. – This species is named in honour of Mr L.J. Toxopeus who collected the holotype, and the types of several other species on which the current revision of the '*Baeturia* and related genera complex' is based.

Papuapsaltria dioedes sp. n.
(figs. 4, 156-164)

Type material. – Holotype ♂: 'New Guinea: NE / Mur Mur P. 2800 m / 28.xii.67-6.i.68' [print]; 'Tawi / Collector / BISHOP' [print], BPBM; Paratypes: PAPUA



Figs. 165-174. *Papuapsaltria woodlarkensis* sp. n.: 165, female genital segment in lateral view, paratype; 166, pygofer in lateral view, holotype; 167, pygofer from aslant, holotype; 168, aedeagal apex, paratype; 169, male caudodorsal beak in dorsal view, holotype; 170, aedeagus in lateral view, paratype; 171, claspers, holotype; 172, male operculum, holotype; 173, female operculum, paratype; 174, female caudodorsal beak in dorsal view, paratype.

NEW GUINEA: 5°15' S / 141°05' E, 2280 m, 4.v.1970, O. McCaw, 1♂, Moul; Bosavi Mt., 2300 m, 7.v.1973, J.L. Gressitt & Goya, 1♂, BPBM; Giluve, 2700 m, J. & M. Sedlacek, 1♂, ZMAN; Giluve Mt., 2500-2650 m, 28.v.1963, J. Sedlacek, 1♂, BPBM; same data but 2500-2750 m, 30.v.1963, 1♀, BPBM; Kepilam, 2420-2540 m, 21.vi.1963, J. Sedlacek, 1♀, BPBM; same data but 2450-2600 m, 22.vi.1963, 1♀, ZMAN; Kiunga, 5°15' S / 141°05' E, 7500 ft, 4.v.1970, O. McCaw, 1♂, Moul; Kubor Range, W Highlands, 2950 m, 23.v.1966, J.L. Gressitt, 1♂, BPBM; Wilhelm Mt., east slopes, Pengagl Camp, 2770 m, 17.vii.1959, sixth Archbold Exped. to Papua New Guinea, L.J. Brass, 1♂, AMNH; same data but 26.vii.1959, 2♀, AMNH.

The generic allocation of this species is somewhat uncertain. *P. dioedes* shares the supposed synapomorphous very short proximal spine on the fore femur with most species of *Papuapsaltria*, while the tegmina, with very long and slender apical areas and a very broad hyaline border, also indicate a relation with this genus. For these reasons the species is preliminary included in *Papuapsaltria*. However, its claspers are very similar to those of *Guineapsaltria pennyi*. The male opercula somewhat resemble those of *Guineapsaltria chinai* and those of *P. goniodes* and *P. angulata*.

Description

Body light yellowish brown to reddish brown. Females smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.1-1.4× as long as body length, of females 1.5-1.6×. Male abdomen 1.4-2.0× as long as head and thorax, of females 1.1-1.4×.

Head: Vertex and postclypeus with short red setae. Postclypeus angularly protruding beyond vertex lobes. Anterior margin of postclypeus sharply curving back at lateral corners, forming almost right angles with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) concave. Vertex with fairly distinct diverging fissures. Distance between lateral ocelli 0.9-1.3× as long as distance between lateral ocellus and eye and 1.4-2.5× the width of frontal ocellus.

Legs: Fore femur very slender (fig. 159) with row of three erect spines. Most proximal spine extremely short, rudimentary, often shorter than middle spine and much shorter than distance to middle spine.

Tegmina: Hyaline, with 8 long and slender apical areas, a distinct hyaline costal area and a very broad hyaline border along hind margin.

Tymbals: Six slightly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin. Lateral band of seven intercalary ridges weakly developed.

Opercula: Male operculum (fig. 163) quite large, but only partly covering tymbal cavity and leaving a wide gap between operculum and abdomen; folded membrane only partly visible in ventral view. Distal part of operculum fairly long, more than twice as long as basal part, and medially elongate, with greatest length at medial margin. Operculum not reaching medially of meracanthus. Lateral margin long and straight, forming an obtuse angle with crest of basal part, close to distolateral corner of basal part, and convexly bent into much shorter, straight distal margin. Medial margin long and straight, distomedial corner almost rectangular. Meracanthus reaching beyond operculum. Female operculum (fig. 164) very short, its distal part shorter than basal part and angularly oblong. Distolateral corner rounded, distomedial corner rectangular, medial margin very short.

Abdomen: Male abdomen strongly inflated. First tergite very short, partly hidden under metanotum. Medial part of 2nd tergite about twice as long as lateral parts. Anterior margin of 2nd tergite strongly concave medially. First and 2nd sternites generally not adjacent. Auditory capsules weakly inflated. Female caudodorsal beak in dorsal view (fig. 161) narrow triangular and bluntly rounded, almost pointed at apex. Ovipositor sheaths almost reaching to apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 157. Dorsal margin weakly convex, concavely bent into straight, erect and very slender caudodorsal beak. Distal margin weakly convex, concavely bent into margin of beak. Ventral margin convex, forming a small angular corner under lateral protuberance. Ventral margins converging towards base of pygofer; basal part of pygofer opening V-shaped (fig. 156). Caudodorsal beak in dorsal view (fig. 160) very slender, oblong, and rounded at apex. Lateral lobe of pygofer strongly curving inwards towards end of distal margin, forming a weakly swollen, bluntly rounded lateral protuberance. Claspers (fig. 162) very different from other species of this genus, almost straight and parallel towards rounded apices. Claspers adjacent, but diverging at half-length, curving around aedeagus. Aedeagus not adjacent to base of anal valves. Claspers almost fused, dorsally separated by narrow furrow between aedeagus and base of anal valves. Apical part of clasper weakly curved down, with large and sharply edged ventral hollow. Aedeagus (fig. 158) weakly S-curved, with long and slender lateral crests. Aedeagal pore round.

Measurements: Body length ♂: 20.0-26.5 mm (x̄ 22.3 mm ± 2.3), ♀: 18.2-21.1 mm (x̄ 20.0 mm ± 0.9); tegmen length ♂: 23.6-31.4 mm (x̄ 27.1 mm ± 2.4), ♀: 29.1-33.3 mm (x̄ 31.0 mm ± 1.5); head length ♂: 1.3-1.7 mm (x̄ 1.4 mm), ♀: 1.5-1.8 mm (x̄ 1.7 mm); pronotum length ♂: 1.8-2.5 mm (x̄ 2.1 mm), ♀: 2.3-2.8 mm (x̄ 2.5 mm); mesonotum length ♂: 4.2-5.2 mm (x̄ 4.7 mm), ♀: 4.7-5.8 mm (x̄ 5.1 mm); head width ♂: 3.4-4.1 mm (x̄ 3.7 mm), ♀: 4.1-4.3 mm (x̄ 4.2 mm); width of pronotal collar ♂: 5.3-7.0 mm (x̄ 5.8 mm), ♀: 6.5-7.3 mm (x̄ 6.8 mm).

Distribution (fig. 4). – *P. dioedes* is found in the central mountain ranges of western Papua New Guinea, at high altitudes, and on Mt. Bosavi, just south of these mountain ranges.

Etymology. – Dioedes (Greek) means swollen and refers to the swollen abdomen of this species.

Papuapsaltria woodlarkensis sp. n.

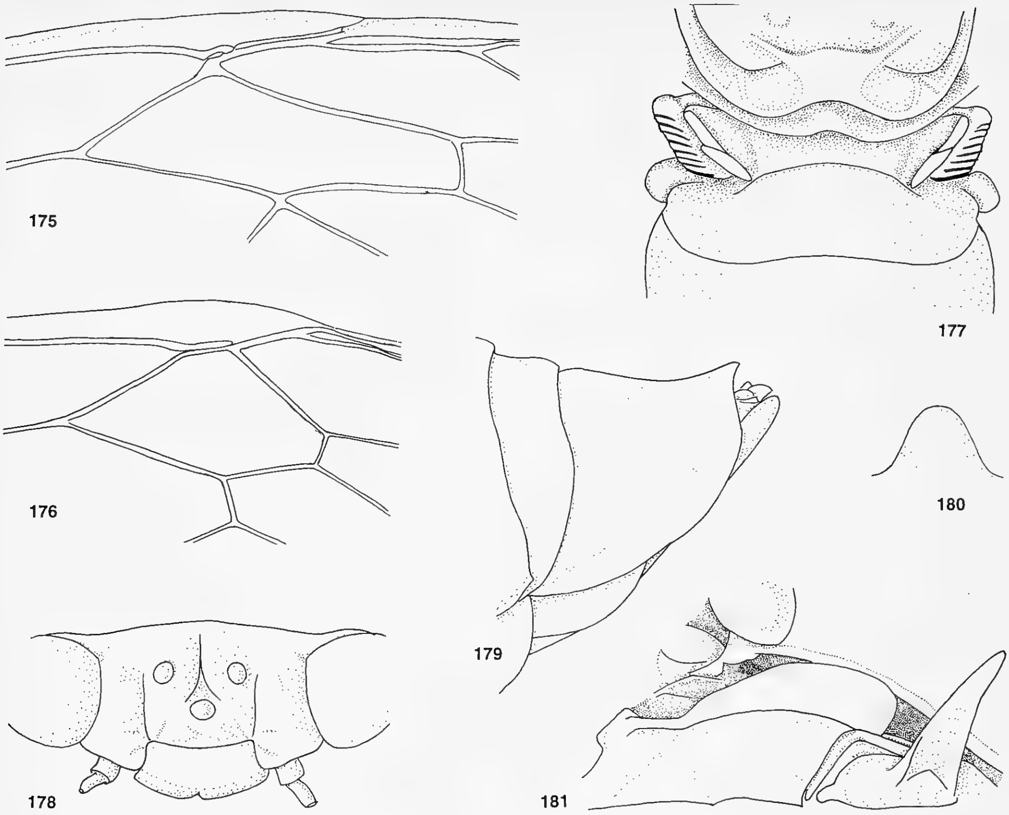
(figs. 4, 10, 165-174)

Type material. – Holotype ♂: 'NEW GUINEA: PAPUA / Woodlark (Murua) / Kulumandau Hill / Feb. 3. 1957' [print]; 'W.W. Brandt / Collector' [print], BPBM. – Paratypes: WOODLARK ISLAND: same data as holotype 1♂, 1♀, ZMAN; 2♀, BPBM; same data but 28-30.i.1957, 1♀; 10.ii.1957, 1♀; 16.ii.1957, 2♀; 25.ii.1957, 1♀; 7-13.iii.1957, 3♀; 12.iii.1957, 3♀; 16-22.iv.1957, 1♂, 1♀, all BPBM; Kulumandau, 0-100 m, 3.xi.1956, 5th Archbold Exped. to New Guinea, L.J. Brass, 1♀, AMNH; same data but 10.xi.1956, 1♂, 1♀, AMNH.

P. woodlarkensis is easily recognized by the conical, thorn-shaped, and inwardly curved protuberances at the ventral margin of the pygofer.

Description

Body of males almost uniformly ochraceous-brown, but tinged with green. Females more reddish brown or bicolorate, with greenish head and thorax and reddish brown abdomen. Females distinctly smaller than males, but with more robust head and thorax, and longer tegmina. Tegmina of males 1.0-1.1× as long as body length, of females 1.2-1.3×. Male abdomen 1.5-1.6× as long as head and thorax, of females 1.2-1.3×.



Figs. 175-181. 175. *Papuapsaltria spinigera* sp. n.: first ulnar area of right tegmen, holotype. 176-181. *Papuapsaltria phyllophora* (Blöte, 1960): 176, first ulnar area of right tegmen, Bokondini; 177, male first and second tergite in dorsal view, Bokondini; 178, male head in dorsal view, Bokondini; 179, female genital segment in lateral view, Bokondini; 180, female caudodorsal beak in dorsal view, Bokondini; 181, female operculum, Bokondini.

Head: Postclypeus slightly angularly protruding, smoothly rounded anteriorly, its anterior margin weakly convex, almost continuous with anterior margins of vertex lobes. Postclypeus not swollen; anterior margin (lateral view) straight. Rows of short parallel ridges form a broad, though weakly developed, band along lorum. Distance between lateral ocelli 0.9-1.2 × as long as distance between lateral ocellus and eye and in males 2.0-2.2 ×, in females 2.2-3.1 ×, the width of frontal ocellus.

Tegmina: Hyaline, with 8 long and slender apical areas, a fairly distinct costal area, and a very broad hyaline border along hind margin.

Legs: Fore femur (fig. 10) with row of three or four erect spines, diminishing in length towards tibia. Proximal spine fairly long, distinctly longer than middle spine and only slightly shorter than distance to middle spine.

Tymbals: Five parallel transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin and a 6th ridge almost reaching ventral margin. Six short intercalary ridges clearly visible.

Opercula: Male operculum (fig. 172) not covering tymbal cavity in ventral view, leaving a wide gap between operculum and abdomen; folded membrane clearly visible in ventral view. Distal part of operculum angularly oblong and distinctly longer than basal part. Lateral margin long and straight, convex to base, ending in almost right angle on crest of basal part and reaching that crest close to lateral corner. Distal part of basal crest very short, and lower than its lateral part. Distolateral corner rounded, distal and medial margins straight, distomedial corner rectangular. Meracanthus longer than operculum, but not reaching to margin of abdominal segment 2. Female operculum (fig. 173) resembling that of male, but much shorter, with its distal part shorter than basal part, and oblong. Lateral margin as in male. Distal margin weakly convex, medial margin short and straight.

Abdomen: Male abdomen strongly inflated. First tergite rather long; medially about half as long as 2nd tergite. Anterior margin of 2nd tergite weakly convex medially. First and 2nd sternites not adjacent. Auditory capsules weakly developed, hardly protruding and not visible in dorsal view. Female abdomen stout. Female caudodorsal beak (fig. 174) oblong and rounded at apex. Ovipositor sheaths reaching distinctly beyond apex of caudodorsal beak (fig. 165).

Male genitalia: Pygofer in lateral view as in fig. 166. Dorsal margin concave, but convexly, almost angularly, bent into straight, short, and stout caudodorsal beak. Distal margin weakly convex between caudodorsal beak and lateral protuberance, forming an obtuse angle with straight margin of caudodorsal beak. Caudodorsal beak in dorsal view (fig. 169) short and broad, weakly convex, almost truncate at apex. Lateral lobe of pygofer with large swollen and bluntly rounded protuberance. Ventral part of pygofer lobe strongly curving inwards towards ventral margin, forming a slender conically rounded, almost thorn-shaped and inwardly directed, protrusion just below lateral protuberance (fig. 167). This protrusion is not visible in lateral view. Ventral margin of pygofer in lateral view weakly concave below lateral protuberance, but convex to base. Ventral half of pygofer opening narrowly oblong, forming a distinctly swollen ridge along its margins (fig. 167). Claspers (fig. 171) very short, hardly reaching beyond pygofer, diverging towards sharply pointed and downwardly directed apices. Clasper forming a weak dorsal crest. Rectangular distodorsal corner of that crest bending mesiad, distally of aedeagus and supporting aedeagus in upright position. Distal margin of clasper almost straight. Apical part of clasper with large, sharply edged hollow, ending at base in weak lateral swelling. Clasper base forming a ring-shaped collar around base of anal valves, which is medially sharply indented around aedeagus. Aedeagus standing erect between claspers, close to anal valves, its apical part slightly curving away from anal valves. Aedeagus (fig. 170) strongly S-curved, with long and distinct lateral crests and a weak dorsal ridge. Apex of aedeagus weakly pointed in lateral view, with oval, almost round, pore (fig. 168).

Measurements: Body length ♂: 19.7-21.0 mm ($\bar{x}$ 20.3 mm ± 0.5), ♀: 18.0-19.8 mm ($\bar{x}$ 18.9 mm ± 0.6); tegmen length ♂: 20.5-21.8 mm ($\bar{x}$ 21.2 mm ± 0.5), ♀: 22.6-24.5 mm ($\bar{x}$ 23.3 mm ± 0.6); head length ♂: 1.4-1.6 mm ($\bar{x}$ 1.5 mm), ♀: 1.6-1.8 mm ($\bar{x}$ 1.7 mm); pronotum length ♂: 2.2-2.3 mm, ♀: 2.2-2.5 mm ($\bar{x}$ 2.3 mm); mesonotum length ♂: 4.0-4.4 mm ($\bar{x}$ 4.2 mm), ♀: 4.2-4.7 ($\bar{x}$ 4.4 mm); head width ♂: 4.0-4.4 mm ($\bar{x}$ 4.2 mm), ♀: 4.3-5.0 mm ($\bar{x}$ 4.8 mm); width of pronotal collar ♂: 5.2-5.7 mm ($\bar{x}$ 5.5 mm), ♀: 5.7-6.4 mm ($\bar{x}$ 6.0 mm).

Distribution (fig. 4). – *P. woodlarkensis* is presumably endemic to Woodlark Island of the D'Entrecasteaux islands.

Etymology. – The name of this species is derived from the type locality: Woodlark island.

Papuapsaltria phyllophora (Blöte, 1960) comb. n. (figs. 4, 176-190)

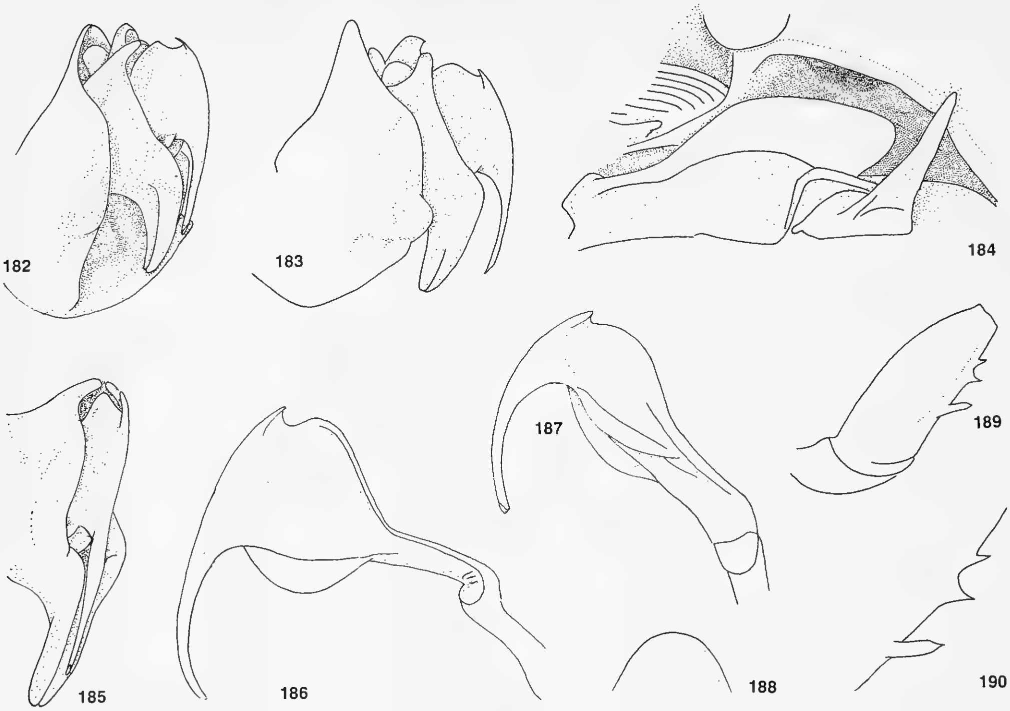
Baeturia phyllophora Blöte, 1960: 79, figs. 45, 46; Duffels & Van der Laan 1985: 254; De Boer 1993a: 16.

The generic allocation of this species is dubious. *P. phyllophora* shares none of the apomorphies on which any of the genera of the '*Baeturia* and related genera complex' are based. Furthermore, the apomorphy of that complex as a whole, an S-curved aedeagus with wing-shaped lateral crests, can hardly be recognized in the strongly deviating aedeagus of *P. phyllophora*; this deviating shape is here regarded as autapomorphous. The small male opercula and smoothly vaulted vertex suggest that the species either belongs to *Guineapsaltria* or to *Papuapsaltria*. The species is preliminary included in *Papuapsaltria* since its ocelli are more closely together than is generally the case in *Guineapsaltria*. Current phylogenetic analysis concerning all species of the '*Baeturia* and related genera complex' indicate that *P. phyllophora* either as the sister group of *Guineapsaltria*, or as part of *Papuapsaltria* both belong to the most parsimonious solutions. Males and females of *P. phyllophora* can easily be recognized by a swelling of the costa at the distal end of the first radial area, and by the quintangular-shaped second ulnar area. Males are unmistakable by their peculiar aedeagus.

Description

Body of males unicoloured red-brown or olive green, of females often darker brown or greenish. Females on average slightly longer than males, but with distinctly more robust head and thorax and longer tegmina. Tegmina of males 1.2-1.4× as long as body length, of females 1.3-1.5×. Male abdomen 1.2-1.5× as long as head and thorax, of females 1.0-1.2×.

Head (fig. 178): Reddish brown or greenish, often reddish along anterior margins of postclypeus and vertex lobes. Vertex and postclypeus with short red-brown setae. Postclypeus very broad in dorsal view, 3.0-4.3× as broad as long and oblong-shaped, hardly protruding beyond vertex lobes. Anterior margin of postclypeus almost continuous with anterior margins of vertex lobes. Postclypeus not swollen, its anterior margin (lateral view) concave. Lateral surface of postclypeus quite smooth, with only weakly developed rows of parallel ridges. Distance between lateral ocelli



Figs. 182-190. *Papuapsaltria phyllophora* (Blöte, 1960): 182, pygofer from aslant, Bokondini; 183, pygofer in lateral view, Bokondini; 184, male operculum, Bokondini; 185, claspers and aedeagus, Bokondini; 186, aedeagus in lateral view, Wau; 187, aedeagus from aslant, Wau; 188, male caudodorsal beak in dorsal view, Bokondini; 189, male fore femur, Bokondini; 190, detail male fore femur, Bokondini.

0.8-1.2 ×, though in most specimens practically 1.0 ×, distance between lateral ocellus and eye and 2.2-3.5× the width of frontal ocellus (1.3× in one female).

Thorax: Red-brown or olive green. Pronotum with very weak medial furrow. Lateral corners of pronotal collar often slightly swollen proximally.

Legs: Ochraceous, fore tibiae and tarsi reddish. Fore femur with row of three erect spines, diminishing in length towards tibia. Proximal spine slightly longer than middle spine, but shorter than distance to middle spine (figs. 189-190).

Tegmina: Hyaline, with 8 fairly short apical areas, a distinct costal area and a broad hyaline border along hind margin. Costa distinctly inflated towards distal end of first radial area. Second ulnar area definitely quintangular shaped, practically quadrangular in all related species (compare figs. 175 and 176).

Tymbals: Eight darkly sclerotized transverse ridges spanning the tymbal from dorsal to ventral margin, sometimes with a partly developed 9th ridge, closely along proximal tymbal margin. Eight short and much lighter coloured intercalary ridges seem to form a band across the tymbal.

Opercula: Male operculum (fig. 184) very small and angular, not covering tymbal cavity, and leaving a narrow gap between operculum and abdomen; folded membrane hardly visible in ventral view. Distal part of male operculum angular, oblong-shaped, and erect. Lateral margin of distal part straight, forming an obtuse angle with straight distal margin, and with crest around distolateral corner of basal part. Medial margin straight, distomedial corner angularly rounded. Meracanthus reaching well beyond operculum, to sternite 2. Female operculum (fig. 182) very similar to that of male, but slightly shorter. Distal part oblong-shaped and erect, with straight margins and almost rectangular distomedial corner.

Abdomen: Male abdomen ochraceous brown or greenish, not inflated. Segmental hind margins sometimes reddish. First tergite short and broad, partly hidden under metanotum. Medial part of 2nd tergite about 1.5× as long as lateral parts (fig. 177). Anterior margin of second tergite almost straight medially. Auditory capsules distinctly swollen and visible in dorsal view (fig. 177). First and 2nd sternites adjacent. Female abdomen more slender than that of males. Female pygofer (fig. 179) robust, in lateral view broader than long. Female caudodorsal beak in dorsal view (fig. 180) stout, broadly rounded at apex. Ovipositor sheaths reaching just beyond apex of caudodorsal beak.

Male genitalia: Pygofer in lateral view as in fig. 183. Dorsal margin slightly convex, concavely bent into stout, straight and erect caudodorsal beak. Distal margin convex between base of beak and lateral protuberance. Ventral margin almost straight. Ventral margins converge to a sharp angle at base of pygofer opening; ventral part of pygofer opening V-shaped (fig. 182). Pygofer lobe curved inwards towards distal margin and forming a small, globularly rounded, lateral protuberance. Caudodorsal beak in dorsal view (fig. 188) short, stout and broadly rounded at apex. Claspers very slender and parallel to rounded apices (fig. 185). Proximal part of clasper very long and straight, adjacent to membranous part of aedeagus. Apical part of clasper long and slender, with very shallow ventral hollow, strongly bent downwards. Dorsal part of clasper base forming a broad rounded ridge at base of anal valves. Dorsal ridges of both claspers distally elongated. Elongated parts curving mesiad, almost fusing, and forming a small hood over aedeagus. Clasper forming a rounded medial protrusion, supporting aedeagus. Aedeagus (figs. 186-187) very peculiar in shape, resembling a pick-axe; consisting of a stem ending in long and slender, recurving, dorsal and ventral protrusions. A square-shaped, semi-transparent membrane connecting dorsal protrusion with stem. This membrane strengthened by a crest along its proximal margin. Ejaculatory duct following ventral protrusion, ending in posteriorly directed pore. Aedeagus with pair of short, semi-circular, wing-shaped crests ventrally along the stem. Aedeagal crests bending slightly laterad and resting on medial protrusions of claspers.

Measurements: Body length ♂: 12.0-15.0 mm ($\bar{x}$ 13.3 mm ± 0.8), ♀: 11.6-15.8 mm ($\bar{x}$ 14.0 mm ± 1.0); tegmen length ♂: 14.6-18.2 mm ($\bar{x}$ 16.8 mm ± 0.7), ♀: 15.6-23.0 mm ($\bar{x}$ 19.1 mm ± 1.7); pronotum length ♂: 1.4-1.7 mm ($\bar{x}$ 1.5 mm), ♀: 1.5-2.0 mm ($\bar{x}$ 1.7 mm); mesonotum length ♂: 2.5-3.2 mm ($\bar{x}$ 2.8 mm), ♀: 2.8-4.1 mm ($\bar{x}$ 3.4 mm); head length ♂: 1.0-1.3 mm ($\bar{x}$ 1.1 mm), ♀ 1.1-1.6 mm ($\bar{x}$ 1.3 mm); head width ♂: 3.0-3.4 mm ($\bar{x}$ 3.2 mm), ♀: 3.1-4.1 mm ($\bar{x}$ 3.5 mm); width of pronotal collar ♂: 3.6-4.2 mm ($\bar{x}$ 3.9 mm), ♀: 4.2-5.4 mm ($\bar{x}$ 4.6 mm).

Material examined. – IRIAN JAYA: Bewani R. territ., 1200 m, 1939, W. Stüber leg., 1♀, RMNH; Bokondini, 10 km E, 40 km N of Baliem Val., 1300 m, 24.xi.1961, L. & S. Quate, 16♂, 11♀, BPBM; same data 2♂, 2♀, ZMAN; Waigeu, Camp Nok, 2500 ft, iv.1938, L.E. Cheesman, 3♂, 1♀, BMNH; same data but iv-v.1938, 2♂, 5♀, BMNH; 1♂, 1♀, ZMAN; PAPUA NEW GUINEA: Arau, 40 km E of Kainantu, 1400 m, 15.x.1959, T.C. Maa, 1♀, BPBM; Arau, Kratke Mts., Valley of Upper Wanton R., 1400 m, 7.x.1959, L.J. Brass, 1♀, AMNH; Baiyer River, 14.i.1978, R.B. Lachlan, 1♀, Moul.; Big Wau Creek, Wau, 1200 m, xii.1965, J. Sedlacek, 1♂, BPBM; Coviak Rdg., Wau, 763 m, 7.xii.1963, H. C., 1♂, 5♀, BPBM; Damanti, Finisterre Mts., Madang Dist., 3550 ft, 2-11.x.1964, M.E. Bacchus, 1♂, 1♀, BMNH; Kumur, Upper Jimi V., 1000 m, 12.vii.1955, J.L. Gressitt, 1♂, BPBM; same data but 13.vii.1955, 1♀, BPBM; Garaina S, 900-1800 m, 8-14.x.1968, 1♀, BPBM; Loloipa, Goilala, Owen Stanley Range, 11-20.xii.1957, W.W. Brandt, 1♀, BPBM; Mafulu, 4000 ft, i.1934, L.E. Cheesman, ♂ holotype *Baeturia phyllophora* Blöte, 1♀ paratype, 1♀ allotype, BMNH; Mt. Missim, Wau, 950-1300 m, xii.1965, J. Sedlacek, 1♀, BPBM; Mt. Missim, Wau, Morobe Dist., 1200-1800 m, 8.xii.1963, H. Clissold, 1♂, 1♀, ZMAN; same data but 1600 m, 17.iii.1963, Gressitt, 1♀; 1800 m, 22.iii.1966, 1♀, both BPBM; Mt. Missim, 7°16' S 146°48' E, 1500-1800 m, 7.i.1970, M. Sedlacek, 1♂, BPBM; Moroka, 1300 m, vii-xii.1895, Loria, 1♀ paratype *Baeturia phyllophora* Blöte, BMNH; Nakata Ridge, Wau, 1800 m, 18.xii.1963, H. Clissold, 1♂, 1♀, BPBM; Sattelberg, Huon Golf, 1898, Biró, 3♂, 2♀, TMB; Upper Baiane, Nr. Bulowat, 1100 m, 3.vi.1979, J.L. Gressitt, 1♀, BPBM; Wanuma, Adelbert Mts., 800-1000 m, 26.x.1958, J.L. Gressitt, 2♂, 5♀, BPBM; Wau, 1200 m, 21.xi.1963, J.L. Gressitt, 1♀, BPBM; same data but 25-30.ix.1964, J. & M. Sedlacek, 1♀; 1-9.ix.1965, J. Sedlacek, 1♀; 11.xii.1965, J. & M. Sedlacek, 1♂; 14.iii.1966, Gressitt & Wilkes, 1♂, 1♀, all BPBM; Wau, 1150-1250 m, 17.ii.1966, J. Sedlacek, 1♀, BPBM; same data but 1100-1300 m, 12.i.1966, 1♂, BPBM; Wau Area, Morobe P., iii-iv.1984, T.R. New, 1♂, Moul; Wau, 10 km S, st. 054, 22.v.1988, J. van Stalle, 1♀, ISNB; Wau, Ecology Inst., 1220 m, 18-20.vi.1981, J. van Goethem, 1♀, ISNB; Wau, Hospital Ck., 1200 m, 17.ii.1965, J. Sedlacek, 1♀, BPBM; same data but 1250-1300 m, 7.iii.1965, 1♀, BPBM; Wau, Morobe Distr., 14.-viii.1972, G.G.E. Scudder, 1♂, BPBM; same data but 1000 m, 1.iii.1963, H.W. Clissold, 1♂; 1090 m, 25.i.1963, J. Sedlacek, 1♀; 1100 m, 26.x.1961, J. Sedlacek, 1♀, all BPBM; Wau, Morobe Distr., 1200 m, 1-20.xi.1961, J. Sedlacek, 1♀; same data but 2-10.xi.1961, J. & M. Sedlacek, 1♀; 19.xi.1961, J.H. Sedlacek, 1♂; 22.xi.1961, J. & J.H. Sedlacek, 1♂; 2.xii.1961, J. Sedlacek, 1♀; 20-26.v.1962, J. Sedlacek, 1♀; 10.iii.1963, J. Sedlacek, 1♀; 15.i.1963, J. Sedlacek, 1♂, all BPBM.

Remark: The female paratype from Kokoda, mentioned by Blöte (1960) does not belong to this species but to *Guineapsaltria stylata* (Blöte, 1960) (see De Boer 1993a).

Distribution (fig. 4). – *P. phyllophora* is distributed throughout northern New Guinea, including the island of Waigeu, and the Huon and Papuan peninsulas, but is not recorded from Cendrawasih.

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References

Anonymous, 1938. Atlas van tropisch Nederland: [i-ix], maps 1-31b, legenda 1-31b, 1-17. Koninklijk Nederlands Aardrijkskundig Genootschap & Topografische Dienst in Nederlandsch-Indie, Amsterdam/Batavia.

Anonymous, 1966. List of New Guinea localities: 1-19. – Bernice P. Bishop Museum, Honolulu.

Anonymous, 1968. The Times atlas of the world: i-xliii, 1-272, pls. 1-123. Times Newspapers Ltd., London.

Blöte, H.C., 1958. On the history of the genus *Baeturia* Stål (Insecta, Homoptera, Cicadidae). – Archives néerlandaises de Zoologie 13 (Suppl. 1): 262-269.

Blöte, H.C., 1960. The genus *Baeturia* Stål as represented in New Guinea (Homoptera, Cicadidae). – Zoölogische Mededelingen, Leiden 37: 61-80.

Boer, A.J. de, 1982. The taxonomy and biogeography of the *nasuta* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Beaufortia 32 (4): 57-78.

Boer, A.J. de, 1986. The taxonomy and biogeography of the *conviva* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Beaufortia 36 (7): 167-182.

Boer, A.J. de, 1990. *Aedeastria,* a new cicada genus from New Guinea, its phylogeny and biogeography (Homoptera, Tibicinidae), preceded by a discussion on the taxonomy of New Guinean Tibicinidae. – Beaufortia 40 (3): 63-72.

Boer, A.J. de, 1991. *Scottotympana,* a new cicad genus from New Guinea, with the description of three new species, their taxonomy and biogeography (Homoptera, Tibicinidae). – Beaufortia 42 (1): 1-11.

Boer, A.J. de, 1992a. The taxonomy and biogeography of the *viridis* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Bijdragen tot de Dierkunde 61 (3): 163-183.

Boer, A.J. de, 1992b. The taxonomy and biogeography of the genus *Thaumastopsaltria* Kirkaldy, 1900, (Homoptera, Tibicinidae). – Beaufortia 43 (3): 17-44.

Boer, A.J. de, 1993a. *Guineapsaltria,* a new genus of the Australian-New Guinean region, with notes on the taxonomy and biogeography (Homoptera, Tibicinidae). – Bijdragen tot de Dierkunde 63 (1): 15-41.

Boer, A.J. de, 1993b. Ten new species of the genus *Aedeastria* De Boer, 1990, with notes on the taxonomy and biogeography (Homoptera, Tibicinidae). – Beaufortia 43 (9): 140-167.

Boer, A.J. de, 1994. The taxonomy and biogeography of the *guttulinervis* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Bijdragen tot de Dierkunde 64 (2): 87-100.

Boer, A.J. de, 1995a. The taxonomy and biogeography of the genus *Gymnotympana* Stål, 1861, (Homoptera, Tibicinidae). – Invertebrate Taxonomy (in press).

Boer, A.J. de, 1995b. The taxonomy and biogeography of the genus *Mirabilopsaltria* (Homoptera, Tibicinidae). – Tropical Zoology (in press).

Distant, W. L., 1892. A monograph of Oriental Cicadidae, Parts 5-7: i-xiv, 97-158; Pls. x-xv. – Trustees Indian Museum, Calcutta.

Distant, W. L., 1906. A synonymic catalogue of Homoptera. Part 1. Cicadidae: 1-207. – Trustees British Museum, London.

Duffels, J.P. & P.A. van der Laan, 1985. Catalogue of the Cicadoidea (Homoptera, Auchenorhyncha) 1956-1980. – Series Entomologica 33: i-xvi, 1-414.

Jacobi, A., 1903. Singcicaden von Ost-Neuguinea. – Gesellschaft naturforschender Freunde Berlin, Sitzungsbericht 1903: 10-15.

Jong, M.R. de, 1985. Taxonomy and biogeography of oriental Prasiini 1: The genus Prasia Stål, 1863 (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 128: 165-191

Kato, M., 1931. Notes on the distribution of Cicadidae in Japanese Empire. – Bulletin de la Société Biogeographique de Japan 2: 36-76.

Kato, M., 1932. Monograph of Cicadidae. 1-450.

Lallemand, V., 1931. Hemiptera-Homoptera. Résultats Scientifiques du Voyage aux Indes Orientales Néerlandaises de LL. AA. RR. le Prince et la Princesse Léopold de Belgique. – Mémoirs du Musée Royal d'Histoire Naturelle de Belgique 4 (1): 71-85.

Metcalf, Z. P., 1963. General catalogue of the Homoptera, VIII. Part 2. Tibicinidae. – North Carolina State College, Raleigh, N.C.: i-iv + 1-492.

Moulds, M.S., 1990. Australian cicadas. – New South Wales University Press, Kensington: 1-217.

Moulton, J. C., 1923. Cicadas of Malaysia. – Journal Federated Malay States Museum 11: 69-182 + pls. 1-5.

Myers, J. G., 1928. Cicadidae. Insects of Samoa and other Samoan terrestrial Arthropoda 2 (2): 55-65. – Trustees of the British Museum, London.

Pigram, C. J. & H. L. Davies, 1987. Terranes and the accretion history of the New Guinea orogen. – BMR Journal of Australian Geology and Geophysics 10: 193-212.

Swofford, D.L., 1993. PAUP: Phylogenetic Analysis Using Parsimony, version 3.1.1. – Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Wheeler, T., 1988. Papua New Guinea a travel survival kit. – Lonely Planet Publications, Victoria, Australia: 1-340.

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A REVIEW OF THE SUBFAMILY KORINNINAE (PHASMIDA: PSEUDOPHASMATIDAE), WITH THE DESCRIPTION OF A NEW SPECIES

Bragg, P. E., 1995. A review of the subfamily Korinninae (Phasmida: Pseudophasmatidae), with the description of a new species. – Tijdschrift voor Entomologie 138: 45-50, figs. 1-9. [ISSN 0040-7496]. Published 15 June 1995.

The subfamily Korinninae is reviewed. A key to genera and species is provided. *Kalocorinnis pulchella* (de Haan), was previously placed in a different suborder, was found to be the senior synonym of *Kalocorinnis calopteryx* Günther. Variation in the males of *K. pulchella* is discussed and illustrated. A new species, *Kalocorinnis wegneri*, from Borneo, is described and illustrated. The female of *Korinnis errans* Günther is illustrated. The egg of *K. wegneri* is the first egg to be described and illustrated from this subfamily.

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Key words. – Phasmida, Korinninae, *Korinnis, Kalocorinnis,* new species, Borneo.

This paper is produced as the result of a visit to Leiden (RMNH) to examine the type specimens of de Haan. During this visit it was discovered that one of de Haan's species appeared to be the same as the paratype of a species described by Günther in 1944 which is also in the RMNH collection. According to the literature however the two species were considered to be in different suborders. Careful cleaning and examination of de Haan's type specimen showed that it had been placed in the wrong suborder by Redtenbacher in 1908.

The RMNH collection has a large number of unidentified specimens, many from Borneo. These were examined and several more specimens of this subfamily were located, including one species which is described here for the first time.

KORINNINAE

Korinninae Günther 1953: 550. – Type genus: *Korinnis* Günther 1932.

The subfamily belongs to the suborder Areolatae and family Pseudophasmatidae. This is a small subfamily which is restricted to south east Asia. The subfamily contains only four species which fall into two genera. The two suborders of Phasmida are distinguished by the presence of a triangular depression on the underside of the apex of the middle and hind tibiae in the Areolatae, and the absence of this feature in the Anareolatae. The use of Bradley & Galil's key to families (1977: 178) places these species in the Pseudophasmatidae because the tarsi have five segments, the first abdominal segment is longer than metanotum, the metanotum is longer than it is wide, and the antennae are long and filiform. The key to subfamilies of Pseudophasmatidae (Bradley & Galil 1977: 200) refers these species to the Korinninae because they possess normally formed elytra, four unarmed carinae on the femora, and they lack ocelli.

The following key serves to distinguish the genera and species of the subfamily.

Key to the subfamily

1. Base of fore femora curved, mesonotum with large tubercules, wings not coloured, or only tinted (*Korinnis* spp.) 2
– Base of femora straight, mesonotum smooth, wings strongly coloured (*Kalocorinnis* spp.) 3
2. Mesonotum evenly tapering and not armed with blunt spines .... *Korinnis errans* Günther
– Mesonotum tapers in two distinct stages and is armed with eight blunt spines ....*Korinnis potameis* Günther
3. Mesonotum evenly tapering and not armed with blunt spines ..... *Kalocorinnis pulchella* (de Haan)
– Mesonotum tapers in two distinct stages and is armed with six blunt spines .... *Kalocorinnis wegneri* **sp.n.**

Ragge (1955), in his study of wing venation in Phasmida, did not examine any representative of the Korinninae. The wing venation agrees with the general pattern which Ragge found in all groups that he examined (1955: 390). In the Korinninae the costa, subcosta, radius, cubitus, and first anal are all unbranched, the media branches near the base to form the anterior and posterior media. Ragge considered an unbranched radius to be unusual, this state occurring only 'in isolated genera (or even species) in two subfamilies (Aschiphasminae and Necrosciinae)'. The only difference within the Korinninae is the length of the subcosta; this is between three quarters and four fifths of the wing length in *Korinnis* but only about two thirds in *Kalocorinnis*. The females of all four members of the subfamily have an operculum with a deep notch in the apex. This condition is rare in Aschiphasmatinae (present in one out of 13 species examined) although not unusual in the Pseudophasmatinae.

The distribution of the subfamily is probably limited to the islands of the East Indies and the Malay Peninsula. All four species occur in Borneo; reliable records from outside Borneo refer to only one species, *Kalocorinnis pulchella* (de Haan).

SYSTEMATIC PART

Kalocorinnis Günther

Kalocorinnis Günther, 1944: 77. – Type species *Kalocorinnis calopteryx* Günther 1944 by original designation [= *K. pulchella* (de Haan, 1842)].

Kalocorinnis pulchella (de Haan) comb.n.

(figs. 1-4)

Phasma (*Necroscia*) *pulchellum* de Haan, 1842: 120, pl. XV fig. 5. – Holotype ♂, Sumatra, Batang Singalang (RMNH) [examined].
Necroscia pulchella (de Haan). – Westwood 1859: 152; Kirby 1904: 377.
Tagesoidea pulchella (de Haan). – Redtenbacher 1908: 565.
Kalocorinnis calopteryx Günther, 1944: 78, fig. 5. – Holotype: ♀, Nordborneo (RMNH) [examined], Paratypes: ♀, Central-Borneo (SMTD); ♂, Peninsular Malaysia, Selangor, Bukit Kutu, 1100m, 13-iii-1931, H.M. Pendlebury (RMNH) [examined]. **Syn. n.**

Material examined. – Holotypes: *Phasma (Necroscia) pulchellum*, ♂; *Kalocorinnis calopteryx*, ♀. Paratype: *Kalocorinnis calopteryx*, ♂. – Others: Midden O-Borneo, 14.viii.1925, H. C. Siebers, 1♀ (RMNH); E. Borneo, 125m Tabang, Bengen River, 28.x.1956, A.M.R. Wegner, 3♂ (RMNH); Sarawak, J.E.A. Lewis, 1♂ (BMNH, 1910-116); Sarawak, Wallace, 1♂ (OXUM); Sabah, Danum Valley, 220m, light trap sample, roadside, secondary forest, 10.ix.1987, A.H. Kirks-Spriggs, 1♀ (NMWC, NMW.Z.1987.094).

Examination of the holotype of *pulchella* showed that it belongs in the subfamily Korinninae; the original description makes no mention of the characteristic which is used to distinguish the two suborders. Direct comparison of de Haan's male holotype, and Günther's male paratype leave no doubt that they are the same species.

Rather unusually for phasmids, the wings of this species are brightly coloured and have a distinctive pattern. In view of the fact that the species had already been described and well illustrated (de Haan 1842), and had been recorded from Borneo (Westwood 1859: 152), Günther's description of *Kalocorinnis calopteryx* as a new species from Borneo might appear strange. However some research into the background suggests a rational explanation of this.

The most recent comprehensive work on Phasmida is the three part monograph by Brunner von Wattenwyl (1907) and Redtenbacher (1906, 1908), this is still used as the basis for identification of phasmids by most workers. Redtenbacher (1908) placed *pulchella* in his 'Tribus Necrosciini' (now the subfamily Necrosciinae). This was presumably based only on de Haan's description and illustration; the species is not represented in Redtenbacher's collection. De Haan's description is quite brief and makes no mention of the feature which distinguishes the two suborders of Phasmida: the sunken triangular area on the middle and hind tibiae. It appears that Günther had not seen de Haan's type specimen; Leiden Museum records show no evidence of a visit by Günther. The illustrations in de Haan's publication (1842) are very accurately drawn but are hand coloured; examination of two copies (RMNH and Oxford University library) has shown that the pattern on the wings varies (although less than can occur in the insects themselves). Westwood (1859: 152) correctly identified Wallace's specimen although it differs considerably from de Haan's specimen (figs. 1, 4). Günther probably did not consider the possibility that Redtenbacher had placed the species in the wrong suborder, the species is so distinctive that he would almost certainly have recognised it despite variations in de Haan's illustrations.

The type specimens have suffered damage since they were originally described. The holotype of *pulchella* has only two legs remaining, the right fore leg and left mid leg; the tarsi of both these legs are missing. Günther illustrated the *calopteryx* holotype (1944: 75, fig. 5) at which time it had one antenna missing, it has since lost both front and both middle legs; the male paratype lacks both front legs, the left mid leg, both antennae, and the end of the abdomen.

This species shows variation in both colour and pattern of the wing patches. There is considerable variation in the shape of the patches of the males (figs. 1-4), this is particularly noticeable in Wallace's specimen which has greatly reduced patches. The wing patches of all three females which have been examined, and the two male types, are cream coloured.

One of the three Tabang males has pale blue-green patches, the other two have white patches with a blue-green tinge to the veins. Wallace's male also has blue-green patches. The BMNH specimen has yellow patches. Table 1 gives measurements of the female collected by Siebers and one of the males collected by Wegner, part of the abdomen of the male is missing.

This species appears to be quite widespread, having been recorded from Borneo, peninsular Malaysia and Sumatra. Within Borneo it has been recorded from Sabah (Günther's male paratype and NMWC specimen), Sarawak (Westwood, 1859: 152, and Lewis) and Kalimantan (Wegner, Siebers, and Günther's female paratype).

Kalocorinnis wegneri sp.n.
(fig. 5)

Type material. – Holotype ♀: East Borneo, 125m Tabang, Bengen River, 3.ix.1956, A.M.R. Wegner (RMNH). – Paratype ♀: Sabah, Sepilok, 23-ii-1983, Shinji Nagai (C.L. Chan).

The holotype is in poor condition; all the internal parts of the head and thorax have been eaten, as have all thoracic sternites; the one remaining antenna is broken; the left hind and mid legs are missing and only one tarsus remains; the abdomen is shrunken and distorted. Despite the poor condition, the wings are very distinctive and this species is unlikely to be confused with any other.

The paratype is in better condition than the holotype, but lacks any front legs, antennae, left mid leg and right mid tarsus. It differs from the holotype by being slightly longer (57 mm), and by being more brightly coloured. It is likely that the colour of the holotype was originally similar to the paratype. The abdomen is much fatter, while some of this is due to dorso-ventral compression during preservation, it clearly shows that the abdomen of the holotype is badly shrunken.

Measurements of the holotype and paratype are given in table 1. Figure 5 is based on the holotype but has been modified to take some account of the damage and distortion of the specimen; the right wing has been omitted.

Head globular, longer than wide, smooth. Eyes prominent. Antennae filiform; light brown at the base, becoming darker (broken off).

Pronotum mid brown, lateral surfaces green in the paratype; smooth, with a deep transverse indentation about one third of the way from the front margin. Mesonotum granulose; narrow, with parallel sides at the anterior; widening and swelling suddenly one third of the way back; with two pairs of laterally pointing blunt spines near the front edge, and one blunt spine on each side, slightly in front of the mid point of the swelling. Anterior third of holotype light brown, posterior portion mid to dark brown; paratype evenly mid brown dorsally and green on lateral surfaces. Metanotum and abdominal segments light brown; paratype with green lateral surfaces. It is possible that when live the whole of the paratype's abdomen may have been green.

Abdominal segments of the holotype are shrunken and distorted, those of the paratype are flattened, but the abdomen appears to narrow evenly along its length. Segments 1-7 becoming evenly shorter, 8th segment noticeably shorter than 7th; 9th and 10th much shorter and of equal length. The slender lamina supraanalis is as long as the 10th segment and tapers to a point. Operculum covered in bristles, with a deep notch at the apex.

Elytra almost circular; with an obvious hump near the outer margin; evenly covered in prominent fine veins.

Wings well rounded. Holotype with costal region chocolate brown, anal region of the wing tessellated dark brown and white, with an arc of large white patches about one two thirds of the way from the base of the wing, and small white triangular spots on the margin between the veins. Paratype with costal region of wings green in front of the main vein and mid brown behind; anal region dark brown with very few white tessellations; an arc of pale blue patches corresponds to the white patches of the holotype; the white triangles on the margin are present but some have a pale blue tint.

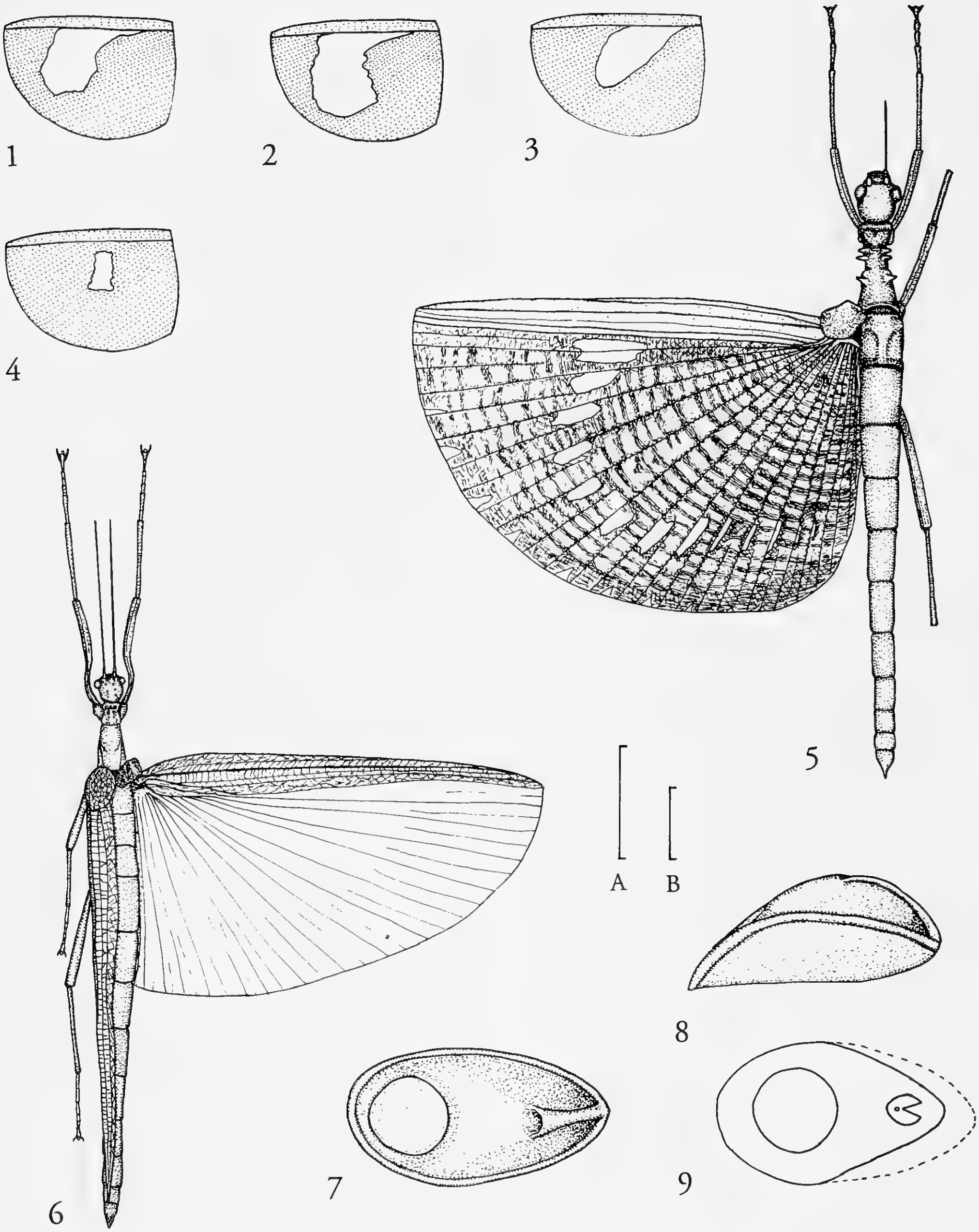
Femora all with four carinae; smooth, apart from fine bristles mainly on the carinae. The fore femora are straight and narrow only slightly at the base. Hind femora slightly enlarged and laterally compressed.

Tibiae with four indistinct carinae; only slightly widened at the apices. Fore and mid tarsi with five segments; first tarsomere one third of the total; fourth tarsomere very short. (Middle tarsi missing from both specimens).

Male: Unknown.

Egg. – Several eggs (figs. 7-9) were removed from the body of the paratype by rehydration and partial dissection of the abdomen. While some eggs appear to be fully developed, there may be some slight differences in surface detail between these and eggs which are laid. Some of the eggs have been slightly damaged during the original preservation or by their subsequent rehydration; this has caused some distortion of the ventral surface, as a consequence the true curvature of the ventral surface may differ slightly from that shown in the illustration (fig. 8).

Whole of capsule mid brown. Capsule twice as



Figs. 1-9. Korinninae. – 1-4. Wing patterns of male *Kalocorinnis pulchella* (de Haan): 1, De Haan's holotype; 2, Günther's paratype; 3, One of Wegner's specimens; 4, Wallace's specimen. – 5. *Kalocorinnis wegneri* sp. n., holotype ♀. – 6. *Korinnis errans* Günther, ♀. – 7-9. Egg of *Kalocorinnis wegneri* n.sp. (removed from paratype): 7, dorsal view; 8, lateral view; 9, internal view of dorsal surface. Scale line A (1 cm) for figs. 5 and 6, scale line B (1 mm) for figs. 7-9.

long as wide, tapering slightly at polar end, dorsal surface sloping steeply towards the ventral surface at the anterior end; ventral surface longitudinally almost flat, laterally sharply convex; dorsal surface strongly convex. A sharp ridge circles the egg, separating the dorsal and ventral surfaces; a similar ridge runs from the micropyle to the polar end. Operculum circular; at the anterior end of the dorsal surface. Micropylar plate indistinct externally; internally the plate is almost circular, open, with a triangular notch at the polar end (fig. 9). Typical measurements: length 3.8 mm, height 1.5 mm, width 2.0 mm.

Etymology. – *Wegneri*, after the collector A.M.R. Wegner.

Korinnis Günther

Korinnis Günther, 1932: 66. – Type species *K. potameis* Günther, 1932 by original designation.

Korinnis potameis Günther

Korinnis potameis Günther, 1932: 67, fig. 1. – Holotype ♀, Kalimantan, Noesa Djangkai on the lower reaches of the River Serawai, 19-xi-1924.
Korinnis potameis. – Günther 1943: 151.

Material examined. – Kalimantan, Mahakam, expedition of Dr Nieuwenhuis, 1894 [det. Günther, 1943: 151], 1♀ (RMNH); same data [det. Günther, but not mentioned in Günther 1943], ♀ nymph (RMNH); Kalimantan Tengah, Sungai Ratu Miri, Ratu Miri logging camp, to lights, 22-viii-1993, P.E. Bragg, 1♀ (P.E. Bragg, PEB-1999).

Table 1 gives measurements of the two adult specimens which have been examined. The specimen collected by the author was kept alive for four days but did not lay any eggs. Colour transparencies (Kodachrome 64 ASA film) were taken and used in conjunction with the preserved specimen for the following description of the coloration of the insect.

Head, pronotum, mesonotum and leading edge of elytra a glossy mid brown. Spines on the mesonotum with black tips. Head with a large almost round pea-green spot between the eyes. Sides and underneath of body, and whole of abdomen, blueish-green; final three abdominal segments with a chocolate brown longitudinal stripe. Costal and subcostal areas of wing blueish-green, radial and medial areas pea-green; radial vein distinctly orangy-brown with a narrow white line on the hind margin of the subcostal area. The anal region of the wing pale rose-pink. Elytra blueish-green on the leading edge, glossy mid-brown on the humped portion, pea-green on the outer trailing edge and bright yellow on the inner trailing edge. All femora, fore tibiae and fore tarsi glossy mid-brown, fore femora yellowish green at the base. Mid and hind tibiae very pale green, brown at apices. Mid and hind tarsi very pale green at the base becoming mid brown at the apices. Antennae very dark brown, almost black, with some pale bands towards the apices.

Remarks. – Maps of Kalimantan are of limited value for finding precise localities, they are often marked 'data incomplete' and not all rivers and villages are named. Attempts to locate Noesa Djangkai on available maps have been unsuccessful, however a village called Nanga Serawai has been located on the confluence of the rivers Melawei and Serawai; this suggests

Table 1. Measurements of specimens examined in detail

	Kalocorinnis			*Korinnis*	
Length (mm)	♂ *pulchella*	♀ *pulchella*	♂ *wegneri*	♀ *potameis*	♀ *errans*
Total	>28	38	53-57	58-59	48
Antennae	>26	>16	>6	25	>13
Head	2.5	3	4.5-5	4	3.5
Pronotum	1.5	2	2	2.5	1.5
Mesonotum	4	5	5.5-6	6.5-7	4.5
Metanotum & median segment	6.5	8.5	10-11	9-10	8
Elytra	1.5	2.5	4-4.5	4.5-5	4
Wing	21	27	40	40-41	35
Fore femora	6.5	7	9	10.5-11.5	9.5
Fore tibiae	5	4.5	7	7-9	7
Fore tarsi	5	4.5	6	6-7	6
Mid femora	5	5	7-7.5	7.5-8.5	7
Mid tibiae	4	3.5	5	5-6.5	5
Mid tarsi	4	3.5	-	4.5-5.5	4.5
Hind femora	8	8	10.5-11	11.5-13	11
Hind tibiae	6.5	6	9	8-10.5	8
Hind tarsi	5	5	7	5.5-7	6

that Noesa Djangkai is probably in the region around 0° 15'S, 112° 45'E. The specimens from Dr. Nieuwenhuis' expedition give 'Mahakam' as the locality; this is rather vague as the Mahakam, in eastern Kalimantan, is one of the longest rivers in Borneo. Neither the Ratu Miri logging camp, or the River Ratu Miri are marked on any available maps; the camp is estimated to be approximately 0° 30'S, 113° 35'E.

Korinnis errans Günther
(fig. 6)

Korinnis errans Günther, 1938: 125. – Holotype ♀, Borneo? [Günther stated that the specimen was incorrectly labelled 'Sibsagar, Nordost Assam, S.E. Peal'] (NZSI).

Material examined. – [from Siebers' collection], 1 ♀ (RMNH); Sabah, Mt Kinabalu, Silau Silau trail, c. 1580m, 10.xi.1991, C. L. Chan (C. L. Chan) ♀; Sabah, Sepilok, 13.vi.1982, C. L. Chan & S. Nagai, 1 ♀ (C. L. Chan).

The female from RMNH which has been examined has no original data label other than the number 181 written in pencil. However there are two labels added by Klante in 1965; the first is a determination label, the second is a note that the specimen is 'without doubt from box 39 of the Siebers collection'. The RMNH collection contains a large number of phasmids collected in Borneo by Siebers in 1925. This supports Günther's suspicions about the locality of the holotype. This is confirmed by the two specimens in the collection of Mr C.L. Chan of Kota Kinabalu, Sabah.

The RMNH specimen agrees with Günther's description. Although the total length is only 3 mm shorter, there are three measurements notably different from those given by Günther: the length of the mesonotum is shorter (4.5 mm compared to 6.5 mm in Günther's description), the fore femora are shorter (9.5 mm compared to 11 mm), and the elytra are larger (4 mm compared to 3 mm); other size differences are minor. The length of the fore femora agree if it is assumed that Günther included the trochanter in his measurement. A complete set of measurements of Siebers' specimen is given in table 1, and the specimen is illustrated in figure 6.

The two specimens from the collection of C.L. Chan appear to differ considerably from each other. The Mt Kinabalu specimen, length 40 mm, is much smaller than the other specimens although the general proportions agree closely with the RMNH specimen. The Sepilok specimen, length 48 mm, has a more slender appearance due to the longer mesothorax (5.5 mm), and longer legs; its proportions agree closely with those given by Günther.

In most respects these specimens agree closely with Günther's description; the differences may be due to intraspecific variation. There is a possibility that there are two species represented here but at present insufficient material is available to determine this with confidence.

It is worth noting that although the other members of the Korinninae have a few hairs on the radius of the wing, these specimens have numerous hairs all over the costal region; although those of the Sepilok specimen are less densely packed than the RMNH and Sepilok specimens.

REFERENCES

Bradley, J. C. & Galil, B. S., 1977. The taxonomic arrangement of the Phasmatodea with keys to the subfamilies and tribes. – Proceedings of the Entomological Society of Washington 79 (2): 176-208.

Brunner von Wattenwyl, K., 1907. *Die Insektenfamilie der Phasmiden*, Volume 2. Leipzig.

Günther, K., 1932. Die von Professor Dr. H. Winkler 1924/25 in Zentralborneo gesammelien Phasmoiden. – Zoologischer Anzeiger 101 (3/4): 65-73.

Günther, K., 1938. Neue und wenig bekannte Phasmoiden aus dem Indian Museum, Calcutta. – Records of the Indian Museum 40: 123-141.

Günther, K. 1943. Die Phasmoiden (Orthoptera) der 'Borneo-Expedition Dr. Nieuwenhuis' aus dem Stromgebiet des oberen Mahakam. – EOS Madrid 19: 149-172.

Günther, K., 1944. Bemerkungen über indomalayische Stabheuschrecken (Orth.), besonders die Gattung *Haaniella* Kby. – Stettiner Entomologische Zeitung 105: 68-79.

Günther, K., 1953. Über die taxonomische Gliederung und die geographische Verbreitung der Insektenordnung der Phasmatodea. – Beiträge zur Entomologie 3 (5): 541-563.

Haan, W. de., 1842. Bijdragen tot de kennis Orthoptera. – in: C. J. Temminck, Verhandelingen over de natuurlijke Geschiedenis der Nederlandsche overzeesche Bezittingen 2: 95-138.

Kirby F.W., 1904. A synonymic catalogue of Orthoptera. Volume 1. London.

Ragge, D.R., 1955. The wing-venation of the order Phasmida. – Transactions of the Royal Entomological Society of London 106: 375-392.

Redtenbacher J., 1906. Die Insektenfamilie der Phasmiden, Volume 1. Leipzig.

Redtenbacher J., 1908. Die Insektenfamilie der Phasmiden, Volume 3. Leipzig.

Westwood, J.O., 1859. Catalogue of the Orthopterous insects in the collection of the British Museum. Part I: Phasmidae. British Museum, London.

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A TAXONOMIC REVISION OF THE PTILOMERINE GENUS *RHYACOBATES* ESAKI (HEMIPTERA: GERRIDAE), WITH FIVE NEW SPECIES FROM CHINA AND ADJACENT COUNTRIES

Andersen, N.M. & P.P. Chen, 1995. A taxonomic revision of the ptilomerine genus *Rhyacobates* Esaki (Hemiptera: Gerridae), with five new species from China and adjacent countries. – Tijdschrift voor Entomologie 138: 51-67, figs. 1-37, table 1. [ISSN 0040-7496]. Published 15 June 1995.

The taxonomy of the lotic-adapted water strider genus *Rhyacobates* Esaki, 1923, is revised, all previously known species redescribed, and five new species described from China and adjacent countries: *R. abdominalis* sp. n. from Guangdong, *R. edentatus* sp. n. from Guangdong and Guangxi, *R. recurvus* sp. n. from Jiangxi, *R. scorpio* sp. n. from Sichuan, all in China, and *R. malaisei* sp. n. from Burma, Thailand, and China (Yunnan). *R. esakii* Miyamoto & Lee, 1963, syn. n. is synonymized with *R. chinensis* Hungerford & Matsuda, 1959. A key to all species of the genus is provided. The status of '*Rhyacobates*' *imadatei* Miyamoto, 1967, is discussed. Finally, the results of a cladistic analysis of relationships between species of *Rhyacobates* and related genera of Ptilomerinae are given.

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Key words. – Gerridae; Ptilomerinae; *Rhyacobates;* taxonomy; key; new species; China, Korea, Burma, Thailand.

The subfamily Ptilomerinae Bianchi, 1896 comprises medium-sized or large water striders which all are strongly adapted to life on the water surface of lotic habitats including torrents and fast-flowing streams and rivers. Except for one genus from Madagascar, the ptilomerines are confined to the eastern Palearctic Region and the Oriental Region including New Guinea (Andersen 1982). Matsuda (1960) presented a very useful account of the taxonomic morphology and generic taxonomy of the Gerridae including most genera of the Ptilomerinae. Apart from the taxonomic revision by Hungerford & Matsuda (1965) of the large genus *Ptilomera* Amyot & Serville and the revision of the genus *Potamometropsis* Lundblad by Zettel (1994), the species taxonomy of the ptilomerine genera is still incompletely known.

The following account of the genus *Rhyacobates* Esaki (1923) is the first part of a series of studies of the classification and phylogeny of ptilomerine genera undertaken by the senior author. It is also a contribution towards improving the knowledge about the fauna of semiaquatic bugs (Heteroptera, Gerromorpha) of China and adjacent countries.

All measurements are in millimeters. 'Length' has been measured from the anterior margin of the head along the central body axis to the posterior margin of the last visible abdominal tergum in apterous (wingless) specimens, or to the apex of the forewings in macropterous (winged) specimens. 'Dealated' specimens are macropterous specimens which have shed their wings by self-inflicted damage or autotomy (see Andersen 1982). 'Width' is the maximum width of the body and is measured across the middle pair of acetabula (coxal cavities). Measurement of the femur does not include the trochanter. Measurements of the distal leg segments (tibia and/or tarsus) are usually inaccurate since these segments are extremely thin and usually coil up when the specimen is dried.

The genital segments of female *Rhyacobates* (segments 8-10) are usually completely withdrawn into the tubular, pregenital abdomen (e.g., figs. 6-7) and difficult to remove for examination and dissection. In order to examine the genital segments (segments 8-10) of the male (fig. 8), the segments are detached from the abdomen (dry specimens may be softened by placing them in alcohol for a few hours), macerated in hot 10% potassium hydroxide (KOH) for about ten minutes, and cleared in lactic acid (50% aqueous solution) for a couple of hours. The phallic organ is pulled out of the pygophore (segment 9) and the distal part of the phallus (vesica) pushed out of the basal part (phallotheca) with fine needles.

The specimens dealt with in this paper were borrowed from or deposited in the following collections (with abbreviations used in the lists of material examined): Entomological Laboratory, Kyushu University, Fukuoka, Japan (ELKU); the Natural History Museum (formerly British Museum, Natural History), London, U.K. (BMNH); the John T. Polhemus collection, Englewood, Colorado, U.S.A. (JTPC); the Nico Nieser collection, Tiel, the Netherlands (NC); Natural History Museum, Stockholm, Sweden (NHMS); Natural History Museum, Vienna, Austria (NHMV); Nankai University, Tianjin, China (NUC); Snow Museum of Entomology, Kansas University, Lawrence, Kansas, U.S.A. (SEMK); National Museum of Natural History, Smithsonian Institution, Washington, D.C., U.S.A. (USNM); Zoological Institute, Academia Sinica, Beijing, China (ZIB); Zoological Museum, University of Copenhagen, Denmark (ZMUC).

Systematic part

Genus ***Rhyacobates*** Esaki

Rhyacobates Esaki, 1923: 387 (descr.). Type species by original designation: *Rhyacobates takahashii* Esaki, 1923; Hungerford & Matsuda, 1960: 8 (key); Matsuda, 1960: 273-276; Andersen, 1982: 424 (key; many further references throughout book).

Esakobates Lundblad, 1934: 22. Type species by monotypy: *Esakobates svenhedini* Lundblad, 1934. Synonymized by Hungerford & Matsuda (1959: 69).

Description. – Chiefly black dorsally and pleurally, covered by silvery pubescence (fig. 1). Head yellowish with median black spot. Pronotum with large median pale spot; pronotal lobe (macropterous form) dark with brownish lateral margins. Mesonotum (apterous form) with median pale stripe not reaching anterior margin. Mesosternum chiefly black, rest of venter yellowish.

Female larger than male, not modified ventrally. Head with anterior margin not bent ventrad; eyes globular. Antenniferous tubercles prominent; antennae almost as long as body in male, slightly shorter in female: first antennal segment longer than three following segments together (fig. 2); second segment not longer than third; fourth segment shortest, curved and with elongate, impressed whitish hair-pad ventrally on distal two fifths (fig. 3). Pronotum of apterous form short, subquadrangular, with lateral margins slightly converging posteriorly. Mesonotum about three times as long as pronotum in male, slightly longer in female. Pronotum of macropterous form large, covering mesonotum and wing bases; posterior margin broadly rounded. Fore leg longer than body (fig. 1); femur robust, slightly tapering apically; tibia with inner apical process more distinct in female than in male; first tarsal segment 1.6–2x as long as second segment in male, longer in female. Middle femur about twice or a little less than twice as long as tibia; femur in male without dense fringe of long hairs on inner margin, with scattered dark pegs or spines ventrally, not forming a distinct row of spines; middle tibia about half as long as femur, with distinct hair-fringe ventrally; middle tarsus less than half as long as tibia, first tarsal segment much longer than second segment. Hind coxae longer than wide, without spine on apical margin; hind femur slightly longer than middle femur; hind tibia about one third as long as femur, without hair-fringe; hind tarsus less than one tenth as long as tibia, first tarsal segment shorter than second segment. Claws absent from both middle and hind legs. Forewing venation very similar to that of *Ptilomera* (Andersen, 1982: fig. 430), with M and Cu separated from near base, connected by a cross-vein before middle of wing.

Male abdomen shortened, seventh segment about 1.5x sixth segment ventrally. Eighth segment reduced in length ventrally (fig. 8), hind margin slightly produced. Pygophore prolonged, rounded on apical margin. Proctiger widened (fig. 10), sometimes expanded laterally in basal parts. Parameres large (fig. 9), symmetrical and falciform, not conspicuously setose. Phallotheca cylindrical but weakly sclerotized; conjunctivum with two pairs of lobes; endosoma with dorsal vesical sclerite only partly sclerotized (fig. 11), bifurcated apically and fused to slender ventral sclerite basally; there are no well-defined lateral sclerites.

Female abdomen moderate in length in most species, posterior segments curved dorsad (fig. 6; apterous form), in some species to oblique or even vertical position. Seventh segment about twice or over twice as long as sixth segment ventrally (fig. 4), tubular, prolonged and enclosing genital segments. Connexivum with postero-lateral corners more or less distinctly prolonged. Hind margin of seventh sternum produced medially but without distinct median lobe. Ovipositor illustrated by Matsuda (1960: fig. 680, *R. lundbladi).*

Type species by original designation and monotypy: *Rhyacobates takahashii* Esaki, 1923.

Biology. – Species belonging to the genus *Rhyacobates* live on the surface of swift streams or small rivers. Esaki (1923: 389-390) aptly characterizes the habitat and behaviour of *Rhyacobates takahashii* as follows: 'This curious water strider was found at first on a very rapid stream in a rocky ravine at Sozan

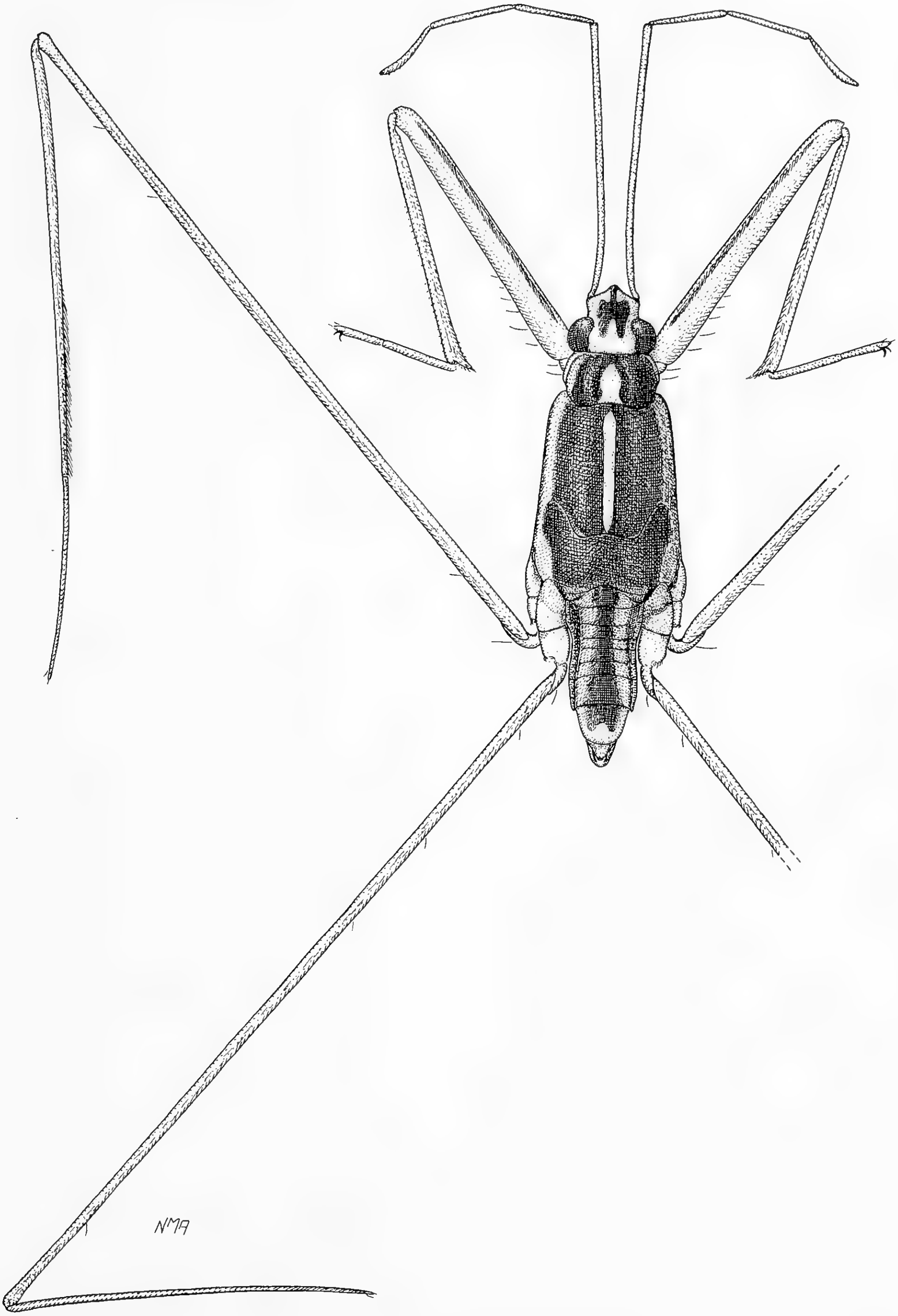


Fig. 1. *Rhyacobates scorpio;* apterous male, dorsal habitus (Reproduced with permission from Andersen, 1982: fig. 448).

[in Taiwan]. The insects glide swiftly on the surface of the water in all directions and are hardly recognizable owing to the disturbance of the water. They look, however, somewhat like whirligig beetles. Some of them were found climbing on the rocks near by. Numerous of specimens in copula were also captured. Numerous examples were found on the Shinten River which is a very much larger stream than the Sozan. Here also they live on a rapid current, but at Shinten only the males and the nymphs of the last instar were found. The nymphs were not seen at Sozan.'

The last observation seems to indicate that the species is protandrous, i.e., that males complete their last moult before the females. The modifications of the female abdomen with genital segments withdrawn into a tubular seventh abdominal segment may be an adaptation to discourage copulation except when the female is newly emerged and teneral.

Comparative notes. – *Rhyacobates* is most closely related to *Heterobates* Bianchi (1896) and *Pleciobates* Esaki (1930). Matsuda (1960: 264-265) pictured these genera as a (presumably monophyletic) group with unresolved mutual relationships in his diagram of 'evolutionary relationships' of genera of the Ptilomerinae. The genus *Potamometroides* Hungerford (1951) from Madagascar was also included but is not considered in the following discussion.

Rhyacobates shares the following characters with *Heterobates* and *Pleciobates:* (a) meso- and metanotum chiefly dark, covered with a dense layer of silvery pubescence; (b) first antennal segment much longer than three following segments together; (c) fourth antennal segment short, curved and with elongate ovate, impressed whitish area in distal two fifths to half; (d) male fore femora relatively slender, without ventral modifications before apex; (e) claws absent from middle and hind tarsi; (f) male parameres moderate in size, falciform, not conspicuously setose; (g) apical segments of female pregenital abdomen strongly modified. According to Matsuda (1960: 204), the basally strongly reflexed connexiva (female abdomen) also unites the three genera. This character, however, is not present in all *Rhyacobates* species.

Rhyacobates differs from both *Heterobates* and *Pleciobates* in the following characters: (h) middle femur of male without ventral row of black spines; (i) eighth abdominal segment of male reduced ventrally, shorter than seventh sternum; (j) posterior segments of female abdomen usually curved dorsad (apterous form); (k) seventh segment of female abdomen tube-like prolonged, completely enclosing the genital segments.

The genus *Heterobates* is above all characterized by the distinctly demarcated, flattened area on the ventral surface of the female body (Matsuda 1960: fig. 684). The hind margin of female abdominal sternum 7 has a square, median lobe (absent in *Rhyacobates* and *Pleciobates).*

The genus *Pleciobates* was not available to Matsuda (1960) for direct study but its affinity was discussed based on the original description by Esaki (1930). In females of the type species, *P. tuberculatus* Esaki, 1930, the seventh abdominal segment is prolonged, with a finger-like process arising from the hind corner of the sixth connexival segment (see also Cheng & Fernando 1969). More recently, Thirumalai (1986) has described two species of *Pleciobates* from southern India in which the females lack this connexival process.

Key to the species of *Rhyacobates*

(male of *R. recurvus* sp. n. not available)

1. Females 2
– Males 10
2. Seventh abdominal segment abruptly turned dorsad at an angle of about 90 degrees (fig. 28). Posterolateral corners of segment with very short process (figs. 29-30). China (Sichuan) .... *R. scorpio* sp. n.
– Seventh abdominal segment not modified as above 3
3. Abdomen distinctly curved dorsad towards the end (figs. 6, 12, 16, 33). Posterolateral corners of seventh abdominal segment either blunt or triangularly produced, but never bilobate 4
– Abdomen almost straight or only faintly curved dorsad towards the end (fig. 18). Posterolateral corners of seventh abdominal segment more or less distinctly bilobate 8
4. Dorsal margin of seventh abdominal segment distinctly shorter than ventral margin when viewed from the side (fig. 16). Posterior margin of seventh abdominal sternum with median, recurved process (fig. 17). China (Guangdong) .... *R. recurvus* sp. n.
– Dorsal margin of seventh abdominal segment almost as long as ventral margin when viewed from the side (figs. 6, 12, and 33). Seventh abdominal sternum at most with a median, pointed but not recurved process (fig. 14) 5
5. Posterior margin of seventh segment (figs. 34-35) without any projections. China (Guangdong, Guangxi) .... *R. edentatus* sp. n.
– Posterior margin of seventh segment with one or two pairs of lateral projections and one median, ventral process 6
6. Posterior margin of seventh segment (fig. 12) with a blunt, angular projection above laterad of which is a faint process (fig. 13). China (Guangdong) .... *R. abdominalis* sp. n.
– Posterior margin of seventh segment with one or

two pairs of prominent, lateral projections. Dorsal margin of segment usually furnished with a row of erect dark hairs 7

7. Posterior margin of seventh segment (fig. 4) with one triangular projection above which is directed obliquely downward. First abdominal tergite swollen. Length 9.1-9.5 mm. Taiwan .... *R. takahashii* Esaki

– Posterior margin of seventh abdominal segment (figs. 6-7) with two projections: one short, triangular projection above laterad of which is a longer, postero-ventrally directed projection. First abdominal tergite with two, distinctly separated swellings. Length 8.0-9.3 mm. China (Neimenggu, Hebei, Hubei, Hunan, Tianjin), Korea .... *R. chinensis* Hungerford & Matsuda

8. Small species, length 7.0-7.6 mm. Posterior margin of seventh abdominal segment with two projections (figs. 18-19): one long, triangular projection above laterad of which is a short, pointed process. Burma, China (Yunnan), Thailand .... *R. malaisei* sp. n.

– Larger species, length 11-12.2 mm. Posterior end of abdomen not modified as before 9

9. Posterolateral corners of seventh abdominal segment (figs. 26-27) with two lobes; inner lobe narrow and pointed, outer lobe broad and rounded at tip. Length 12.2 mm. China (Zhejiang) .... *Rhyacobates lundbladi* Hungerford

– Posterolateral corners of seventh abdominal segment as above, but inner lobe very small (figs. 24-25) and outer lobe broad and obliquely cut off at tip. Length 11-12 mm. China (Fujian, Sichuan) .... *Rhyacobates svenhedini* Lundblad

10. Small species, length 6.0-7.2 mm 11

– Large species, length 7.5 mm or more 13

11. Middle and hind femora subequal in length. Proctiger with small, hook-shaped process on each side (fig. 21). Length 6.0-6.5 mm .... *R. malaisei* sp. n.

– Middle femur shorter than hind femur. Proctiger laterally widened (fig. 10), but without hook-shaped processes 12

12. Parameres rather broad in middle one-third, with apices more or less suddenly narrowed (fig. 9) .... *R. chinensis* Hungerford & Matsuda

– Parameres slender and falciform, with distinctly hook-shaped apices (as viewed from behind) .... *R. takahashii* Esaki & *R. abdominalis* sp. n.

13. Eighth segment distinctly impressed ventrally, with transverse ridge in basal part. Length 8.4 mm .... *R. svenhedini* (Lundblad)

– Eighth segment not modified ventrally as before 14

14. Length 7.5 mm .... *R. lundbladi* (Hungerford)

– Length 8.0-8.1 mm .... *R. scorpio* sp. n.

Rhyacobates takahashii Esaki
(figs. 2-5)

Rhyacobates takahashii Esaki, 1923: 388, pl. 1. Holotype female [not examined] from Taiwan, Sosan near Taihoku (ELKU); Esaki, 1925: 60; Matsuda, 1960: 273-276, figs. 656-658, 660, 663, 674-676, 678.

Material. – TAIWAN: 2♂ 2♀ (apterous), Formosa, Keishinryo, 15.iv.1965, leg. T. Saigusa (det. S. Miyamoto) (JTPC); 1♂ (apterous), Ural, Taipei, Taiwan, July 1957, leg. L.C. Chen (JTPC); 1♂ 1♀ (apterous), Taiwan, Shinten near Taihoku, 7.vi.1940, leg. S. Miyamoto (*R. takahashii*, det. Esaki) (USNM).

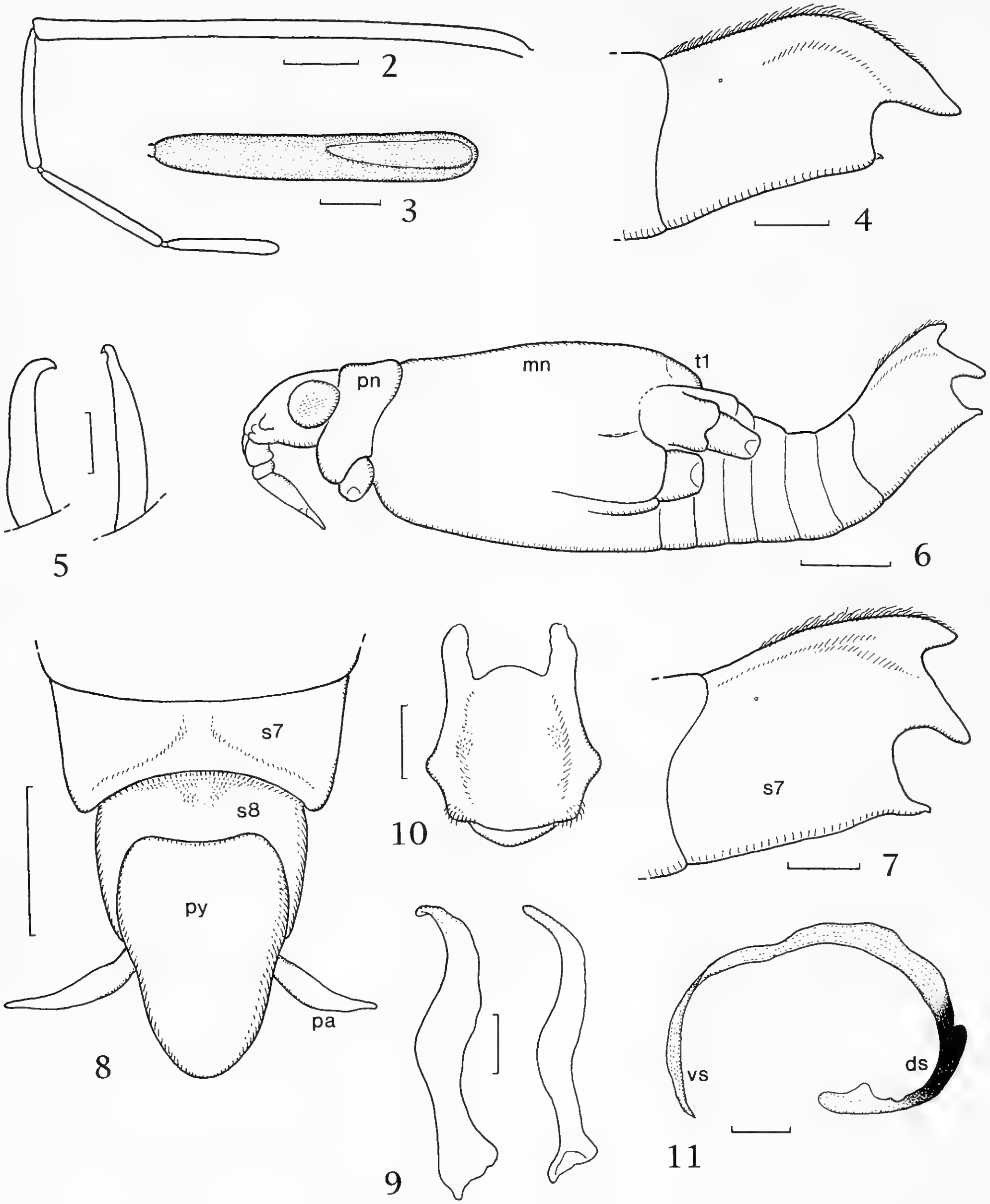
Descriptive notes. – The original description (Esaki, 1923) of the apterous male and female of *R. takahashii* is excellent and well illustrated, and leaves no doubt about the identity of this species. The length is given as 6.5 mm (male) and 9.5 mm (female). Matsuda (1960) offers useful illustrations of both sexes of this species including details of head, appendages, male genitalia, and female abdomen.

The apterous specimens examined by us have the following dimensions: length ♂ 6.8, ♀ 9.1; width of head ♂ 1.2 mm, ♀ 1.4; width of thorax ♂ 1.8, ♀ 2.6. Colour pattern as in generic description. Antennal segments 1-4 of male measure: 3.52 : 0.98 : 1.05 : 0.82. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 3.60 : 3.00 : 1.00 : 0.62; middle leg: 10.05 : c. 4.9 : c. 2.0 (segment 1+2); hind leg: 10.92 : c. 3.2 : 0.10 : 0.20.

Male genital segments have the following structure (Matsuda 1960: figs. 658, 674): eighth segment slightly impressed ventro-laterally; pygophore large, ovate; proctiger with small, angular projection on each side; parameres (fig. 5) slender and falciform, with distinctly hook-shaped apices (as viewed from behind). Miyamoto & Lee (1963: fig. 5) illustrated the vesical sclerites and Miyamoto (1967: fig. 58) the structure of the male endosomal conjunctivum.

Abdomen of apterous female curved upward towards the end. First abdominal tergite with a median, yellowish brown swelling. Connexiva reflected, margins of third to fifth segment almost meeting each other above the tergites. Seventh abdominal segment slightly longer than two preceding segments together ventrally; dorsal margin describing a regular curve when viewed from the side (fig. 4), furnished with dense, erect pubescence; posterior margin with a triangular projection above which is directed obliquely downward; median, ventral process small but sharp, continued as a low carina on seventh sternum.

Esaki (1925: 60, figs. 11-12) described and illustrated the macropterous form.



Figs. 2-11. – 2-5. *Rhyacobates takahashii,* 2 left antenna, 3 fourth antennal segment, ventral view, 4 abdominal end of female, lateral view, 5 left paramere of male, two different views. Scales 2, 4 0.5 mm, 3 0.2 mm, 5 0.1 mm. – 6-11. *Rhyacobates chinensis,* 6 female body, lateral view (mn mesonotum, pn pronotum, t1 first abdominal tergum), 7 abdominal end of female, lateral view (s7 seventh abdominal sternum), 8 abdominal end of male, ventral view (pa paramere, py pygophore, s7 seventh abdominal sternum, s8 eighth abdominal sternum), 9 left paramere of male, two different views, 10 proctiger of male, dorsal view, 11 vesical sclerites of male, lateral view (ds dorsal sclerite, vs ventral sclerite). Scales 6 1 mm, 7, 8 0.5 mm, 9, 11 0.1 mm, 10 0.2 mm.

Rhyacobates chinensis Hungerford & Matsuda (figs. 6-11)

Rhyacobates chinensis Hungerford & Matsuda, 1959: 69. Holotype [not examined] from China, Neimenggu [Inner Mongolia], Djalantun, Great Khingan Mts. (SEMK).

Rhyacobates esakii Miyamoto & Lee, 1963: 43. Holotype male [examined]: Korea (S), Nam Te Cheon (ELKU). **Syn. n.**

Rhyacobates takahashii Esaki; Esaki, 1940: 128 (Miyamoto & Lee, 1963: 43)

Material. – CHINA: Paratypes 1♂ 1♀ (apterous)(*R. chinensis),* Djalantun, Gr. Khingan, VI.38, Bot. from M. Weymarn (JTPC). – *Hebei:* 7♂ 31♀ (apterous), 1♀ (macropterous), Wu-Ling Shan (40.6N, 117.4E), VIII.29.1973, leg. Liu Shengli (NUC, ZMUC); 6♀ (apterous), same locality, VIII.1974 (NUC); *Hubei:* 1♀ (apterous), Shen-Nong-Jia Nat. Res., Song-Bai (31.7N, 110.6E), VII.17.1977, leg. Zou Huan-guang (NUC); *Hunan:* 6♂ 6♀ (apterous), Zhang-jia-jie Nat. Res. (29.1N, 110.4E), Jin-bian Stream, X.14.1985, leg. Zou Huan-guang (NUC); 1♂ (apterous), NW-Hunan, Bez. Dayong, Wulingvuan, Zhiangjiajie, Forest NP, Shuiraosinum, X.30.1993, 600 m, leg. H. Schönmann (NHMV); *Neimenggu* [Inner Mongolia]: 11♂ 10♀ (apterous), Xilin Gol Meng (43.9N, 116.0E), livestock breeding farm, VIII.1974, leg. Jiang Zhong-ming (NUC); *Tianjin:* 2♂ 3♀ (apterous), Ji County (40.0N, 117.3E), Xia-Ying Xiang, Chang-zhou Village, VII.29, 1985, leg. Liu (NUC). KOREA: Holotype ♂ (apterous) (*R. esakii*): Nam Te Cheon, Sam Bangcheon, Ham Nam, 31.vii.1937, leg. K. Doi (ELKU); 3♂ 3♀ (apterous), S. Korea, Seolak Mt., 8.9.1976, collector unknown (ex Lee coll.) (*R. chinensis,* det. P. Chen & J.T. Polhemus) (JTPC).

Description. – Apterous form: Dimensions. Length ♂ 6.4-6.8, ♀ 8.0-9.3; width of head ♂ 1.2-1.3 mm, ♀ 1.4-1.5; width of thorax ♂ 1.9-2.1, ♀ 2.8-3.2.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite in female. Connexival margin brownish in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative lengths of antennal segments (1-4): 3.50 : 0.93 : 0.98 : 0.83. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.50 : 3.00 : 0.90 : 0.56; middle leg: 10.30 : 5.80 : c. 3.5 (1st + 2nd tarsal segment); hind leg: 11.20 : c. 3.6 : 0.11 : 0.21. Eighth segment ventro-laterally impressed (fig. 8); pygophore large, ovate; proctiger (fig. 10) with a small angular projection on each side. Parameres (fig. 9) rather broad in middle one-third, with apices more or less suddenly narrowed. Phallic conjunctivum with two pairs of lobes, of which the anterior one is sclerotized on dorsal wall; dorsal sclerite of vesica partly sclerotised (fig. 11), with a hook-shaped distal part; ventral sclerite short and elongate leaf-like (see also Miyamoto & Lee, 1963: 44 and fig. 2).

Female robust. Relative lengths of antennal segments (1-4): 4.50: 1.15 : 1.20 : 0.93. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 4.40 : 3.80 : 1.75 : 0.93; middle leg: 12.30 : 7.20 : c. 3.9 (1st + 2nd tarsal segment); hind leg: 13.00 : c. 5.0 : 0.16 : 0.24. Abdomen relatively short, with distal half distinctly curved upward to oblique (fig. 6) or nearly vertical position. First abdominal tergite swollen and with a pair of prominent, widely spaced tubercles. Connexiva erect on first two segments, converging along dorsal midline of third through sixth segments. Tube-like seventh abdominal segment (fig. 7) as long as three preceding segments together ventrally; dorsal margin describing a regular curve; posterior margin with a short, triangular projection above terminating each connexivum, laterad of which is a longer, postero-ventrally directed projection; median, ventral process slender and sharp, sometimes continued as a low, longitudinal carina on ventral surface of seventh sternum.

Comparative notes. – Miyamoto & Lee (1963) described *Rhyacobates esakii* from Korea, seemingly without knowing *R. chinensis* Hungerford & Matsuda (1959) described from Neimenggu, China. A comparison between a pair of paratypes of the former species and the holotype male and a topotypical female of the latter species, lead us to the conclusion that they are conspecific. *R. chinensis* can be separated from *R. takahashii* by the slightly larger size, paired swellings of the first abdominal tergite of female, more distinctly curved female abdomen, and especially by having five instead of three apical projections on the seventh abdominal segment of the female. The parameres of *R. chinensis* males are more robust and less curved, and the structure of the vesical sclerites is different (see Miyamoto & Lee, 1963: figs. 2 and 5). While males of *R. chinensis* are rather uniform in structure throughout the geographical range of the species, the shape and relative size of the apical projections of the female abdomen seem to be quite variable although characteristic of the species.

So far, *R. chinensis* has been recorded from Neimenggu Province [Inner Mongolia] (Hungerford & Matsuda, 1959), Hebei, Hubei, and Hunan Provinces, China, and from North, central and South Korea (Miyamoto & Lee, 1963). The records by Esaki (1940) of *R. takahashii* from Kullin, Kiangsi [Jiangxi] and Jehol, Manchuria [Heilongjiang], both localities in China, and from Korea, probably refer to *R. chinensis.*

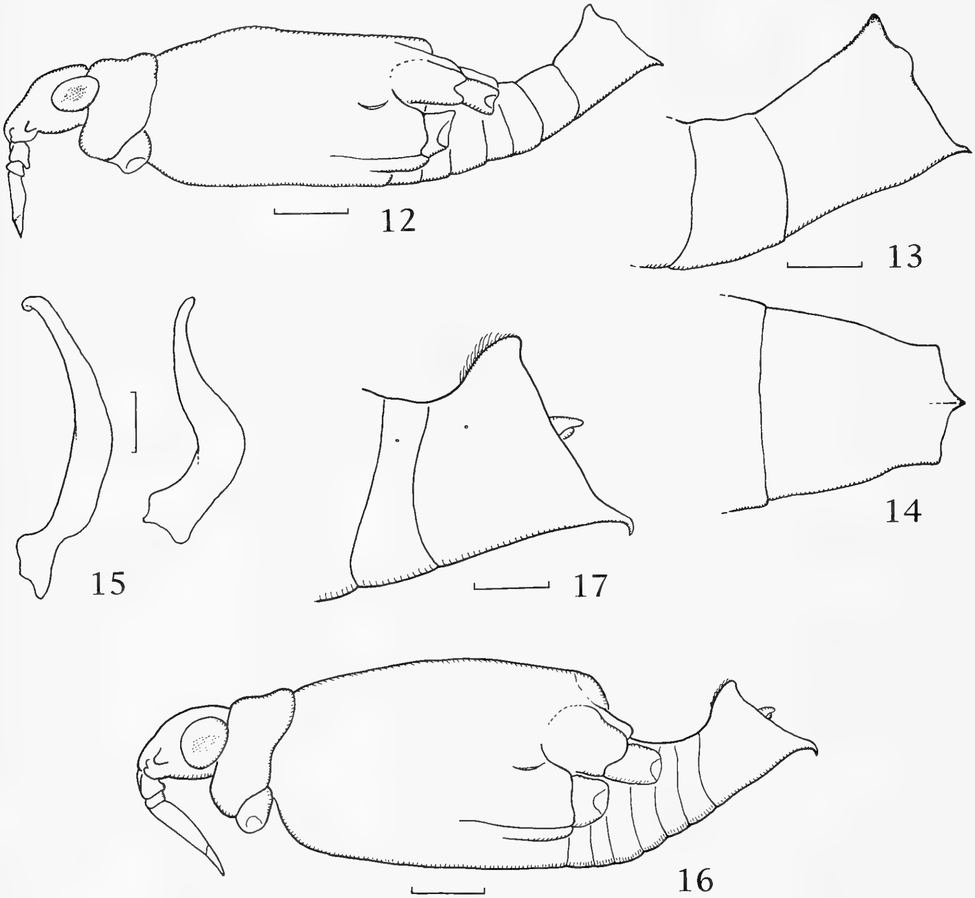
Rhyacobates abdominalis sp. n.
(figs. 12-15)

Type material. – CHINA: Holotype ♀ (apterous): Guangdong Province, Ruyang Nat. Res., Lao-Peng Stream, 1100 m, VIII.14. 1990, leg. P.P. Chen, C9012 (NUC). – Paratypes 9♂ 8♀ (apterous), same label data as above (NC, NHMV, NUC, ZMUC).

Description. – Apterous form. Dimensions. Length ♂ 6.2-6.8, ♀ 8.6-9.3; width of head ♂ 1.2-1.3, ♀ 1.47-1.52; width of thorax 1.9-2.2, ♀ 3.1-3.3.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown to blackish. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite in female. Connexival margin brownish yellow in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative length of antennal segments (1-4): 3.15 : 0.89 : 1.05 : 0.84. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.37: 2.64 : 0.95 : 0.62; middle leg: 9.20 : 5.20 : c. 3.0 (1st + 2nd tarsal segment); hind leg: 8.98 : c. 3.84 : 0.12 : 0.18. Eighth segment ventro-laterally impressed; pygophore large, ovate; proctiger with a small angular projection on each side. Parameres (fig. 15) relatively slender, broad on basal 2/5, tapering towards hook-shaped apices.



Figs. 12-17. – 12-15. *Rhyacobates abdominalis,* 12 female body, lateral view, 13 abdominal end of female, lateral view, 14 abdominal end of female, ventral view, 15 left paramere of male, two different views. Scales 12 1 mm, 13–14 0.5 mm, 15 0.1 mm. – 16-17. *Rhyacobates recurvus,* 16 female body, lateral view, 17 abdominal end of female, lateral view. Scales 16 1 mm, 17 0.5 mm.

Female robust. Relative length of antennal segments (1-4): 4.06 : 1.10 : 1.31 : 0.96. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 4.24 : 3.51 : 1.95 : 0.91; middle leg: 12.55 : 7.09 : c. 4.23 (1st + 2nd tarsal segment); hind leg: 12.38 : c. 6.1 : 0.14 : 0.18. Abdomen relatively short, with distal half distinctly curved upward to oblique position (fig. 12). First abdominal tergite slightly swollen. Connexiva erect, only converging distally along mid-line of seventh segment, or never converging. Tube-like seventh abdominal segment (fig. 13) ventrally as long as two preceding segments together; dorsal margin describing a regular curve; posterior margin with a short, angular projection above terminating each connexivum, laterad of which is a blunt projection; median ventral process (fig. 14) slender and sharp, sometimes continued as a low, longitudinal carina on ventral surface of seventh sternum.

Etymology. – *abdominalis* refers to the structure of the female abdomen.

Comparative notes. – Females of *R. abdominalis* sp. n. share the distinctly curved abdomen with the two preceding species, but the projection terminating each connexivum is much shorter. The median process of seventh sternum is slender and sharp, but not recurved as in the following species.

Rhyacobates recurvus sp. n.
(figs. 16-17)

Type material. – CHINA: Holotype ♀ (apterous): Lushan [Lu Shan in Jiangxi Province], 9.VIII.30, leg. Chenfu Wu (BMNH).

Description. – Apterous form. Dimensions. Length ♀ 7.7; width of head ♀ 1.4; width of thorax ♀ 2.7.

Colour as in generic description. Head with one large, median spot and two smaller, posterior black spots. Antennae dark brown to blackish. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite in female. Connexival margin brownish yellow in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Female stout. Relative lengths of antennal segments (1-4): 3.70 : 1.10 : 1.22 : 0.88. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 4.18 : 3.35 : 1.48 : 0.88; middle leg: 11.50 : ? : ? : ?; hind leg: 12.12 : c. 4.0 : ? : ?. Abdomen very short, with distal half distinctly curved upward to oblique or nearly vertical position (fig. 16). First abdominal tergite slightly swollen. Connexiva erect on first two segments, converging along dorsal mid-line of third through sixth segments, reflexed above abdominal tergites. Tube-like seventh abdominal segment (fig. 17) longer than three preceding segments together ventrally; dorsal margin distinctly shortened; posterior margin angular above, almost straight below, ventrally produced into a median, hook-shaped process.

Male unknown.

Etymology. – *recurvus* refers to the recurved median process of the female seventh abdominal sternum.

Comparative notes. – The short, distinctly curved abdomen and recurved median process of seventh sternum separates the female of *R. recurvus* sp. n. from those of other *Rhyacobates* species known to us.

Rhyacobates malaisei sp. n.
(figs. 18-23)

Type material. – BURMA: Holotype ♂ (apterous): N. Burma, Bumgahtuang-Hpungan, river, 17.III.1934, leg. R. Malaise (NHMS). – Paratypes 2♂ 4♀ (apterous), same label data as holotype (NHMS, ZMUC). THAILAND: 4♂ 3♀ (apterous), Chiang Mai Prov., Nam Chai R. above hydro station intake at Fang Hort. Stat, CL 2197, 15.xi.1985, leg. J.T. & D.A. Polhemus (JTPC). CHINA: 2♂♂ (apterous), Yunnan, 100 km W Kunming, Diaolin Nat. Res. V.22-VI.6.1993, leg. E. Jendek & O. Sousa (NHMV).

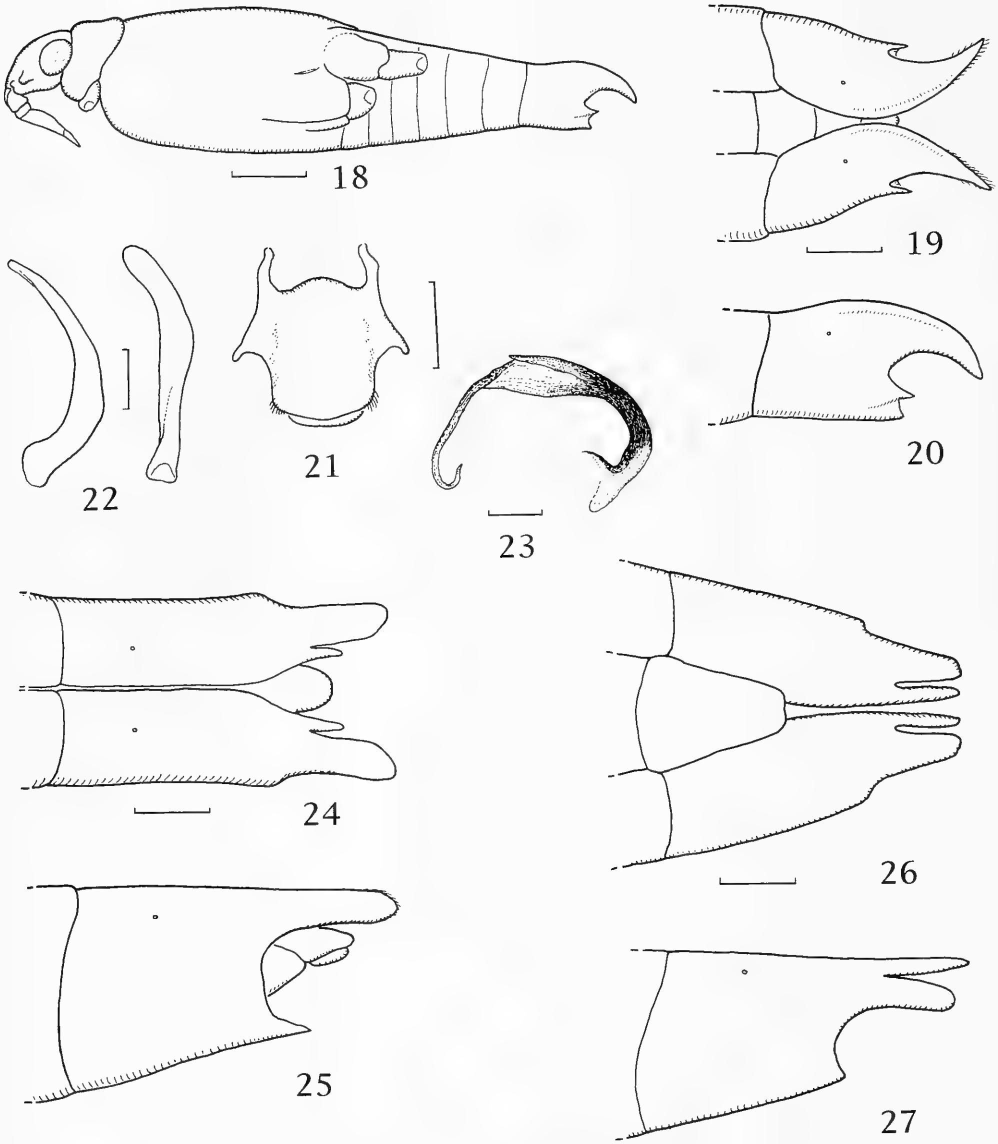
Description. – Apterous form. Dimensions. Length ♂ 6.0-6.5, ♀ 7.0-7.6; width of head ♂ 1.1-1.2, ♀ 1.1-1.2; width of thorax ♂ 1.7-1.9, ♀ 2.1-2.3.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with a broad, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum does not extend onto metanotum and first abdominal tergite. Connexival margin chiefly blackish, connexival processes of female light brownish. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative lengths of antennal segments (1-4): 2.70 : 0.78 : 1.05 : 0.75. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 2.90 : 2.28 : 0.75 : 0.48; middle leg: 8.60 : 4.45 : 1.85 : 0.35; hind leg: 8.82 : 2.10 : 0.10 : 0.18. Eighth segment ventro-laterally impressed; pygophore large, ovate; proctiger widened (fig. 21), with a small hook-shaped projection on each side.

Parameres (fig. 22) rather broad, almost spatulate, in distal part. Armature of phallic vesica as illustrated (fig. 23).

Female elongate. Relative lengths of antennal segments (1-4): 2.85 : 0.70 : 0.92 : 0.75. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 2.80 : 2.30 : 1.10 : 0.72; middle leg: 8.20 : 4.65 : 1.92 : 0.28; hind leg: 8.10 :



Figs. 18-27. – 18-23. *Rhyacobates malaisei,* 18 female body, lateral view, 19 abdominal end of female, dorsal view, 20 abdominal end of female, lateral view, 21 proctiger of male, dorsal view, 22 left paramere of male, two different views, 23 vesical sclerites of male, lateral view. Scales 18 1 mm, 19, 20 0.5 mm, 21, 23 0.1 mm, 22 0.2 mm. – 24-25. *Rhyacobates svenhedini,* 24 abdominal end of female, dorsal view, 25 abdominal end of female, lateral view. Scale 24, 25 0.5 mm. mm. – 26-27. *Rhyacobates lundbladi,* 26 abdominal end of female, dorsal view, 27 abdominal end of female, lateral view. Scale 26, 27 0.5 mm.

2.18 : 0.12 : 0.15. Abdomen relatively long, almost straight in lateral view (fig. 18). First abdominal tergite not modified. Connexiva erect on first segment, reflexed upon abdominal tergites, running parallel to each other for most of the abdominal length, meeting each other towards the end. Tube-like seventh abdominal segment shorter than two preceding segments together ventrally; dorsal margin describing a regular curve (fig. 20); posterior margin (fig. 19) with a long, triangular projection above terminating each connexivum, laterad of which is a small, pointed process; hind margin of seventh sternum straight, without median process.

Etymology. – Named for the Swedish entomologist René Malaise, the collector of the type series from northern Burma.

Comparative notes. – This is the first *Rhyacobates* species known from outside China and Korea (the status of '*Rhyacobates*' *imadatei* Miyamoto from Borneo and Thailand is discussed below). Apterous females of *R. malaisei* sp. n. can be separated from other species by their nearly straight abdomen and very characteristic structure of the abdominal end. The shape of the male proctiger and parameres is also unique.

Rhyacobates svenhedini (Lundblad)
(figs. 24-25)

Esakobates svenhedini Lundblad, 1934: 23-25, fig. 10, plate 2. Holotype male [examined]: China, N.E. Szechuan [Sichuan] (NHMS).

Material. – CHINA: Holotype ♂ (apterous): Kina [China], N.O. Szechuan [Sichuan], Sven Hedin Exp. Ctr. Asien, leg. Dr. Hummel (NHMS). – Paratypes 1♂ 2♀ (apterous), same label data as holotype (NHMS, JTPC, ZMUC). – 1♀ (apterous), Fukien [Fujian], S. China, Kienow: Fengio, leg. T. Maa (JTPC); 3♀ (apterous), Ku-ling, Sichuan, collector unknown (ZIB).

Descriptive notes. – Lundblad (1934) gave excellent descriptions and illustrations of both the apterous male and female of *R. svenhedini*. He gives the length as about 9 mm (male) and 12 mm (female), but the apterous specimens examined by us have the following dimensions: length ♂ 7.5, ♀ 11.0; width of head ♂ 1.3, ♀ 1.6; width of thorax 2.2, 2.7. Colour pattern (see Lundblad 1934: plate 2, fig. 4) as in generic description except that the dark mark on the dorsal head surface is reduced, distinctly bifid or dissolved in smaller spots posteriorly (Lundblad 1934: fig. 10A). Antennal segments 1-4 of male measure: 4.46 : 1.18 : 1.22 : 0.97. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 4.60 : 3.78 : 1.25 : 0.67; middle leg: 12.85 : 6.42 : 2.71 : 0.46; hind leg: 12.64 : 3.38 : 0.12 : 0.19.

Male genital segments have the following structure: eighth segment slightly impressed ventro-laterally; pygophore large, ovate; proctiger slightly expanded on each side; parameres slender and falciform (Lundblad 1934: figs. 10H-I), with hook-shaped apices (as viewed from behind).

Abdomen of apterous female relatively long, moderately curved upward towards the end. First abdominal tergite not swollen. Connexiva reflected with margins converging posteriorly as in the female illustrated by Lundblad (1934: plate 2, fig. 4) or the connexiva are meeting each other above the tergites. Seventh abdominal segment shorter than two preceding segments together ventrally; dorsal margin only moderately curved when viewed from the side (fig. 25); posterolateral corners of each connexivum (fig. 24) usually produced into two lobes: one long, posteriorly directed outer lobe and a much smaller, pointed inner lobe (lacking in one paratype); posterior margin of seventh sternum angularly produced in middle, but without a median tooth.

Comparative notes. – When describing *Esakobates svenhedini*, Lundblad (1934) compared it with *Rhyacobates takahashii* Esaki (1923). The structure of the female abdomen, however, are quite different in the two species. *R. svenhedini* seems to be closest to the *R. lundbladi* Hungerford but separated by the shape and size of the lobes arising from the posterolateral corners of each connexivum (compare figs. 25 and 27).

Rhyacobates lundbladi (Hungerford)
(figs. 26-27)

Esakobates lundbladi Hungerford, 1957: 33-36, pls 1-2. Holotype male [not examined]: China, Zhekiang, Tien um Shan (SEMK).

Rhyacobates lundbladi (Hungerford); Matsuda, 1960: 274-276, figs. 659, 661, 671, 672, 677, 679, 680.

Type material. – CHINA: Paratype 1♂ (dealated macropterous), Tien um Shan, China, 9.21.37, leg. E. Suenson (JTPC).

Descriptive notes. – The original description of *R. lundbladi* Hungerford (1957) is excellent and well illustrated and leaves no doubt about the identity of this species. The type series is only composed of macropterous, although dealated, males and females, which makes it difficult to compare with other *Rhyacobates* species which usually are known only in the apterous adult form. Matsuda (1960) offers useful illustrations of structural details of head, female abdomen and ovipositor, and male terminalia. Hungerford (1957) gives the following dimensions of the apterous form: length ♂ 8.4, ♀ 12.2; width across pronotum ♂ 2.6, ♀ 2.64. Colour as in generic description except as follows for the pronotum of the macropterous form (Hungerford, 1957: plate 1); pronotum black, margined on the sides and rear with yellowish brown, a large triangular or nearly round yellowish brown spot on anterior part of pronotum with a median line of same colour on pronotal lobe which may surpass humeri. Antennal segments 1-4 of male measure: 4.30 : 1.10 : 1.32 : 1.00. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment): fore leg: 4.40 : 3.52 : 1.32 : 0.84; middle leg: 12.25 : 6.30 : 2.42 : 0.46; hind leg: 12.36 : c. 4.3 : 0.13 : 0.22.

The male genital segments have the following structure (Hungerford, 1957: plate 2; Matsuda, 1960: figs. 672, 679): eighth segment distinctly impressed ventrally, with transverse ridge basally; pygophore large, ovate; proctiger slightly expanded on each side; parameres slender and falciform, with faintly hook-shaped apices.

Abdomen of apterous female relatively long, only slightly curved upward towards the end. First abdominal tergite not swollen. Connexiva more or less vertical but on last segment reflected and meeting each other above the seventh tergite. Seventh abdominal segment shorter than two preceding segments together ventrally; dorsal margin almost straight when viewed from the side (fig. 27); posterolateral corners of each connexivum (fig. 26) produced into two, posteriorly directed lobes: outer lobe broad and rounded at tip; inner lobe narrow and pointed; posterior margin of seventh sternum only slightly produced in middle.

Comparative notes. – Hungerford (1957) placed this species in Lundblad's genus *Esakobates* together with *E. svenhedini* (see above), but later (Hungerford & Matsuda, 1959) synonymized this genus with *Rhyacobates*. The relatively long and moderately curved female abdomen unites *R. lundbladi* and *svenhedini*, but the relative size and shape of the connexival lobes is quite different in the two species (compare figs. 25 and 27). The ventral modifications of the eighth abdominal segment may be helpful in distinguishing the males.

Rhyacobates scorpio sp. n.

(figs. 1, 28-32)

Type material. – CHINA: Holotype ♀ (apterous): Szechuan [Sichuan], Song Ch'i, Kuanhsien, 3500-5000', August 1938, leg. D.C. Graham (USNM). – Paratypes 1♂ 6♀ (apterous), same label data as holotype (JTPC, USNM, ZMUC); 3♂ 6♀ (apterous), Song Ch'i Hsien, July 1938, leg. D.C. Graham (JTPC, USNM); 3♂ 4♀ (apterous), 1 nymph, Wen Chuan, 4000-6000', August 1938, leg. D.C. Graham (USNM); 4♂ 5♀ (apterous), Ku-ling, collector unknown (ZIB); 5♂ 3♀ (apterous), 1 nymph., Mt. Emei (29.5N, 103.3E), Jie-Yin Temple, VII.14, 1957, leg. Zheng Le-yi (NUC, ZMUC).

Description. – Apterous form. Dimensions. Length ♂ 8.0-8.1, ♀ 9.7-9.9; width of head ♂ 1.5, ♀ 1.6-1.7; width of thorax ♂ 2.6-2.7, ♀ 3.4-3.5.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with an elongate triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite of female. Connexival margins brownish yellow in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male rather stout with relatively short abdomen. Relative lengths of antennal segments (1-4): 4.60 : 1.45 : 1.55 : 1.15. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 4.90 : 4.20 : 1.40 : 0.90; middle leg: 12.95 : c. 7.5 : c. 3.0 : 0.52; hind leg: 13.50 : c. 5.5 : 0.18 : 0.25. Eighth segment ventro-laterally impressed; pygophore large, ovate; proctiger with a narrow, angular projection on each side. Parameres slender and falciform (fig. 31), with weakly hook-shaped apices (as viewed from behind). Armature of phallic vesica as illustrated (fig. 32).

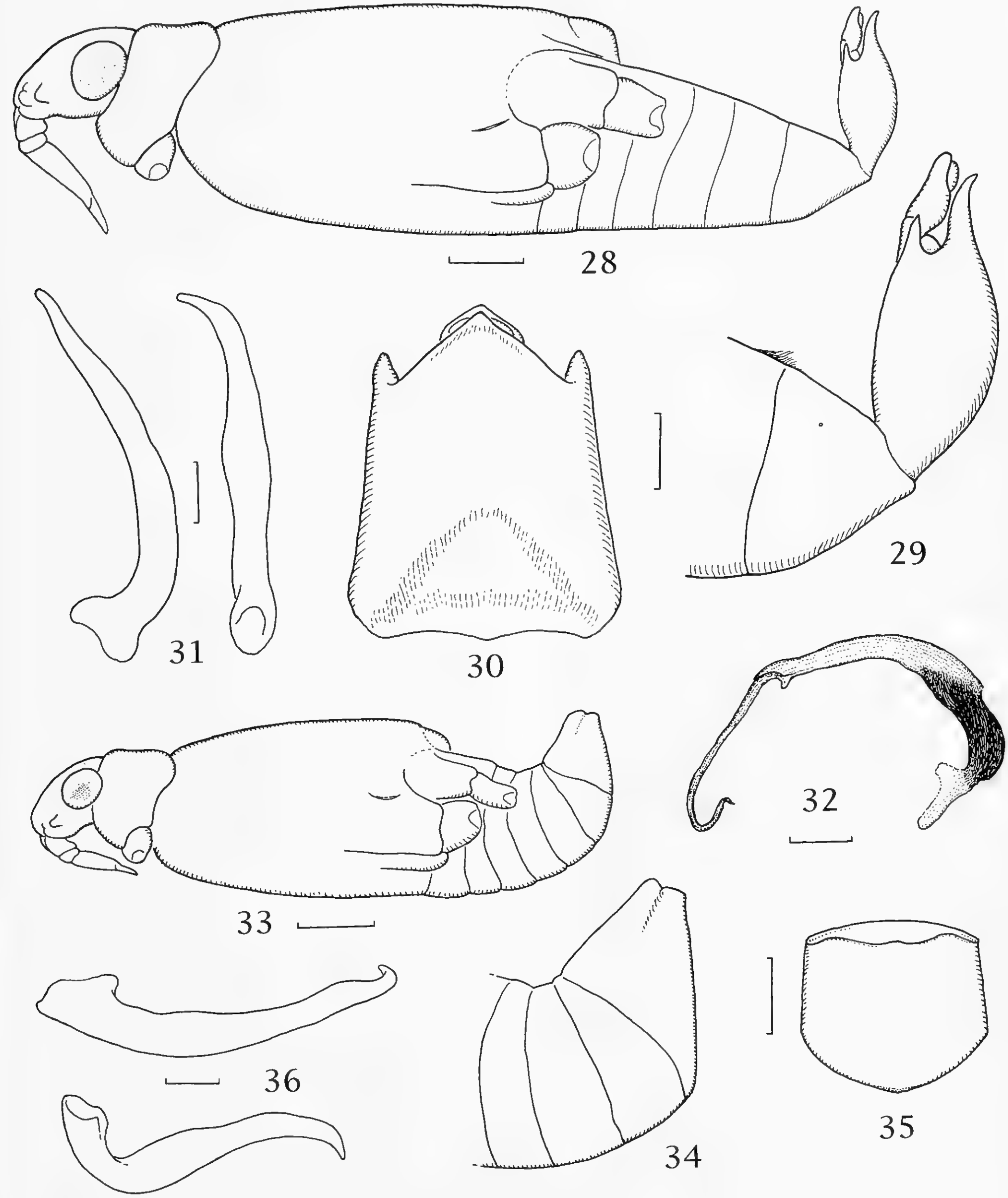
Female stout with relatively short abdomen. Relative lengths of antennal segments (1-4): 4.98 : 1.45 : 1.68 : ?. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 5.12 : 4.30 : 2.28 : 1.15; middle leg: 13.90 : 8.52 : 4.72 : 0.58; hind leg: 14.42 : 5.30 : 0.20 : 0.28. Abdomen relatively short, curiously bent upwards towards end (fig. 28). First abdominal tergite distinctly swollen. Connexiva narrow, erect on first to sixth segment, reflexed upon seventh tergite. Sixth sternum depressed medially toward posterior margin. Seventh abdominal segment (fig. 29) dorso-ventrally flattened, about as long as two preceding segments together, bent upwards at a right angle to the preceding abdominal segments (fig. 28); posterior margin (fig. 30) with a short, pointed process terminating each connexivum; hind margin of seventh sternum distinctly produced in middle.

Etymology. – *scorpio* refers to the peculiar, upturned abdominal end of the female, resembling the way a scorpion carries its tail.

Comparative notes. – Females of *R. scorpio* sp. n. are immediately recognized by the very characteristic shape of the abdomen. Males can be separated from those of other *Rhyacobates* species by their larger size and slender parameres.

Rhyacobates edentatus sp. n.
(figs. 33-36)

Type material. – CHINA: Holotype ♀ (apterous): Guangdong Province, Lian County (24.7N, 112.3E), Yao-An Xiang, X.28.1962, leg. Zheng Le-yi & Cheng Han-hua



Figs. 28-36. – 28-32. *Rhyacobates scorpio,* 28 female body, lateral view, 29 abdominal end of female, lateral view, 30 abdominal end of female, ventral view, 31 left paramere of male, two different views, 32 vesical sclerites of male, lateral view. Scales 28 1 mm, 29, 30 0.5 mm, 31, 32 0.1 mm. – 33-36. *Rhyacobates edentatus,* 33 female body, lateral view, 34 abdominal end of female, lateral view, 35 abdominal end of female, ventral view, 36 left paramere of male, two different views. Scales 33 1 mm,

(NUC). – Paratypes 5♂ 3♀ (apterous), 1♂ (macropterous), 1 nymph, same label data as holotype (NUC, ZMUC); 1♀ (apterous), Guangxi, Bez. Lipu, 120 km S Guilin, 80 km E Liuzhou, Siuren, XI.12.1993, 360 m, leg. H. Schillhammer (NHMV).

Description. – Apterous form. Dimensions. Length ♂ 6.0-6.6, ♀ 7.6-8.0; width of head ♂ 1.2-1.3, ♀ 1.5; width of thorax ♂ 1.7-1.8, ♀ 3.0-3.1.

Colour as in generic description. Median black spot of head posteriorly bifurcated. Antennae dark brown. Pronotum with a large, triangular brownish yellow spot in middle. Median, brownish yellow stripe of mesonotum extends onto metanotum and first abdominal tergite in female. Connexival margin brownish in female. Prosternum, legs and distal parts of acetabula light brown. Mesosternum chiefly dark with a median subtriangular, yellowish spot.

Male elongate with relatively short abdomen. Relative lengths of antennal segments (1-4): 3.00 : 0.77 : 0.93 : 0.65. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.18 : 2.63 : 0.95 : 0.53; middle leg: 9.05 : 4.58 : c. 2.3 (1st + 2nd tarsal segment); hind leg: 9.08 : c. 2.93 : 0.10 : 0.15. Eighth segment ventro-laterally impressed; pygophore large, ovate; proctiger with a small angular projection on each side. Parameres (fig. 36) slender with broader base; apices hook-shaped.

Female robust. Relative lengths of antennal segments (1-4): 3.70 : 1.00 : 1.20 : 0.90. Relative lengths of leg segments (femur: tibia: first tarsal segment: second tarsal segment); fore leg: 3.86 : 3.16 : 1.90 : 0.90; middle leg: 13.05 : 6.10 : c. 2.50 (1st + 2nd tarsal segment); hind leg: 13.3 : c. 4.40 : 0.14 : 0.18. Abdomen relatively short, with distal half distinctly curved upward to oblique or nearly vertical position (fig. 33). First abdominal tergite not swollen. Connexiva erect on first two segments, converging along dorsal midline of third through sixth segments. Seventh abdominal sternum (fig. 35) half as long as three preceding sterna together; dorsal margin straight, posterior margin slightly arched, without any projections or processes (fig. 34).

Etymology. – *edentatus* refers to the absence of any projections or processes on the female abdominal end.

Comparative notes. – The female abdomen of *R. edentatus* is relatively short and wide and the seventh abdominal segment is lacking any of the projections or processes found in most of the other *Rhyacobates* species

Classification of *Rhyacobates imadatei* Miyamoto

Miyamoto (1967: 238-241) described *Rhyacobates imadatei* from Brunei (N. Borneo) and northern Thailand. Through the courtesy of Drs S. Miyamoto and O. Tadauchi (ELKU), we have been able to examine the holotype ♂ and allotype ♀ (both apterous) labelled 'Amo, Brunei, 24.ii.1962, leg. G. Imadaté'. The following brief description will serve to clarify the taxonomic position of this species.

Dimensions. Length ♂ 6.7-7.2, ♀ 9.5-10.0; width of head ♂ 1.8-1.2, ♀ 1.3-1.4; width of thorax ♂ 2.05-2.1, ♀ 2.8-3.0.

Colour. Head yellowish brown with median black markings. Pronotum black with large yellow marking in middle. Mesonotum all black.

Female bigger than male, not modified ventrally. Antenna with first segment much longer than the three following segments together; second segment distinctly shorter than third segment; fourth segment curved, with elongate, impressed whitish area in distal two thirds. Middle femur of male with distinct row of dark spines along ventral margin. Middle and hind legs with small but distinct claws. Eighth abdominal segment of male shorter than seventh sternum; pygophore prolonged, narrowed posteriorly; proctiger widened with angular lateral projections. Parameres long and slender but not conspicuously setose. Female abdomen relatively long. Seventh segment prolonged but not enclosing genital segments; connexival corners with a short spinose process. Seventh sternum flattened but otherwise simple, without median lobe or process.

The completely dark mesonotum, the distinct row of dark spines ventrally on middle femur of male, and the distinct claws on middle and hind tarsus, excludes *R. imadatei* from the genus *Rhyacobates* as defined here. However, the classification of '*Rhyacobates*' *imadatei* Miyamoto cannot be settled until the generic taxonomy of the Ptilomerinae has been further clarified.

PHYLOGENY

A cladistic analysis of phylogenetic relationships between the species of *Rhyacobates* was performed using the parsimony program Hennig86 (Farris 1988). The species '*Rhyacobates*' *imadatei* (see above) and the genera *Heterobates* and *Pleciobates* were also included as well as a hypothetical 'ancestor' composed of character states common in other ptilomerine gerrids (Matsuda 1960; Andersen 1982).

The following characters and character states were considered:

1. Colour of meso- and metanotum: uniformly dark (0), dark with median pale stripe (1).

2. Relative length of first antennal segment: subequal to or shorter than three distal segments together

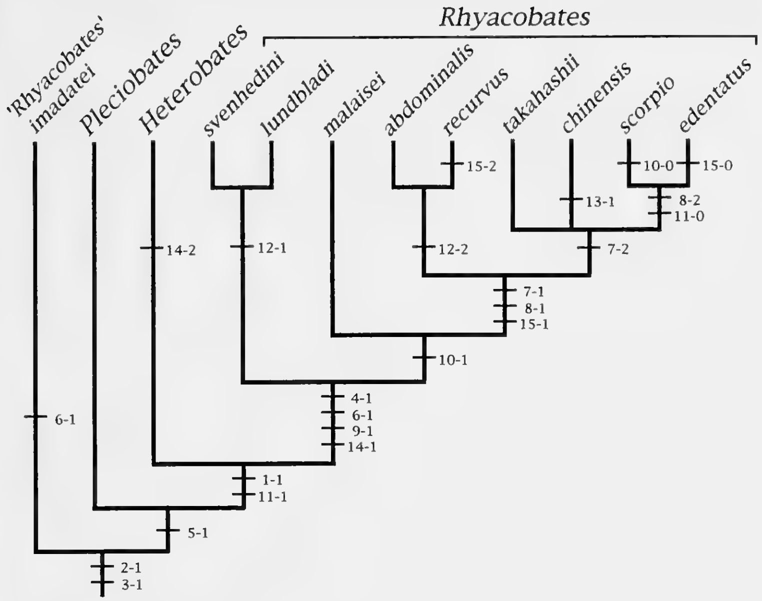


Fig. 37. Cladogram showing phylogenetic relationships between the species of *Rhyacobates,* the genera *Heterobates* and *Pleciobates,* and '*Rhyacobates*' *imadatei.* Numbers on internodes refer to apomorphic character states. See text for further explanations.

(0), much longer than the three distal segments together (1).

3. Ventral surface of fourth antennal segment: with an elongate ovate, impressed whitish area in distal two fifths to one half (1), impressed area shorter than before (0).

4. Ventral row of dark spines on middle femur of male: present (0), absent (1).

5. Middle and hind tarsal claws: present (0), absent (1).

6. Ventral length of eighth abdominal segment of male: longer than seventh sternum (0), shorter than seventh sternum (1).

7. First abdominal tergite of apterous female: not modified (0), slightly swollen (1), distinctly swollen (2).

8. Shape of dorsal abdomen of apterous female (lateral view): almost straight (0), distinctly curved dorsad towards apex (1), abruptly turned dorsad to nearly vertical position towards apex (2).

9. Abdominal laterotergites (connexiva) of apterous female: almost parallel throughout (0), reflexed and converging towards each other along dorsal midline (1).

10. Seventh abdominal segment of female: prolonged, longer than fifth and sixth sterna together, almost completely enclosing the genital segments (1), shorter, at least distal parts of genital segments visible (0).

11. Posterior margin of seventh abdominal segment of female: not modified or at most with a small process (0), modified, with angular projections (1).

12. Posterior margin of seventh abdominal segment of female (if modified): with one large, angular projection (0), with one small and one large projection (1), with one small, angular projection (0).

13. Posterolateral margin of seventh abdominal segment of female: simple or slightly produced (0), with triangular process (1).

14. Posterior margin of seventh abdominal sternum of female: simple, straight (0), angularly produced in middle (1), with square median lobe (2).

15. Posterior margin of seventh abdominal sternum of female (if angularly produced): simple (0); pointed (1), pointed and recurved (2).

The character state matrix is shown in Table 1. The states of all characters were coded as additively (ordered) except for the characters 8, 12, and 14 where the states were coded as non-additively (unordered).

Using the hypothetical 'ancestor' as outgroup, the Hennig86-analysis found only one most parsimonious tree, 25 steps long (Consistency Index = 0.80 and Retention Index = 0.86). This tree (or cladogram) is shown in fig. 37 with synapomorphies (given as character number and state) inserted on the internodes. The cladogram supports the monophyly of the genus *Rhyacobates,* excluding '*Rhyacobates*' *imadatei.* Four monophyletic species-groups are delimited in *Rhyacobates:* (1) *svenhedini* + *lundbladi,* (2) *malaisei,* (3) *abdominalis* + *recurvus,* and (4) *takahashii* + *chinensis* + *scorpio* + *edentatus.* Finally, the genus *Heterobates* is placed as the sister-group of

Table 1. Character state matrix for the species of *Rhyacobates*, '*Rhyacobates*' *imadatei*, the genera *Heterobates* and *Pleciobates*, and a hypothetical 'ancestor'. ? = missing observation, - = character not applicable. Further explanation in text.

Taxon	Character no				5					10					15
Rhyacobates															
takahashii	1	1	1	1	1	1	2	1	1	1	1	0	0	1	1
chinensis	1	1	1	1	1	1	2	1	1	1	1	0	1	1	1
abdominalis	1	1	1	1	1	1	1	1	1	1	1	2	0	1	1
recurvus	1	1	1	?	1	?	1	1	1	1	1	2	0	1	2
malaisei	1	1	1	1	1	1	0	0	1	1	1	0	0	1	0
svenhedini	1	1	1	1	1	1	0	0	1	0	1	1	0	1	0
lundbladi	1	1	1	1	1	1	?	?	?	0	1	1	0	1	0
scorpio	1	1	1	1	1	1	2	2	1	0	0	–	0	1	1
edentatus	1	1	1	1	1	1	2	2	1	1	0	–	0	1	0
R. imadatei	0	1	1	0	0	1	0	0	0	0	0	–	0	0	–
Pleciobates	0	1	1	0	1	0	0	0	0	0	0	–	0	0	–
Heterobates	1	1	1	0	1	0	0	0	0	0	1	0	0	2	–
Ancestor	0	0	0	0	0	0	0	0	0	0	0	–	0	0	–

Rhyacobates. It must be emphasized, however, that the relationships between *Rhyacobates* and other ptilomerine genera depicted in fig. 37 are preliminary, awaiting a more comprehensive cladistic analysis of the genera of Ptilomerinae.

As here defined, *Rhaycobates* has a predominantly East Asian distribution with one species (*R. malaisei* sp. n.) found in the border region between SE China, Burma, and Thailand. Until a more comprehensive cladistic analysis of the genera of Ptilomerinae is available, speculations about the historical biogeography of *Rhyacobates* and its allies are premature.

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We are grateful to Liang Aiping, Beijing (ZIB); Le-yi Zheng, Tianjin (NUC); John T. Polhemus, Englewood, Colorado (JTPC); the late Peter D. Ashlock, Lawrence, Kansas (SEMK); M.D. Webb, London (BMNH); R.C. Froeschner, Washington, D.C. (USNM); Per Lindskog, Stockholm (NHMS); Herbert Zettel, Vienna (NHMV); and S. Miyamoto and O. Tadauchi, Fukuoka, Japan (ELKU) for making types and other material available for study. We also thanks Dan A. Polhemus, Honolulu, for offering useful comments on an earlier version of the manuscript.

References

Andersen, N.M., 1982. The Semiaquatic Bugs (Hemiptera, Gerromorpha). Phylogeny, adaptations, biogeography, and classification. – Entomonograph 3: 1-455.

Cheng, L. & C.H. Fernando, 1969. A taxonomic study of the Malayan Gerridae (Hemiptera: Heteroptera) with notes on their biology and distribution. – Oriental Insects 3: 97-160.

Esaki, T., 1923. An interesting new water strider from Formosa. – Philippine Journal of Science 22(4): 387-391.

Esaki, T., 1925. New or little-known water striders from the Oriental region. Philippine Journal of Science 26(1): 57-65.

Esaki, T., 1927. Revision of the *Ptilomera*-group of the Gerridae, with descriptions of three new species (Heteroptera). – Eos 3: 251-268.

Esaki, T., 1930. New or little-known Gerridae from the Malay Peninsula. – Journal of the Federated Malay States Museum 16: 13-24.

Esaki, T., 1940. Some aquatic and semiaquatic Heteroptera from China. – Notes d'Entomologie Chinoise 7: 123-130.

Farris, J.S., 1988. Hennig86, version 1.5. Program and documentation. – J.S. Farris, Port Jefferson Station, New York.

Hungerford, H.B., 1951. An interesting new gerrid from Madagascar (Hemiptera). – Journal of Kansas Entomological Society 24: 131-133.

Hungerford, H.B., 1957. A new Gerrid from China (Gerridae, Hemiptera). – Journal of Kansas Entomological Society 30: 33-36.

Hungerford, H.B. & R. Matsuda, 1958. Another new generic entity of the Gerridae. – Entomological News 69: 258-260.

Hungerford, H.B. & R. Matsuda, 1959. Synonymy of the genera *Rhyacobates* Esaki 1923 and *Esakobates* Lundblad 1934, and a description of a new species of *Rhyacobates* from China (Hemiptera: Gerridae). – Journal of Kansas Entomological Society 32: 69-72.

Hungerford, H.B. & R. Matsuda, 1960. Keys to subfamilies, tribes, genera and subgenera of the Gerridae of the World. – Kansas University Science Bulletin 41: 3-23.

Hungerford, H.B. & R. Matsuda, 1965. The genus *Ptilomera* Amyot and Serville (Gerridae: Hemiptera). – Kansas University Science Bulletin 45: 397-515.

Lundblad, O.M., 1934. Schwedisch-Chinesische Wissenschaftliche Expedition nach den Nordwestlichen Provinzen Chinas. – Arkiv för Zoologie 27A (14): 1-31, pls. 1-2.

Matsuda, R., 1960. Morphology, evolution and a classification of the Gerridae (Hemiptera-Heteroptera). – Kansas University Science Bulletin 41: 25-632.

Miyamoto, S., 1967. Gerridae of Thailand and North Borneo taken by the Joint Thai-Japanese Biological

Expedition 1961-62. – Nature and Life in Southeast Asia 5: 217-257.
Miyamoto, S. & C. Lee, 1963. Water striders of Korea (Hemiptera, Heteroptera). – Kontyû 31: 33-47.
Thirumalai, G., 1986. On Gerridae and Notonectidae (Heteroptera: Hemiptera: Insecta) from the Silent Valley, Kerala. – Records of the Zoological Survey of India 84: 9-33.
Zettel, H., 1994. Revision der Gattung *Potamometropsis* Lundblad (Insecta: HeteropteraL Gerridae). – Annalen des Naturhistorischen Museums Wien (B) 86: 75-98.

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NINE NEW SPECIES OF *PSEUDOVELIA* AND A NEW *XIPHOVELIA* (HETEROPTERA: VELIIDAE) FROM SULAWESI (INDONESIA) AND MINDANAO (PHILIPPINES)

Notes on Malesian aquatic and semiaquatic bugs (Heteroptera), V.

Nieser, N., 1995. Nine new species of *Pseudovelia* and a new *Xiphovelia* (Heteroptera: Veliidae) from Sulawesi (Indonesia) and Mindanao (Philippines). Notes on Malesian aquatic and semiaquatic bugs (Heteroptera) V. – Tijdschrift voor Entomologie 138: 69-87, figs. 1-58, table 1 [ISSN 0040-7496]. Published 15 June 1995.

Nine new species of *Pseudovelia* from Sulawesi (including the northern islands of Sangihe and Karakelong) and Mindanao are described: *P. aflia* sp. n., *P. afrofila* sp. n., *P. epimekta* sp. n., *P. koutali* sp. n., *P. mystax* sp. n. and *P. pyrokrene* from Sulawesi; *P. sangihe* sp. n. from Sangihe; *P. argyropardala* sp. n. from Karakelong and Mindanao and *P. kalami* from Mindanao. Additional data on two species and a revised key to *Pseudovelia* of the Oriental Region are also given. Finally a new species of *Xiphovelia*: *X. skoteina* sp. n. from Sulawesi is described.

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Key words. – Sulawesi, Karakelong, Sangihe, Mindanao; Veliidae; *Pseudovelia*, key, new species; *Xiphovelia*, new species.

The present paper belongs to a series on the Nepomorpha and Gerromorpha of Sulawesi started by P. P. Chen and N. Nieser (papers listed in Nieser & Chen 1993). The series is a contribution to the Fauna Malesiana programme and is based on specimens mainly collected by the staff members of the Zoological Museum Amsterdam and the National Museum of Natural History Leiden, Dr. G. Zimmermann (Marburg, FRG) and the author.

Veliidae constitutes the second largest family of Gerromorpha but as its species are on average distinctly smaller and often more cryptic than Gerridae they are less well known. There are six subfamilies of which five are represented in the Oriental region. Most often encountered are the Rhagoveliinae with its principal genus *Rhagovelia.* Its representatives live on streams, often on exposed sites. The Sulawesi fauna has been revised recently by Nieser & Chen (1993). Veliinae, which are with *Velia* the predominant subfamily in Europe are represented with 1 species only in the Oriental Region (Andersen 1982). The endemic subfamily Perittopinae consists of a few cryptic species rare in collections. Haloveliinae with an Oriental-Papuan distribution live mostly on sheltered sites in mangrove or on coral banks.

Pseudovelia belongs to the large cosmopolitan subfamily Microveliinae. Representatives of this subfamily are characterized by having one segmented fore tarsi and two segmented middle and hind tarsi. They are small to very small insects many of which have more or less cryptic habits. Due to this they have been relatively little studied. On the other hand it is a species rich taxon with considerable morphological differentiation. Expectations are that detailed studies in the future will reveal that there are several more genera to be distinguished. Especially the large genus *Microvelia* as conceived at present appears to be polyphyletic; from time to time a distinct group in *Microvelia* is split off as a genus. This is the way in which *Pseudovelia* came to existence. The key to genera below may serve sort out oriental Microveliinae.

METHODS

Measurements are in mm, and are presented as the range or mean of five specimens, taken from the sample containing the holotype (if available). Length and width refer to the maximum value of the specified body part, if unspecified they refer to body length and width. Length is measured in dorsal view from anterior margin of head to apex of abdomen (inclusive genital segments) in apterous and to apex of hemielytra in macropterous specimens. If the tibial comb projects, length of tibia is measured to apex of comb, leg measurements are presented in Table 1. Width of head is measured across eyes. Antennal measurements have been lumped for sexes due to considerable overlap, on average the means in males tend to be 0.01 mm below and those in females 0.01 mm above the lumped mean for each segment. Angles are given in radians ('π').

The apical tarsal segments have, apart from the claws, a dorsal and a ventral arolium placed in the ventral incision. Of these the dorsal one is always bristle shaped and, except for fig. 10, not drawn in the figures. The ventral arolium is usually narrow but may be broad, blade-like, as in figs. 45 and 52. Pilosity is omitted in the drawings except when it is striking or diagnostic.

Depositories registered according to Arnett, Samuelson & Nishida (1993): BMKB (Kota Batu, Brunei), JTPC (Englewood, Co., U.S.A.), MBBJ (Bogor, Indonesia), MUDH (The Hague, The Netherlands), NHMW (Wien, Österreich), NMSC (Singapore), RMNH (Leiden, The Netherlands), SEMC (Lawrence, Kan. U.S.A.), USCP (Cebu City, Philippines), ZMAN (Amsterdam, The Netherlands), ZMUC (København, Danmark). Not registered: BPUH (Bagian Pertanian Universitas Haluoleo, Kendari, Sulawesi), NC (Nieser Collection, Tiel, The Netherlands), PCHC (P. P. Chen Collection, Beijing, P. R. China), ZC (Zimmermann Collection (Goßfelden (Marburg) B.R.D.).

Some additional data on the localities in Sulawesi Tenggara sampled by N. Nieser can be found in Nieser & Chen (1991). Specimens collected by Nieser are in NC unless otherwise specified.

SYSTEMATIC PART

Key to Oriental genera of Microveliinae

Adapted from Andersen 1982.

1. Claws all subterminal, inserted very close to the apex of tarsus (Irian) .... *Velohebria*
– Claws all preterminal, inserted distinctly before apex of tarsus 2
2. Larger species, length at least 3.5 mm. First antennal segment slender and very long, at least 3/4 the width of head between eyes 3
– Smaller species, length less than 3.5 mm. First antennal segment shorter and stouter 5
3. Femora modified (with hair tufts, tubercles etc.) on posterior surface (at least in males).............. 4
– Femora not modified on posterior surface (Oriental) .... *Neoalardus*
4. Eyes distinctly removed from lateroanterior angles of pronotum (W Malaysia) ...... *Lathriovelia*
– Eyes touching or very close to anterolateral angles of pronotum (Oriental) .... *Baptista*
5. First antennal segment incrassate, extending more than 2/3 of its length beyond apex of head. Apical cells of forewings reduced (or macropterous form unknown) 7
– First antennal segment more slender and usually much shorter; if not, then with normal forewing venation or shortened pronotal lobe (apterous form) 6
6. Middle tarsi with three leaflike structures subapically (claws and ventral arolium, fig. 52) (Oriental) .... *Xiphovelia*
– Middle tarsi not modified as above (Cosmopolitan) .... *Microvelia*
7. Parameres very small, segment 8 of male strongly modified ventrally (Palaeotropical and Far Eastern) .... *Pseudovelia*
– Parameres large, segment 8 in male not strongly modified (Himalayan) .... *Geovelia*

Genus ***Pseudovelia*** Hoberlandt, 1950

The genus *Pseudovelia* was erected somewhat laconically by Hoberlandt (1950 p. 38: 'Stout antennae and chiefly long first antennal joint, extending by more than 2/3 of its length beyond the apex of head are the characters on the basis of which it is possible to establish for these species a separate subgenus, *Pseudovelia* subg. n.'). Recently the genus has been thoroughly redescribed in a revision of the Oriental species by Andersen (1983). For practical purposes characteristics mentioned in the key to genera above will serve to recognize the genus. Apart from body size and relative length of (parts of) appendages good diagnostic characteristics on the species level are mainly found in secondary sexual characteristics of males. The parameres which are very small and look more or less the same in different species (fig. 2) in this genus are of little use. However, the ventral structure of first genital segment and the length of the well developed tibial combs on fore leg, which curve around the apical spur-like process on tibia provide excellent characteristics.

The following key is based on that in Andersen (1983) with insertion of the new species. *P. tjurupensis* (Lundblad), which is only known in female sex, is not included.

Key to males of *Pseudovelia* in the Oriental Region

1. Eyes densely hairy. Ventral arolium leaflike flattened (fig. 25) 2
– Eyes naked except for two ocular setae. Ventral arolium bristle-like 3
2. Length (apterous form) ♂ 2-2.2, ♀ 2.5-2.8 mm. male hind tarsus distinctly shorter than tibia; tarsal segment 1 with a row of long bristles along its entire length [Indian Subcontinent to Thailand and Sumatera] ....
.......*P. sexualis* (Paiva) [= *P. crassipes* (Lundblad)]
– Length (apterous form) ♂ 2.8, ♀ 3.0-3.2 mm. Male hind tarsus as long as tibia; tarsal segment 1

with a basal tuft of long bristles [S. China (Fu Jian)] .... *P. longitarsa* Andersen

3. Ventral lobes of head strongly produced backwards (fig. 46). Hind tarsus of male distinctly longer than tibia; tarsal segment 1 modified, twice as long as segment 2 [Thailand] .... *P. buccula* Andersen
– Ventral lobes of head not produced backwards. Hind tarsus not as above 4
4. Fore tibia swollen proximally and distally, resulting in a strongly sinuate posterior margin (Fig. 56) [N. Mindanao] .... *P. kalami* sp. n.
– Fore tibia less broad, its posterior margin evenly and gently curved 5
5. First genital segment of male with 2-5 spine-like processes or tubercles ventrally 6
Remark: under strong magnification the spine-like processes turn out to consist of a basal tubercle with a small acute tuft of closely packed bristles on top.
– First genital segment of male not as above 11
6. Head apart from the silvery hairs at inner margins of eyes also with a patch of silvery hairs mediocaudally 7
– Head mediocaudally at most with very few isolated silvery hairs not forming a patch 9
7. Segment 1 of male hind tarsus distinctly shorter than segment 2, ventral side of first genital segment of male anteriorly with a suboval cup shaped structure (fig. 50) [W. Malaysia] .... *P. lundbladi* Andersen
– Segment 1 of male hind tarsus subequal to or slightly longer than segment 2, segment 8 ventrally without cup shaped structure 8
8. First genital segment of male with one large median triangular process at base of ventral depression, in addition one slender median and a pair of lateral process near its posterior margin [Sumatera] .... *P. hypodonta* Lundblad
– First genital segment of male with two small tubercles at base and three near caudal margin of ventral depression (fig. 9) [N. Borneo] .... *P. borneensis* Andersen
9. Larger and relatively more slender species , ♂ L 2.4, W 0.83 mm. Apical comb on fore tibia of male about half as long as tibia (fig. 22), ventral impression of first genital segment bordered by five elongate and sharp processes (consisting of densely packed bristles) (figs. 20, 21) [N. Sulawesi] .... *P. epimekta* sp. n.
– Shorter and relatively chubbier species, ♂ L 2.0-2.15, W 0.80-0.84 mm. Tibial comb of male about one third the length of tibia (fig. 1), ventral impression of first genital segment bordered by 4-5 shorter processes (figs. 8, 39), ... 10
10. Ventral impression of first genital segment bordered by five processes, two pairs laterally and a single mediocaudally (figs. 3, 8) [N. Sulawesi] . ... *P. aflia* sp.n.
– Ventral impression of first genital segment bordered by four processes, a mediocaudal one absent (figs. 39, 40) [Sangihe I.] .... *P. sangihe* sp. n.
11. Trochanter of male fore leg distally with a short stout process (fig 25), first genital segment ventrally with a large spoon-shaped process (fig. 26) [N. Sulawesi] .... *P. koutali* sp. n.
– Trochanter of male fore leg more or less rounded, first genital segment ventrally at most with a cushion-like plate, no distinct ventrally directed projection 12
12. Segment 1 of male hind tarsus with ventral row of long (as long as segment, fig. 44) bristle-like hairs 13
– Segment 1 of male hind tarsus without distinct ventral row of long hairs which are as long as segment 14
13. Tibial comb 3/4 the length of fore tibia (fig. 16), length of antenna 2/3 body length (1.4/2.2) [Karakelong I., SE Mindanao] .... *P. argyropardala* sp. n.
– Comb on fore tibia of male 2/3 the length of tibia (fig. 19), length of antenna slightly less than 2/3 body length (1.18/2.0) [Philippines] .... *P. reiseni* Polhemus
14. Smaller (length of ♂ up to 2.2 mm) grey-blackish species, with a distinctly contrasting transverse orange patch anteriorly on pronotum 15
– Larger (length ♂ 2.2mm or more), brownish species, anterior orange pronotal mark not strongly contrasting 16
15. Comb on fore tibia of male about one third the length of tibia, impression ventrally on first genital segment with a transverse rim in caudal part (fig. 12) [N. Sulawesi] .... *P. afrofila* sp. n.
– Comb on fore tibia of male slightly more than half the length of tibia, ventral impression on first genital segment simple [Sri Lanka] .... *P. gnoma* Polhemus
16. Second genital segment of male with a tuft of bristles on each side; first genital segment ventrally with a broad cushion reaching across the segment in apical half (figs. 30, 31). [Hind tarsus ± half as long as tibia] [N. Sulawesi] .... *P. mystax* sp. n.
– Second genital segment of male without tufts of bristles laterally; first genital segment ventrally with a less strongly chitinized impression in apical half (fig. 36) 17
17. Length of antenna in male about 2/3 the length of body, hind tarsus 2/3 the length of hind tibia [SE. Sulawesi] .... *P. pyrokrene* sp. n.
– Length of antenna in male less than half the body length, hind tarsus about half the length of hind

tibia. [Thailand, West Malaysia to Jawa] .... *P. feuerborni* Lundblad

Pseudovelia aflia sp. n.
(figs. 1-6, 8)

Type material. – Holotype apterous ♂, INDONESIA, Sulawesi Utara, near Danau Mooat, temporary stream in hills (W of Desa Kankenturan), 21. Nov. 1985, leg. G. Zimmermann (RMNH). Paratypes 14♂ 7♀ apt., 1♂ 2♀ macr., same data as holotype, distributed as follows: 1♂ (macr.) 1♀ (allotype) RMNH; 2♂ 2♀ PCHC; 1♂ JTPC; 1♂ MBBJ; 4♂ 3♀ (1♀ macr.) NC; 4♂ 3♀ (1♀ macr.) ZC; 1♂ ZMAN; 1♂ ZMUC.

Description. – Apterous specimens. Dimensions. Length ♂ 2.00-2.13, ♀ 2.40-2.52; width of head ♂ 0.50-0.52, ♀ 0.52-0.54; width of pronotum ♂ 0.68-0.72, ♀ 0.73-0.78; width (across metanotum/first abdominal tergite) ♂ 0.80-0.84, ♀ 0.92-0.98. Colour and pilosity. Generally pale brownish with a greyish tinge, suture between body sclerites blackish, legs and antennae light brown. Patches of silvery hairs along inner margins of eyes rather inconspicuous; laterally on first abdominal tergite and mediocaudally on tergites 2-6, variable and indistinct in some specimens. Body clothed with rather short and sparse, erect brownish pilosity.

Length of antennal segments I-IV, 0.40: 0.25: 0.24: 0.42. Anterior quarter of pronotum and swollen anterolateral angles smooth, posterior three quarters coarsely punctate. Lateral margins distinctly indented about halfway on anteroposterior line, greatest width just anterior of indentation. Ventral arolia bristle like. Middle tibia with about six long erect hairs on inner side of apical half. Hind tibia with slightly denser and thicker pilosity apically.

Male. Elongate, connexiva roughly horizontal, lateral margins parallel to slightly diverging in anterior, converging in posterior half. Length of antenna two thirds of body length (1.3/2.1). Pronotum one and three quarters as wide as its median length (0.74/0.42), distinctly narrower than width across metanotum. Anterior trochanter rounded. Apical comb on fore tibia relatively short, ± one third (0.2/0.6) tibial length (fig. 1), consisting of about 90 teeth of equal width except for a small group of narrower teeth in the middle. First segment of hind tarsus apart from the normal pilosity with about 7 long (longer than diameter of segment) cilia ventrally. Abdominal tergite 1 large, coarsely punctate, tergites 1 and 2 nearly flat, in lateral view level with or raised slightly above connexiva. Pregenital tergite ± one fifth the dorsal median length of abdomen. First genital segment with a large ventral impression with five spine-like processes on its margin (figs. 3, 4, 8).

Female. Oval shaped, bulkier than male. Connexiva slanting ± 0.25π upward, their lateral margin evenly curved with its greatest width on tergite 4. Length of antenna slightly over half the length of body (1.30/2.45). Pronotum twice as wide as long as its median length (0.78/0.41), distinctly narrower than width across metanotum. Abdominal tergites 1-2, only slightly convex dorsally, in lateral view hardly rising above the margin of connexiva. Caudal apices of connexiva remaining considerably removed from each other, leaving tergite 7 visible. Tergite 8 oriented horizontally, fully visible in dorsal view. Pregenital segment large, its sternite slightly more than one fourth the median length of abdominal venter (0.50/1.75). Genital segments relatively large and protruding caudally, more or less U-shaped in caudal view (figs. 5, 6).

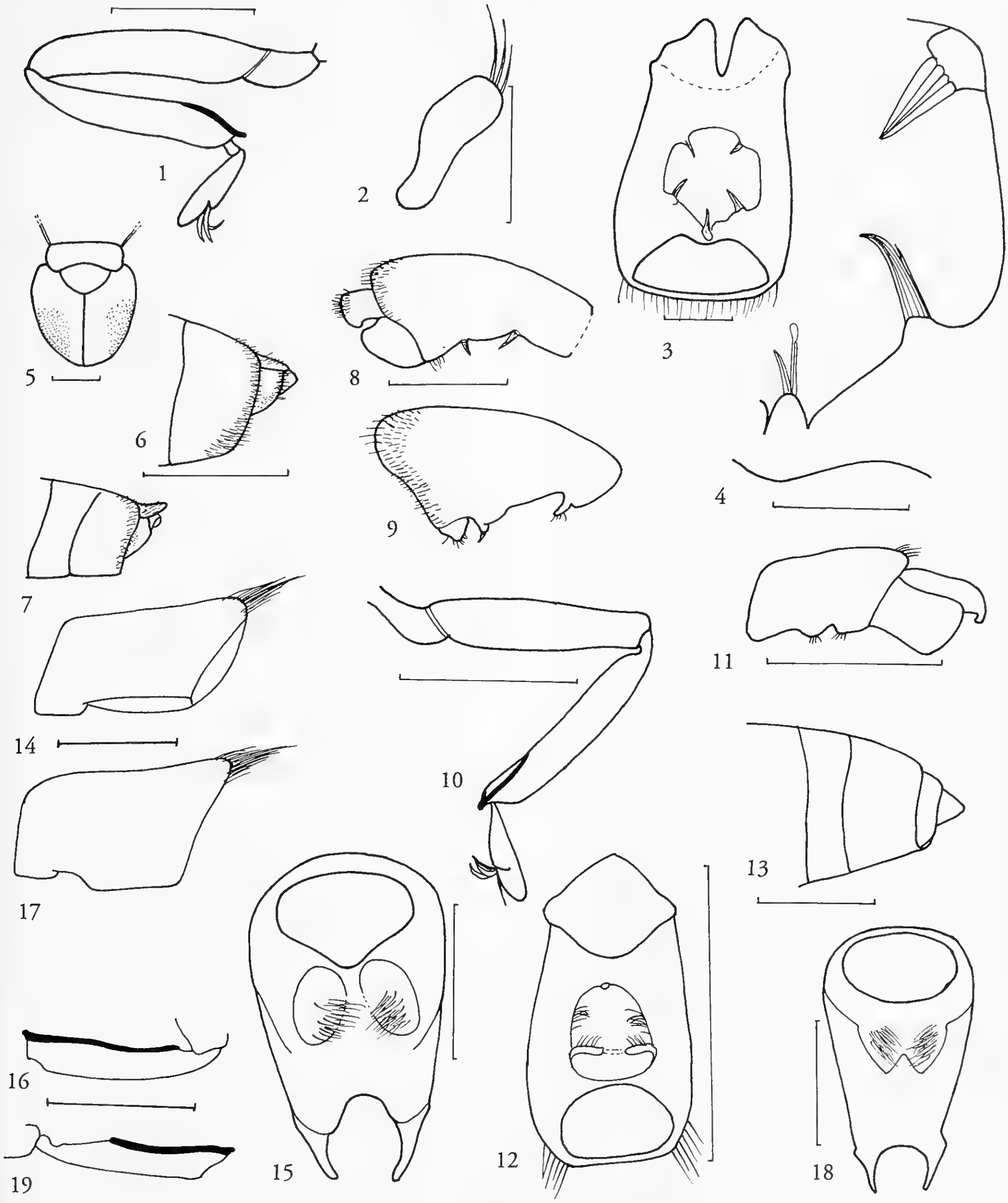
Macropterous form. – Structurally essentially as apterous form except for the usual modifications of macropters in the subfamily. Length ♂ 2.2, ♀ 2.3-2.5; humeral width of pronotum ♂ 1.00, ♀ 1.00-1.10. Hemielytra light grey-brown with an, usually ill defined, elongate sordid white stripe at base. Venation rather indistinct, two elongate basal cells, of which the one near hind (inner) margin seems two be divided. In addition two shorter apical cells. Base of abdomen with distinct lateral (near connexival sutures) keels on tergites 1-3 and a sorter, less distinct sublateral pair on tergites 1 and 2.

Etymology. – *Aflios* (Greek adjective meaning poor, meagre) refers to the comparatively poor pilosity on body.

Comparative notes. – The male genitalia are somewhat similar to those of *P. borneensis* Andersen (figs. 8, 9) but *P. aflia* lacks the patch of silvery hairs mediocaudally on head, and the detailed structure of 1st genital segment in ♂ is different in that the rim of the impression is thicker in *P. aflia* and the warts on which the ventral groups of bristles are placed are less strongly developed. Females of *P. borneensis* have tergite 8 somewhat more produced caudally and abdominal segment 7 somewhat less pilose laterally (figs. 6, 7). The male genitalia also remind those of *P. buccula* Andersen, an aberrant species with ventral lobe of head strongly produced caudally (fig. 46) and first segment of hind tarsus very long. For comparison with *P. epimekta* see under that species.

Pseudovelia afrofila sp. n.
(figs. 10-13)

Type material. – Holotype apterous ♀, INDONESIA: Sulawesi Utara, Sungai Girian (NE slope of G. Klabat, E of Manado), mountain stream with rapids, bottom boulders to coarse sand, specimens collected



Figs. 1-6. *Pseudovelia aflia.* Paratypes: 1-4 male; 1 fore leg, 2 paramere, 3 first genital segment (segment 8) in ventral view, 4 detail of ventral impression of segment 8; 5-6 apex of abdomen of female, 5 caudal, 6 lateral view. – 7 lateral view of apex of abdomen of female of *P. borneensis* 8-9 lateral view of segment 8 of male, 8 *P. aflia*, 9 *P. borneensis.* – 10-13. *Pseudovelia afrofila.* 10-12 male allotype, 10 fore leg, 11 genital segments, lateral view, 12 segment 8, ventral view, 13 female paratype, apex of abdomen, lateral view. – 14-16 *Pseudovelia argyropardala.* Male paratypes: 14 segment 8 lateral view, 15 segment 8 ventral view, 16 fore tibia. – 17-19 *P. reiseni* male: 17 segment 8 lateral view, 18 segment 8 ventral view, 19 fore tibia.
Scale line for figs. 3 and 5: 0.1mm; figs. 10-13, 16 and 19: 0.5mm; figs. 1, 6, 8, 14, 15, 17 and 18: 0.25 mm; figs. 2 and 4: 0.05mm. Figs. 7 and 9 after Andersen (1983).

on patch of foam behind boulder, 23. June 1994, N9452, leg. N. Nieser (ZMAN). Paratype 1♂ (allotype) and 1♀, same data as holotype, (NC). All apterous.

Description. – Apterous specimens. Dimensions. Length ♂ 2.10 , ♀ 2.35-2.40; width of head ♂ 0.55, ♀ 0.58-0.60; width of pronotum ♂ 0.72, ♀ 0.80-0.85; width (across third abdominal tergite) ♂ 0.90, ♀ 1.08-1.10. Colour and pilosity. Generally dull dark grey, anterior third of pronotum pale orange, one female with an indication of orange median line; lateral halves of connexiva (dorsally and ventrally) and distal rims of acetabula brownish; antennae and legs pale yellowish to light brown, proximally lighter than distally. Patches of silvery hairs along inner margins of eyes distinct, a narrow longitudinal stripe medially on vertex shining black (due to lack of basic pilosity). Silvery hairs laterally on first abdominal tergite and on posterior parts of remaining tergites indistinct. Body covered with velvety pilosity superposed with distinct erect brownish pilosity, giving the specimens a hairy look more obvious dorsally than ventrally.

Length of antennal segments I-IV, 0.41: 0.24: 0.29: 0.43. Anterior third of pronotum and anterolateral angles smooth, posterior two thirds coarsely punctate. Greatest width of pronotum about halfway anteroposterior line, lateral margins convex without pronounced humeral angles or indentation. Ventral arolia bristle like. Middle tibia with about 5 long (twice as long as the width of tibia) hairs in apical half of inner side. First segment of hind tarsus ventrally with a few longer cilia twice as long as the width of segment.

Male. General shape elongate oval with a truncate caudal apex, connexiva more or less horizontal, their lateral margins convergent in posterior half. Length of antenna 2/3 the length of body (1.4/2.1). Pronotum less than twice as broad as its median length (0.7/0.4). Anterior trochanter rounded. Fore tibia with grasping comb one third the length of tibia (0.2/0.6, fig. 10), consisting of about 80 coarse teeth. Hind tibia with ciliation apically denser but not modified. First abdominal tergite large, flat dorsally, raised about as high as the edge of connexiva. Pregenital segment about one fifth the length of abdomen. First genital segment ventrally with a large impression with strongly chitinized margin in posterior half, otherwise little modified (fig. 11, 12). Second genital segment lying within first, without special features.

Female. General shape broadly oval, connexiva nearly horizontal, distinctly tapering in posterior 3/5 of abdomen. Length of antenna more than half the length of body (1.4/2.4). Pronotum nearly twice as wide as its median length (0.80/0.45), distinctly narrower than width across metanotum. Abdominal tergites 1-3, somewhat convex dorsally, in lateral view first three rising above the margin of connexiva. Caudal apices of connexiva remaining considerably removed from each other, leaving tergite 7 visible, tergite 8 slanting ventrally 0.16 π, tergites 8 and 9 fully visible in dorsal view. Segment 7 large, its tergite two thirds as long as wide (0.22/0.33),its sternite slightly more than one third the median length of abdominal venter (0.42/1.10). Genital segments well developed, basal part of gonocoxa retracted into abdomen (fig. 13).

Macropterous form unknown.

Etymology. – *Afrofilos* (aphrophilos) is a greek composite adjective meaning 'foam loving'.

Comparative notes. – The general shape (especially in females) and colour of this species is not similar to any species known from Sulawesi. It is apparently similar to *P. gnoma* Polhemus from Sri Lanka, which is unknown to me, the characteristics in the key will suffice to distinguish the species.

Remarks. – The species was found together with *P. koutali* in a patch of foam behind some boulders at an edge of the stream. Andersen (1983) reports the apparently related *P. gnoma* also from 'in foam in river' other species have, however, also been found on patches of foam.

Pseudovelia argyropardala sp. n.
(figs. 14-16, 44, 48-49)

Type material. – Holotype apterous ♂, INDONESIA: Sulawesi Utara, Pulau Karakelong, Sungai Ambela at inlet of irrigation canal for desa Ambela, large open river bed in disturbed rain forest, transition from mountain to lowland stream, only a little water (sluices in dam open), actual stream about 2m wide, 0.3-0.5m wide, water turbid, 30 Nov. 1994, N9493, leg. N. Nieser (RMNH). – Paratypes (adults only), same data as holotype 6♂ 11♀ apterous, 3♂ 5♀ macropterous, 8 lvIV-V, distributed as follows: 1♀ apt. (allotype), 1♂ 1♀ macr. RMNH, 1♂ 1♀ NHMW, 1♂ 1♀ NMSC, 1♂ 1♀ PCHC, 1♂ apt., 1♀ macr. SEMC; P. Karakelong, Sungai (at desa) Pampalu, about 200 m upstream of mouth, open lowland stream through agricultural area, mostly some shade, bottom sand and pebbles, 1. XII. 1994, N9495, leg. N. Nieser, 2♂ 1♀; P. Karakelong, Sungai Ambela at foot of waterfall, mountain stream in primary rainforest, *Pseudovelia* under overhanging rocks at edges of pond, 2. XII. 1994, N9497, leg. N. Nieser, 4♂ 12♀ apt., 1♂ 2♀ macr., 20 lv IV/V (1♀ JTPC, 1♀ MBBJ, 1♀ MUDH, 1♂ SEMC, 1♀ ZC, 1♂ 1♀ ZMUC; P. Karakelong, Sungai Sawang, lowland stream through agricultural area, very turbid after rain, *Pseudovelia* on patch of foam at edge, 3. XII. 1994, N9498, leg. N.

Nieser, 1♂ 1♀ apt., 6 lvIV/V. Pulau Salibabu, Lirung, narrow stream on very steep rocks draining, small shallow pools with much plant debris connected by trickles of water, shaded by remnants of forest, ± 350m asl., 24. XII. 1994, N9483, leg. N. Nieser 5♂ 11♀ apt., 1♀ macr. – PHILIPPINES, Mindanao: Sarangani (S. Cotabato) prov. Siquel River, pool (area ± 20 m^2, 0.2 m deep) at edge of river bed, slightly turbid stagnant water, under overhanging grassy bank, 23. XI. 1993, N9351, leg. N. Nieser, 2♀ apt., 2♂ 2♀ macr. (1♂ 1♀ macr. USCP); Lake Sebu area, stream at Bakdolong, lowland stream aspect, sand/ mud bottom, *Pseudovelia* at edge, 3.XII.1993, N9364, leg. N. Nieser, 1♀ apt.; Stream at Bakdolong, mountain stream aspect, bottom with well sized pebbles, *Pseudovelia* at edge, 3 & 4. XII. 1993, N9366, leg N. Nieser, 5♂ 10♀ apt., 1♂ 2♀ macr.(1♂ 2♀ apt to resp: NHMW, RMNH, USCP, ZMAN, 1♂ 1♀ apt. & 1♂ 1♀ macr. JTPC); stream at Bakdolong, upstream across the agricultural area, beginning of hilly area, narrow stream in limestone, shaded by shrubs and trees on the banks, *Pseudovelia* from pools mostly under overhanging ridges or tree roots, 10. XII. 1993, N9379, leg. N. Nieser, 29♂ 37♀ apt., 2♂ 4♀ macr.; Lake Sebu area, just upstream of third waterfall, edge upstream of a large boulder in mountain stream, slopes with remnants of primary forest, 7. XII. 1993, N9371, leg. N. Nieser, 2♂ 2♀ apt., 1♀ macr. (1♂ 1♀ apt. BMKB, 1♂ 1♀ apt. 1♀ macr. SEMC); Lake Sebu area, just down stream of second waterfall at edge of spray area, sheltered edge downstream of boulders, 8. XII. 1993, N9373, leg. N. Nieser, 1♂ 1♀ apt.

Description. – Apterous specimens. General shape elongate oval. Dimensions. Length ♂ 2.18-2.40, ♀ 2.53-2.75; width of head ♂ 0.56-0.59, ♀ 0.56-0.60; width of pronotum ♂ 0.77-0.80, ♀ 0.78-0.81; width (♂ across posterior margin of thorax, ♀ across abdominal tergites 4-5) ♂ 0.88-0.92, ♀ 0.94-1.03. Colour and pilosity. Generally dark grey to blackish with striking silvery spots dorsally on abdomen. Transverse band anteriorly, lateral margin and narrow median longitudinal stripe on pronotum and lateral half of connexiva brick red. Legs pale yellowish, bases and apices of segments usually darker, antennae light brown, base of rostrum pale, apical segment dark. Bands of silvery hairs along inner margins of eyes distinct; patches of silvery hairs posterior margin of metanotum, laterally on first abdominal tergite, medially on tergites 2 and 3, mediocaudally on connexiva 3-6, posterior part of tergite 6 and most of tergite 7. Compared to other species in the region the silvery patches are more strongly contrasting in this species. Body clothed with long light brown pilosity which is more erect and distinct dorsally than ventrally, especially in lateral view the species appears hirsute dorsally. Antennae and legs also rather hirsute.

Length of antennal segments I-IV, 0.38 : 0.30 : 0.32 : 0.44. Anterior quarter of pronotum slightly swollen, smooth except for a row of pits along anterior margin, coarse punctation on posterior three quarters obscured by dense pilosity. Lateral margins of pronotum smoothly curved, not or hardly indented, greatest width about halfway. Ventral arolia bristle like. Middle tibia with about six long erect hairs on inner side of apical half, becoming distinctly shorter apically. Denser and thicker pilosity apically not obvious.

Male. Connexiva roughly horizontal to slanting 0.25π upward, lateral margins nearly parallel in anterior, converging in posterior half. Length of antenna about two thirds of body length (1.45/2.2). Pronotum less than twice as wide as its median length (0.8/0.45 - 0.8/0.5), narrower than width across metanotum (0.8/0.9). Anterior trochanter rounded. Apical comb on fore tibia long, slightly over three quarters (0.5/0.65) tibial length (fig. 16), consisting of over 300 teeth of which the proximal and distal groups are much finer than those from the central interval. First segment of hind tarsus apart from the normal pilosity with a group of about 20 long (about as long as length of segment, fig. 44) cilia ventrally. Abdominal tergite 1 large, smooth, sloping downward posteriorly; tergites 2-7 flat, horizontal, in lateral view concealed by the connexiva. Pregenital tergite ± one fifth the dorsal median length of abdomen. First genital segment with a pair of ventral impressions, beset with cilia, dorsocaudal pilosity long (figs. 14, 15).

Female. Larger and bulkier than male but of same general form. Connexiva slanting 0.3π upward to nearly vertical (nearly horizontal in gravid specimens), their lateral margins nearly parallel in anterior, converging in posterior half. Length of antenna slightly more than half the length of body (1.45/2.6). Pronotum twice as wide as its median length (0.9/0.45), distinctly narrower than width across metanotum. Abdominal tergite 1 large, coarsely punctate, ± horizontal, in lateral view visible dorsally of connexiva, tergites 2-3 gradually sloping downward posteriorly, less distinctly punctate than tergite 1; tergites 4-8 flat, horizontal, in lateral view concealed by the connexiva (except in gravid females). Caudal apices of connexiva rounded, remaining considerably removed from each other, leaving tergite 7 visible. Tergite 8 oriented horizontally, fully visible in dorsal view. Pregenital segment large, its sternite about one fourth the median length of abdominal venter (0.35/1.4). Genital segments largely retracted within abdomen, more or less U-shaped in caudal view (figs. 48, 49).

Macropterous form. – Structurally essentially as apterous form except for the usual modifications of macropters in the subfamily. Length ♂ 2.55-2.60, ♀ 2.60-2.70; humeral width of pronotum ♂ 1.06-1.08, ♀ 1.12-1.15. Pronotum dark grey-brown with a lighter T-shaped mark, anterior transverse leg broad, posterior longitudinal leg narrow, disc of pronotum distinctly punctate. Hemielytra grey-brown with basal angles largely white, apical cells brownish with lighter centres and membrane greyish. Venation distinct, two elongate basal cells and two shorter apical cells. Lateral keels at base of abdomen long, reaching base of tergite 4, medial pair less distinct, reaching caudal margin of tergite 2; silvery pilosity on abdomen less developed especially anteriorly.

Etymology. – *Argyropardalos*, a greek adjective meaning 'with silvery spots', referring to the distinct patches of silvery pilosity on abdomen of most specimens.

Comparative notes. – Size in combination with pilosity, greyish colour and distinct patches of silvery hairs on abdomen sets this species apart from other Sulawesi species. This species is very similar to *P. reiseni* Polhemus from Luzon and Mindanao males of which are, however, smaller and have a relatively shorter fore tibial comb of somewhat over 200 teeth which are all coarse distally (in *argyropardala*, which has about 300 teeth in tibial comb, there is a row of very fine teeth near the distal spur) and the ventral impression on first genital segment of male less distinctly paired and much smaller (see key and figs. 14-19). Females show considerable overlap and only the smaller females of *P. reiseni* (L about 2.4) are reliably distinguishable from the larger females of *P. argyropardala* (L about 2.7).

Pseudovelia epimekta sp. n.

(figs. 20-24)

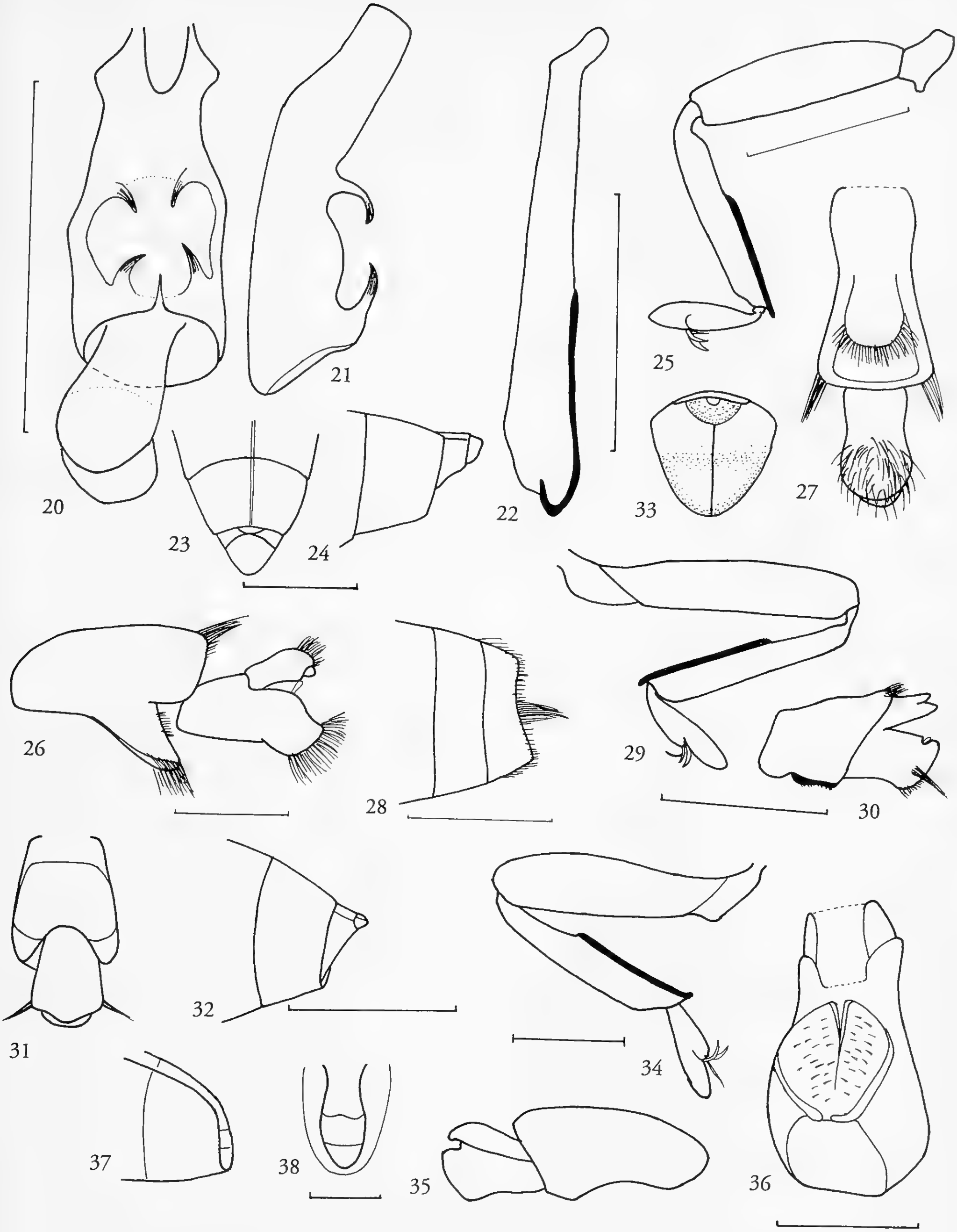
Type material. – Holotype apterous ♂, INDONESIA, Sulawesi Utara, Dumoga Bone N. P., Tumpah, ruhige Abschnitt am Moos (quiet stretch at marshland), 28. Oct. 1985, leg. G. Zimmermann (RMNH). Paratypes 2♀, same data as ♂ (1♀ NC, 1♀ allotype ZC). All apterous.

Description. – Apterous specimens. Dimensions: length ♂ 2.40, ♀ 2.50-2.65; width of head ♂ 0.53, ♀ 0.58-0.59; width of pronotum ♂ 0.68, ♀ 0.72-0.73; greatest width (across mesothorax) ♂ 0.83, ♀ 0.86-0.89.

Colour. Generally dark grey to blackish, eyes very dark brown. Head with grey stripes at inner margins of eyes. Pronotum with strongly contrasting anterior orange transverse band not interrupted in the middle, disk of pronotum medium brown with a very narrow median orange-like stripe. Connexiva somewhat brownish, more distinctly so on ventral side. Antennal segments 1-3 medium brown, segment 4 pale, whitish. Segments 2-3 of rostrum largely yellowish brown (in frontal view). Acetabula on both sides of suture brownish, legs sordid white to light brownish, apical part of femorae and basal part of tibiae medium brown.

Silvery pilosity at lateral margins of abdominal tergite 1, most of tergites 2-3,6, hind margin of tergite 5 and median part of tergite 7, quite variable especially on 6 and 7. Sparse, scattered longer erect bristles dorsally. Venter with well developed medium long somewhat yellowish pilosity, slightly denser on genital segments. Tuft of bristles at end of metasternal scent channels strongly developed. Pilosity of appendages normal, first antennal segment with two distinct erect bristles on anterior side.

Body elongate spindle-shaped, greatest width across mesothorax, subequal to width across posterior margin of abdominal segment 4 (depending on slanting of connexiva this is narrower in 1♂ 1♀ and very little wider in 1♀). Head over three fourths as long as wide (0.45/0.55), longer than median length of pronotum (0.45/0.40). Eyes small, width of an eye only slightly more than one third the interocular space (0.12/0.32). Length of antennal segments I-IV = 0.62: 0.31: 0.42: 0.64. First antennal segment distinctly longer than head, relatively slender, elongate club-shaped and softly curved, with two distinct erect bristles. Second slightly narrower, third and fourth narrowest, subequal. Rostrum nearly reaching base of metasternum. Pronotum more than half as long as wide (0.4/0.7), covering meso and metanotum except for lateroposterior angles of metanotum. Disk shallowly and indistinctly pitted, with an indistinct transverse impression halfway, somewhat more distinct in the male than in the females. Anterior transverse orange band of pronotum smooth, slightly swollen. Propleura with some coarse punctures, most distinctly a row at dorsal margin of acetabulum and another near posterior margin. Fore femur somewhat flattened on under surface in apical part. Arolia bristle-like. Connexiva with lateral margins nearly straight, subparallel on segment 1-4, converging in caudal part, slanting upward about 0.16π. Connexiva widest on segment 4, about half as wide as corresponding tergite. Median length of abdominal tergites 1-7 three times the median length of pronotum (1.40/0.45) in male, slightly more in female (1.60/0.45). Abdominal tergite 1 large, raised above dorsal margin of connexiva in lateral view, somewhat more so in females than in males, tergites 2-3 declivous, tergites 2-5 each about half as long as tergite 1, tergites 6 and 7 progressively longer, especially in male. Abdominal venter flattened in male, indistinctly so in female, with a



Figs. 20-24. *Pseudovelia epimekta.* 20-23 male holotype: 20 genital segments ventral view, 21 segment 8 lateral view, 22 fore tibia, 23-24 apex of abdomen, 23 male, ventral view, 24 female, lateral view. – 25-28, *Pseudovelia koutali*, paratypes: 25-27 male 25 fore leg, 26-27 genital segments, 26 lateral view, 27 ventral view, 28 female apex of abdomen, lateral view. – 29-33, *Pseudovelia mystax.* Paratypes: 29-31 male, 29 fore leg, 30-31 genital segments, 30 lateral view, 31 ventral view, 32-33 female apex of abdomen, 32 lateral view, 33 caudal view. Scales 0.5 mm. – 34-38 *Pseudovelia pyrokrene.* Paratypes, 34-36 male, 34 fore leg, 35 genital segments, lateral view, 36 segment 8 ventral view, 37-38 female apex of abdomen, 37 lateral view, 38 caudal view. Scale line for figs. 20-25, 28-32, 34-35: 0.5mm; figs. 26-27, 36-38: 0.25mm.

narrow, shallow, mediolongitudinal groove on sternites 5-7, sternites 6 and 7 progressively longer than preceding ones.

Male. Length of antenna five sixth the length of body (2.0/ 2.4). Comb on fore tibia long (fig. 22), about half as long as tibia consisting of about 200 teeth which are distinctly stouter in apical part. Otherwise legs without obvious characters, first segment of hind tarsi with a few longer hairs. Tergite 7 half as long as preceding abdominal tergites together. Genital segments relatively large but segment 8 nearly fully retracted within abdomen. Sternite 8 with five curved, sharply pointed processes, one, narrower, mediocaudal, one pair subcaudal and one pair halfway, surrounding a ventral impression (figs. 20-21). Parameres very small, nearly vestigial.

Female. Length of antenna slightly over three quarters the length of body (2.0/2.6). Abdominal tergite 8 horizontal, comparatively large, covering gonocoxae in dorsal view, over half as long as tergite 7 (0.18/0.3), covering gonocoxae in dorsal view. Gonocoxae large, well visible in ventral view. (figs. 23-24).

Macropterous form unknown.

Etymology. – *Epimektes*, a greek adjective meaning elongate, referring to shape of body, especially of female.

Comparative notes. – This species belongs to the *hypodonta* group of species (Andersen 1983). Segment 8 of male is most similar to that of *P. borneensis*, especially in lateral view, the mediocaudal process in *P. borneensis* is, however, stouter, more triangular. *P. borneensis* is, moreover, smaller, of lighter colour and has the first antennal segment relatively shorter and stouter. The first genital segment of the male has a similar form to that of *P. aflia* described above, but it is longer (when isolated from body 0.55 in *P. epimekta*, 0.44 in *P. aflia*) and has more solid ventral warts with bristles (figs. 3, 8, 20, 21). *P. epimekta* is, moreover, generally longer and relatively more slender than *P. aflia* with a distinctly longer first antennal segment (0.6 and 0.4 respectively). *P. aflia* and *P. epimekta* have a few silvery hairs at base of head but these are not recognizable as a silvery patch.

Pseudovelia kalami sp. n.
(figs. 56-58)

Type material. – Holotype apterous ♂ (only specimen known, right middle leg lacking, genitalia in microvial), PHILIPPINES; Mindanao, Surigao del Norte prov., Oslao, narrow mountain stream through coconut groove, bottom stones, pebbles and coarse sand, water colourless, clear, sampled at quiet edges, 29 Mar. 1993, leg. N. Nieser, N9332 (RMNH).

Apterous specimen. – General shape elongate, nearly parallel sided except anterior and posterior regions. Dimensions. Length ♂ 2.49, width (across posterior half of mesothorax) 1.02, width of pronotum 0.96, width of head ♂ 0.63.

Colour and pilosity. Generally blackish with striking silvery spots dorsally on abdomen. Transverse band on anterior half of pronotum, and lateral rim of connexiva dark orange brown. Legs, coxae trochanters and basal part of femurs yellowish, remaining parts brownish, antennae and rostrum also brownish. Bands of silvery hairs along inner margins of eyes distinct, in addition a small spot of silvery hairs mediocaudally on head; patches of silvery hairs: lateroposterior angles of metanotum, laterally on first abdominal tergite, mediocaudally on tergites 6 and 7, mediocaudally on connexiva 3-5, posterior part of tergite 6 and most of tergite 7. Compared to most species in the region the silvery patches are more strongly contrasting in this species. Body clothed with long light brown pilosity which is more erect and distinct dorsally than ventrally.

Length of antennal segments I : II : III : IV, 0.55 : 0.46 : 0.45 : 0.40. Length of antenna three quarters of body length (1.86/2.49). Hind margin of ventral lobe of head produced slightly backwards. Pronotum less than twice as wide as its median length (0.96/0.6), only slightly narrower than width across metanotum. Anterior half of pronotum slightly swollen, smooth except for some pits caudally, coarse punctation on posterior half obscured by dense pilosity. Lateral margins of pronotum smoothly curved, not indentate, greatest width about halfway.

Anterior trochanter rounded. Fore tibia proximally and distally thickened, resulting in a sinuate posterior margin, tibial comb runnig nearly the entire length of tibia (fig. 56). Middle tibia without long erect hairs on inner side. Denser and thicker pilosity apically not obvious. First segment of hind tarsus apart from the normal pilosity with a group of about 15 long (about 3 times as long as diameter of segment) cilia ventrally. Ventral arolia bristle like.

Connexiva roughly horizontal, lateral margins parallel anteriorly, converging on segments 5-7. Abdominal tergite 1 large, smooth, only slightly sloping downward posteriorly; tergites 2-7 flat, horizontal, in lateral view concealed by the connexiva. tergites 1 and 7 twice (0.3) as long as tergites 2-6 (0.15). Abdominal venter with a large and broad median impression. First genital segment with a large central impression bordered by a very high rim caudally ending in a pair of tufts of small bristles, surface of the impression anteriorly and medially also with small bristles (figs. 57-58).

Comparative notes. – General shape and colour similar to *P. argyropardala*, which is slightly smaller.

The small but distinct spot of silvery hairs mediacaudally on the head reminds of *P. pyrokrene* and *P. borneensis.* The form of the anterior tibia and the strongly developed rim around the ventral depression of first genital segment in male are, however, unique within the genus. Females will probably be recognizable by the relatively long antennal segments especially segment 2.

Etymology. – Kalami is a Greek noun, meaning tibia, in apposition, referring to the characteristic fore tibia of male.

Pseudovelia koutali sp. n.
(figs. 25-28)

Type material. – Holotype apterous ♂, INDONESIA, Sulawesi Utara, Dumoga Bone River, downstream of bridge, 22. Oct. 1985 leg. G. Zimmermann (RMNH). Paratypes 11♂ 8♀, same data as type, distributed as follows: 1♀, allotype, RMNH; 1♂ MBBJ; 2♂ 2♀ PCHC; 4♂ 2♀ NC; 3♂ 3♀ ZC; 1♂ ZMAN; Sulawesi Utara, Sungai Girian (NE slope of G. Klabat, E of Manado), mountain stream with rapids, bottom boulders to coarse sand, specimens collected on patch of foam behind boulder, 23. VI. 1994, N9452, leg. N. Nieser, 9♂ 7♀ (1♂ 1♀ JTPC, 1♂ 1♀ MUDH, 1♂ 1♀ NHMW, 1♂ 1♀ SEMC). All apterous.

Description. – Apterous specimens. Dimensions. Length ♂ 2.32-2.40, ♀ 2.80-2.92, width of head ♂ 0.54-0.56, ♀ 0.60-0.62; width of pronotum ♂ 0.78-0.80, ♀ 0.80-0.83; width (across metanotum/first abdominal tergite) ♂ 0.83-0.88, ♀ 0.97-1.03. Colour and pilosity. Generally dark brown, antennae, T-shaped mark on pronotum, lateral margin of connexiva medium brown, legs medium to light brown, coxae, trochanters and basal parts of femurs yellowish. Patches of silvery hairs along inner margins of eyes, caudolaterally on first abdominal tergite, the disks of tergites 2 and 3 and small patches medially on tergites 4 and 5. Body mostly covered with quite long, erect brownish pilosity.

Length of antennal segments I-IV 0.43 : 0.30 : 0.30 : 0.40. Anterior quarter of pronotum smooth, posterior three quarters coarsely punctate. Anterolateral angles of pronotum only slightly swollen. Ventral arolia bristle like. Middle tibia with about 6 long (twice as long as the width of tibia) hairs in apical half of inner side.

Male. General shape elongate, connexiva slanting to a variable angle, usually about 0.5π, their lateral margins convergent in posterior half. Length of antenna over half the length of body (1.4/2.4). Pronotum broader than its median length (0.7/0.5) with lateral angles about midway, very broadly rounded. Anterior trochanter with a distinct ventral tubercle (fig. 25). Fore tibia with grasping comb occupying about two thirds of the length of tibia ((0.35/0.58), consisting of about 150 teeth of equal thickness except for a group of about 25 very fine ones just proximally of the tibial spur. Hind tibia straight, with ciliation along inner margin denser in apical part, with a patch of slightly thicker cilia at extreme apex. Hind tarsal segments of subequal length, first tarsal segment ventrally with normal pilosity only. First abdominal tergite large, raised about as high as the edge of connexiva. Pregenital segment large, about one third the length of abdomen. Genital segments largely retracted within abdomen, first genital segment ventrally with a large spoon-shaped appendage (figs. 26-27).

Female. General shape bulkier than male, with connexiva tapering more strongly. Length of antenna half the length of body (1.4/2.8) or very slightly less. Pronotum wider than long (0.8/0.6), greatest width relatively more posteriorly than in male and more distinctly narrower than width across metanotum. Anterior trochanter without tubercle and tibia without comb. Pilosity of hind tibia less conspicuous than in male, basal segment of hind tarsus distinctly shorter than apical (0.2/0.3). First abdominal tergite large, convexly swollen dorsally, in lateral view distinctly rising above the margin of connexiva. Connexiva vertical, strongly converging posteriorly with apical pilosity meeting across midline and covering tergite 7. Pregenital segment large, about two fifth the length of abdomen. Genital segments small, retracted into abdomen with a distinct tuft of darker bristles, situated dorsally on the vertically oriented tergite 8, pointing caudally (fig. 28).

Etymology. – *Koutali,* a Greek noun meaning spoon, refers to the spoon shaped ventral appendage on first genital segment of male.

Comparative notes. – The male differs from other species in the genus by the tubercle on fore trochanter and the characteristic spoon shaped appendage ventrally on first genital segment. The female is characterised by the short pregenital segment and the caudal tuft of dark bristles. With the key to oriental species by Andersen (1983) this species runs to *P. gnoma* Polhemus from Sri Lanka, which is a smaller species (♂ 2.1-2.2, ♀ 2.6-2.8) with different structure of first genital segment of male. The male of *Microvelia magnifica* Lundblad which might, judging from the figures by Lundblad (1933), also be a *Pseudovelia* or a related genus different from *Microvelia* s. str. also has a ventral tongue on segment 8, but this structure is sharper apically (ventrally) and the anterior trochanter is rounded. The female of *M. magnifica* has the last segment of connexiva meeting over the tip of abdomen.

Pseudovelia mystax sp. n.

(figs. 29-33)

Type material. – Holotype apterous ♂, Sulawesi Utara, Danau Alea, 22 Nov. 1985, leg. G. Zimmermann (ZMAN). – Paratypes, 15♂ 41♀, same data as holotype, distributed as follows: 2♀ (including allotype) ZMAN; 2♀ BPUH; 2♂ 2♀ PCHC; 1♂ 2♀ JTPC; 1♂ 2♀ MBBJ; 3♂ 8♀ NC; 1♂ 2♀ RMNH; 6♂ 20♀ ZC; 1♂ 1♀ ZMUC. All apterous.

Description. – Apterous specimens. Dimensions. Length ♂ 2.20-2.26, ♀ 2.70-2.87, width (across metanotum/first abdominal tergite) ♂ 0.80-0.85, ♀ 0.95-1.003. Colour and pilosity. Generally brick red to light castaneous, sutures between body sclerites mostly blackish, coxae, trochanters and most part of femurs yellowish. Patches of silvery hairs along inner margins of eyes rather inconspicuous, more distinct laterally on first abdominal tergite and lining the sutures between tergites. Body clothed with quite long, erect brownish pilosity, more dense laterally and on venter than on dorsum.

Length of antennal segments I-IV 0.49: 0.32: 0.33: 0.46. Anterior quarter of pronotum and swollen anterolateral angles smooth, posterior three quarters coarsely punctate. Greatest width of pronotum about halfway anteroposterior line, lateral margins convex without pronounced humeral angles or indentation. Ventral arolia bristle like. Middle tibia with about 5 long (twice as long as the width of tibia) hairs in apical half of inner side.

Male. General shape elongate with a truncate caudal apex, connexiva usually more or less horizontal, their lateral margins convergent in posterior third. Length of antenna slightly less than 3/4 the length of body (1.6/2.25). Pronotum twice as broad than its median length (0.8/0.4). Anterior trochanter rounded. Fore tibia with grasping comb occupying somewhat more than half the length of tibia ((0.4/0.7, fig. 29), consisting of over 250 fine teeth except at the spur where they are distinctly coarser. Hind tibia with ciliation along inner margin apically denser but not modified. First segment of hind tarsus ventrally with normal pilosity only. First abdominal tergite large, together with second convex dorsally raised about as high as the edge of connexiva. Pregenital segment about one fifth the length of abdomen. First genital segment ventrally strongly chitinized in posterior half, otherwise little modified (figs. 30-31). Second genital segment lying within first with a pair of tufts (about 6 each) of laterally pointing whisker-like bristles which are visible even when the segment is retracted.

Female. General shape bulkier than male, with connexiva usually more or less vertical, tapering only slightly (but more distinctly than in male) posteriorly. Length of antenna more than half the length of body (1.55/2.75). Pronotum twice as wide as its median length (0.82/0.42), distinctly narrower than width across metanotum. Abdominal tergites 1-3, convex dorsally, in lateral view 1 distinctly, 2 just rising above the margin of connexiva. Caudal apices of connexiva remaining considerably removed from each other, leaving tergite 7 visible, tergite 8 oriented horizontally, fully visible in dorsal view. Pregenital segment large, its sternite slightly less than one third the median length of abdominal venter. Genital segments small, retracted into abdomen, more or less triangular in caudal view (figs. 32-33).

Macropterous form unknown.

Etymology. – *Mystax*, a noun in apposition meaning moustache or upper lip in Doric, referring to the 'caudal whiskers' of the male.

Comparative notes. – This species at first sight resembles *P. aflia* and *P. pyrokrene* because of similar general colour and shape. The bristles on segment 9 of the male separate *P. mystax* from other *Pseudovelia* in tropical Asia. The apex of abdomen in caudal view of the female is more broadly triangular than in other species although the difference with *P. aflia* is very slight.

Pseudovelia pyrokrene sp. n.

(figs. 34-38)

Type material. – Holotype ♂, INDONESIA, Sulawesi Tenggara, Kecamatan Mowewe, Sungai Mowewe, lowland stream, 28 Feb. 1989, N8922, leg. N. Nieser (ZMAN). Paratypes: same data als holotype 3♂ 12♀ distributed as follows: 1♀ (allotype) ZMAN, 1♀ MBBJ, 1♀ BPUH, 2♂ 4♀ NC, 1♂ 2♀ PCHC, 2♀ RMNH, 1♀ ZC. Road Kolaka-Kendari km 20, mountain stream, under overhanging rock, 3. Mar. 1989, N8934, leg. N. Nieser 1♀; Sungai Mokowu (± 3°49'S 121°40'E), 30. X. 1989, 1 ♂; same, 6.XI.1989, 2 ♂ 1 ♀, leg. J. van Tol (RMNH). All apterous.

Additional specimens 1 lvV, same data as holotype; P. Buton, 1st mountain stream along road Bau-Bau to Bunga, 8. III. 1989, N8935, leg. N. Nieser, 1♀ apt.

Description. – Apterous specimens. Dimensions. Length ♂ 2.30-2.44, ♀ 2.71-2.90, width (across metanotum/first abdominal tergite) ♂ 0.79-0.80, ♀ 0.91-0.93. Colour and pilosity. Generally brick red/-light castaneous to dark brown, sutures between body sclerites mostly blackish, rostrum, basal part of first antennal segment, coxae, trochanters and basal half of femurs lighter, yellowish to light brown. Patches of silvery hairs, distinctly contrasting, along inner margins of eyes lateral and caudal margin of first abdominal tergite, most of tergites 2, 3, 6 and 7 less distinct on tergites 4 and 5. Body clothed with quite sparse but distinct long pilosity, in addition to the dense short pilosity covering body.

General shape elongate. Length of antennal segments I-IV 0.44 : 0.30 : 0.34 : 0.50. Anterior quarter of pronotum and swollen anterolateral angles smooth, posterior three quarters coarsely punctate. Greatest width of pronotum about halfway anteroposterior line, lateral margins convex without pronounced humeral angles or indentation. Ventral arolia bristle-like. Middle tibia with about 5 long (twice as long as the width of tibia) hairs in apical half of inner side. First abdominal tergite coarsely punctate.

Male. Connexiva slightly slanting upward laterally, their lateral margins moderately convex, inner margins hardly convergent posteriorly. Length of antenna about 2/3 the length of body (1.6/2.35). Pronotum one and a third times as broad than its median length (0.74/0.55), slightly narrower than the width across metanotum. Anterior trochanter with a nearly perpendicular angle apically (fig. 34). Fore tibia with grasping comb occupying half the length of tibia ((0.3/0.6), consisting of nearly 150 coarse teeth except a few proximal ones and a row of 20 just before the spur, which are narrow. Hind tibia virtually straight, with ciliation along inner margin apically denser but a dark patch of small spines absent. First segment of hind tarsus ventrally with normal pilosity only. First abdominal tergite large, slightly convex dorsally raised just above the edge of connexiva. Pregenital segment about one fifth the length of abdomen. First genital segment ventrally with a large subcircular impression with a chitinized margin in posterior half, otherwise little modified (figs. 35-36). Second genital segment lying mostly within first, without structural peculiarities.

Female. Connexiva vertical in most specimens, distinctly converging posteriorly. Length of antenna more than half the length of body (1.58/2.79). Pronotum 1.4 as wide as its median length (0.8/0.56), only slightly narrower than width across metanotum. Abdominal tergites 1 large, somewhat convex dorsally, in lateral view raised slightly above the margin of connexiva, tergites 2 and 3 declining, remainder of abdominal dorsum horizontal. Caudal apices of connexiva remaining considerably removed from each other, leaving tergite 7 visible, tergite 8 oriented horizontally, fully visible in dorsal view. Pregenital segment large, its sternite slightly less than half the median length of abdominal venter. Genital segments small, retracted into abdomen, more or less U-shaped in caudal view (figs. 37-38).

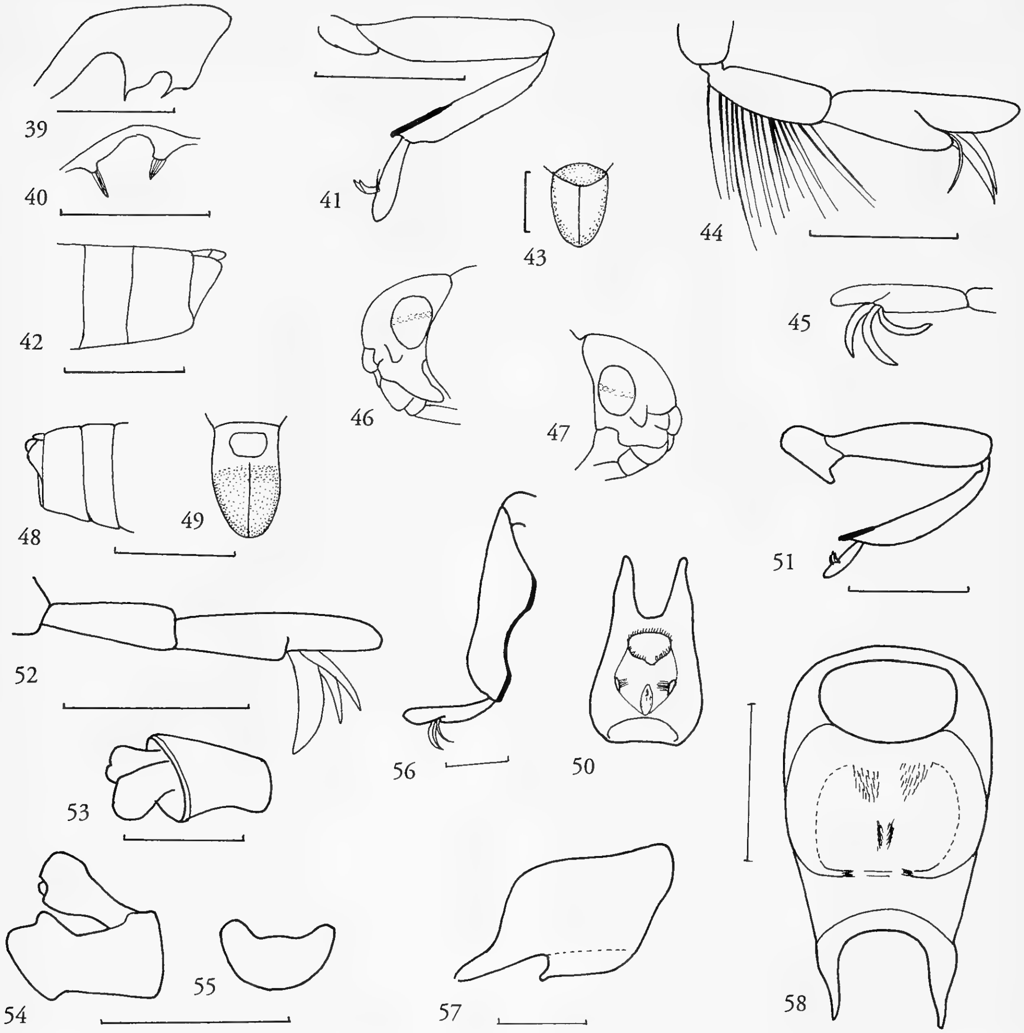
Macropterous form unknown.

Etymology. – *Pyrokrene*, a greek noun in apposition, refers to the similarity with *P. feuerborni*.

Comparative notes. – The ventral impression of first genital segment of male is of similar shape, but relatively larger, as in *P. feuerborni* Lundblad, in addition the male of *P. feuerborni* has a slightly curved hind tibia with a group of small spines apically which is lacking in *P. pyrokrene* which has hind tibia virtually straight and the fore tibial comb of *P. feuerborni* consists of 45 coarse proximal and a 'hardly countable number' of fine teeth in the distal part (lauter winzigen, kaum zählbaren Dornen, Lundblad 1934: 335). *P. feuerborni* is only known from macropterous specimens but in sofar comparison with apterous specimens gives clues, it appears quite related to *P. pyrokrene*. In general shape the female reminds of *P. koutali* but lacks the tuft of caudally directed dark bristles on tergite 8.

Pseudovelia sangihe sp. n. (figs. 39-43)

Type material. – Holotype apterous male: INDONESIA: Sulawesi Utara, Pulau Sangihe, Laine, Sungai Laine at waterfall, at edge of pothole between plants (*Hydrilla*) and floating plant debris, shade, '*Pseudovelia* especially at spots with some foam', 12.XI.1994, N9463, leg. N. Nieser (ZMAN). Paratypes (adults only), same data as holotype 8♂ 4♀ apt., 4♂ 2♀ macr., 22 larvae III/V distributed as follows; 1♀ apt. (allotype) 1♂ 1♀ macr. ZMAN, 1♂ apt., MBBJ, 1♂ apt. NMSC, 1♂ 1♀ apt., 1♂ macr. RMNH, 1♂ apt. SEMC; P. Sangihe, Lelepu, Sungai Lelepu, mainly lowland stream aspect, shaded pools under overhanging vegetation, no foam, 13.XI.1994, N9464, 1♂ 5♀ apt., 1♂ macr., 2 lvV (1♀ MBBJ, 1♂ 1♀ MUDH, 1♀ NHMW, 1♂ macr., 1♀ SEMC, 1♀ ZMUC); P. Sangihe, Desa Utaurano, Sungai Apanukang, pothole, at edge between vegetation, no foam, 14.XI.1994, N9465A, 3♂ 6♀ apt., 1♀ macr. [S. Apanukang is an upstream tributary of S. Laine near Naha, which is different from S. Laine at Laine]; P. Sangihe, Sungai Masalihe, mountain stream in rather deep (c. 20m) gorge, Pseudovelia from puddles at edge of stream bed, 16.XI.1994, N9468, 4♂ 4♀ apt.(1♂ 1♀ JTPC, 1♂ NHMW, 1♀ SEMC, 1♂ 1♀ ZC, 1♂ 1♀ ZMUC); P. Sangihe, Sungai Kendahe, bridge at Poto, mountain stream, pools at edge of stream bed, 17.XI.1994, N9471, 3♂ 4♀ apt.; P. Sangihe, smaller stream near N9471, 17.XI.1994, N9473, 6♂ 1♀ apt., 1♂ macr., 2 lvV; P. Sangihe, mountain stream at Bowokulu, rather small stream with rocky bottom and large boulders, parts with strong current alternating with virtually stagnant pools, *Pseudovelia* at edges under overhanging rocks, 19.XI.1994, N9477, 2♂ 8♀ apt. (1♂ 1♀ PCHC).



Figs. 39-43. *Pseudovelia sangihe.* Paratypes: 39-43 male, 39-40 segment 8, 39 lateral view, 40 detail of rim of ventral impression on segment 8 ventrolateral view, 41 fore leg, 42-43 female apex of abdomen, 42 lateral view, 43 caudal view. – 44 *Pseudovelia argyropardala.* Male paratype hind tarsus. Scale 0.25 mm. – 45 Tarsal segment (*P. sexualis*) illustrating blade like ventral arolium. – 46-47 Head of *Pseudovelia* in lateral view: 46 *P. buccula* illustrating caudally prolonged ventral lobe, 47 *P. lundbladi* with normal ventral lobe. – 48-49 *Pseudovelia argyropardala* female paratype apex of abdomen, 48 lateral view, 49 caudal view. – 50 *Pseudovelia lundbladi* male segment 8 in ventral view. – 51-55 *Xiphovelia skoteina.* Male paratypes: 51 middle tarsus, 52 fore leg, 53 genital segments lateral view, 54-55 segment 9, 54 lateral view, 55 caudal view. – 56-58 *Pseudovelia kalami* holotype male; 56 fore tibia and tarsus, 57-58 segment 8, 57 lateral view, 58 ventral view.
Scale lines for figs. 41, 48, 51: 0.5mm; 39-40, 42-58: 0.25 mm.

Description. – Apterous specimens. Dimensions. Length ♂ 2.12-2.15, ♀ 2.36-2.45; width (across abdominal tergites 4-5) ♂ 0.72-0.76, ♀ 0.92-0.96; width of head ♂ 0.50-0.51, ♀ 0.52-0.56. Colour and pilosity. Dorsally pale orange to pale brick red, head darker, brownish, anterior third of pronotum lighter; lateral and ventral parts lighter than dorsum. Coxae and basal 3/4 of femurs yellowish, remainder of appendages darker, brownish; sutures between body sclerites and spiracles blackish, especially on abdomen. Bands of silvery hairs along inner margins of eyes distinct; patches of silvery hairs laterally on first abdominal tergite, covering most of tergites 2 and 3 and mediocaudally on tergite 6. Body clothed with rather short light brown pilosity which is more distinct ventrally than dorsally. Antennae and legs with usual pilosity.

Length of antennal segments I-IV, 0.43 : 0.28 : 0.31 : 0.47. Anterior third of pronotum smooth, coarse punctation on posterior two thirds sparse and rather indistinct. Lateral margins of pronotum smoothly curved, not or hardly indented, greatest width on posterior third. Ventral arolia bristle like. Middle tibia with about seven long erect hairs on inner side of apical half, becoming distinctly shorter apically. Hind tibia with slightly denser and thicker pilosity apically.

Male. Elongate, connexiva roughly horizontal to slanting slightly upward, lateral margins diverging in anterior, converging in posterior half. Length of antenna slightly more than two thirds of body length (1.5/2.1). Pronotum one and a half times as wide as its median length (0.6/0.4), narrower than width across metanotum. Anterior trochanter rounded. Apical comb on fore tibia relatively short, ± one third (0.2/0.6) tibial length (fig. 41), consisting of about 140 teeth of equal width. First segment of hind tarsus apart from the normal pilosity with 2-3 long (longer than diameter of segment) cilia ventrally. Abdominal tergite 1 large, smooth, sloping downward posteriorly; tergites 2-7 flat, horizontal, in lateral view concealed by the connexiva. Pregenital tergite ± one fifth the dorsal median length of abdomen. First genital segment with a large ventral impression, anteriorly and posteriorly with a pair of spine-like structures, consisting of closely packed bristles (figs. 39, 40).

Female. More broadly oval than male. Connexiva nearly horizontal to slanting 0.16π upward, their lateral margin evenly curved with its greatest width on tergite 4-5. Length of antenna slightly less than two thirds the length of body (1.5/2.4). Pronotum slightly over one and a half as wide as its median length (0.65/0.4), distinctly narrower than width across metanotum. Abdominal tergite 1 large, smooth, sloping downward posteriorly; tergites 2-7 flat, horizontal, in lateral view concealed by the connexiva (except in gravid females). Caudal apices of connexiva rounded, remaining considerably removed from each other, leaving tergite 7 visible. Tergite 8 oriented horizontally, fully visible in dorsal view. Pregenital segment large, its sternite slightly more than one fourth the median length of abdominal venter (0.3/1.1). Genital segments relatively large and protruding caudally, more or less U-shaped in caudal view (fig. 42, 43).

Macropterous form. – Structurally essentially as apterous form except for the usual modifications of macropters in the subfamily. Length ♂ 2.15-2.36, ♀ 2.30-2.35; humeral width of pronotum ♂ 0.85-0.90, ♀ 0.90-0.92. Pronotum brown with a lighter T-shaped mark, anterior transverse leg broad, posterior longitudinal leg narrow, disc of pronotum indistinctly punctate. Hemielytra grey-brown with basal cells largely sordid white and apical cells brownish with lighter centres and membrane greyish. Venation distinct, two elongate basal cells and two shorter apical cells. Lateral keels on basal part of abdomen reaching to the caudal margin of tergite 4, medial keels reaching onto basal part of tergite 2.

Etymology. – *Sangihe* is the Sangirese name for the island where this species was found (Sangir in bahasa Indonesia).

Comparative notes. – (See key). The male genitalia are of a similar shape as in *P. aflia*, *P. borneensis* and *P. epimekta*. Of these *P. borneensis* has an additional mediocaudal ventral projection on first genital segment (fig. 9); *P.epimekta* has the first genital segment and first antennal segment distinctly longer and *P. aflia* has the ventral spine-like groups of bristles less developed.

Pseudovelia borneensis Andersen

(figs. 7, 9)

Pseudovelia borneensis. – Andersen 1983: 264, figs. 35-38.

Material. – BRUNEI DARUSSALAM: Labi Road, Kota Teraja, mountain stream, on foam upstream of log, 15. IV. 1993, N9343A, 1♂ 6♀ apt., 3♂ 6♀ macr.(1♀ apt. 1♀ macr. BMKB, 1♀ macr. NMSC, 1♀ macr. NHMW, 1♀ apt. RMNH, 1♀ apt. ZMAN); Kuala Belalong, small stream behind Field Study Centre, 16. IV. 1993, N9345, leg. N. Nieser, 1♂ 2♀ apt.

Distribution. – Northern Borneo (Sarawak, Brunei, Sabah).

Remarks. – *P. borneensis* was described from macropterous specimens. The apterous form agrees structurally with the macropterous except for absence of wings and reduction of thorax. Dimensions of apterous form: L ♂ 2.35, ♀ 2.43-2.52; width of head ♂ 0.55, ♀ 0.56-0.60; width of pronotum ♂ 0.70, ♀ 0.72-0.77; width ♂ 0.81, ♀ 0.82-0.88. The connexiva of apterous females are nearly vertical whereas in macropters they slant laterally. The pattern of silvery hairs on head and pronotum is identical in both forms, the patch medially on hind margin of head may be rather insignificant in some specimens, both apters and macropters. Apters have patches of silvery hairs laterally on abdominal tergite 1, nearly the whole of tergites 2 and 3 and the posterior 2/3 of tergites 6 and 7.

Pseudovelia reiseni Polhemus

(figs. 17-19)

Pseudovelia reiseni Polhemus 1976: 272-273

Material. – PHILIPPINES: Luzon, Laguna, Los Baños,

Table 1 Measurements of leg segments of Microveliinae described in this paper.

	femur	tibia	tars1	tars2
Pseudovelia aflia				
♂ fore leg	0.61	0.57	0.30	
♂ middle leg	0.72	0.73	0.17	0.28
♂ hind leg	0.81	0.88	0.20	0.27
♀ fore leg	0.65	0.53	0.32	
♀ middle leg	0.73	0.71	0.18	0.29
♀ hind leg	0.86	0.90	0.19	0.27
Pseudovelia afrofila				
♂ fore leg	0.70	0.60	0.29	
♂ middle leg	0.82	0.74	0.12	0.30
♂ hind leg	0.88	0.92	0.16	0.28
♀ fore leg	0.69	0.54	0.30	
♀ middle leg	0.78	0.90	0.14	0.26
♀ hind leg	0.82	0.90	0.14	0.26
Pseudovelia argyropardala				
♂ fore leg	0.63	0.61	0.31	
♂ middle leg	0.83	0.80	0.15	0.30
♂ hind leg	0.84	0.88	0.19	0.32
♀ fore leg	0.66	0.60	0.34	
♀ middle leg	0.82	0.81	0.15	0.30
♀ hind leg	0.91	1.00	0.17	0.31
Pseudovelia epimekta				
♂ fore leg	0.85	0.82	0.40	
♂ middle leg	0.96	1.00	0.25	0.30
♂ hind leg	1.12	1.30	0.41	0.30
♀ fore leg	0.88	0.83	0.40	
♀ middle leg	0.99	1.34	0.25	0.27
♀ hind leg	1.21	1.34	0.42	0.31
*Pseudovelia kalami**				
♂ fore leg	0.80	0.75	0.30	
♂ middle leg	1.03	1.04	0.20	0.38
♂ hind leg	0.98	1.01	0.33	0.30
Pseudovelia koutali				
♂ fore leg	0.68	0.59	0.30	
♂ middle leg	0.82	0.82	0.20	0.30
♂ hind leg	0.86	0.87	0.24	0.26
♀ fore leg	0.69	0.63	0.35	
♀ middle leg	0.93	0.89	0.20	0.30
♀ hind leg	0.98	1.06	0.20	0.30
Pseudovelia mystax				
♂ fore leg	0.77	0.68	0.38	
♂ middle leg	0.93	0.94	0.19	0.33
♂ hind leg	0.99	1.11	0.22	0.32
♀ fore leg	0.81	0.70	0.38	
♀ middle leg	1.01	0.98	0.20	0.36
♀ hind leg	1.08	1.19	0.21	0.33
Pseudovelia pyrokrene				
♂ fore leg	0.70	0.60	0.31	
♂ middle leg	0.89	0.83	0.19	0.30
♂ hind leg	0.91	0.92	0.34	0.30
♀ fore leg	0.71	0.59	0.33	
♀ middle leg	0.87	0.82	0.19	0.28
♀ hind leg	0.98	0.99	0.23	0.31

	femur	tibia	tars1	tars2
Pseudovelia sangihe				
♂ fore leg	0.65	0.58	0.28	
♂ middle leg	0.83	0.79	0.17	0.30
♂ hind leg	0.87	0.95	0.21	0.26
♀ fore leg	0.61	0.57	0.29	
♀ middle leg	0.78	0.78	0.15	0.29
♀ hind leg	0.88	0.96	0.18	0.25
Xiphovelia skoteina				
♂ fore leg	0.49	0.39	0.20	
♂ middle leg	0.56	0.51	0.18	0.26
♂ hind leg	0.54	0.64	0.13	0.19
♀ fore leg	0.52	0.39	0.24	
♀ middle leg	0.61	0.53	0.19	0.28
♀ hind leg	0.59	0.69	0.13	0.22

* Measurements based on single specimen.

stream from Tampalit Falls, 15. XI.1993, leg. H. Zettel, 3♂ (2♂ NHMW, 1♂ NC); Luzon, Infanta, small pool (10x1.5m, up to 0.2 deep) at edge of river bed near mouth of Agos River, many gelatinous algae, 4. IV. 1993, N9335, leg. N. Nieser, 1♂ 1♀. Mindanao, Sarangani (S. Cotabato) prov. Siquel River, pool (area ± 20 m^2, 0.2 m deep) at edge of river bed, slightly turbid stagnant water, under overhanging grassy bank, 23. XI. 1993, N9351, leg. N. Nieser, 3♂; Lake Sebu area, just down stream of second waterfall at edge of spray area, sheltered edge downstream of boulders, 8. XII. 1993, N9373, leg. N. Nieser, 8♂ 1♀ (1♂ BMKB); stream, just downstream of dam at Lopo, under low overhanging grassy bank, 9. XII. 1933, N9377B, leg. N. Nieser, 3♂ 1♀ (2♂ 1♀ macr.; 1♂ apt., 1♂ macr. USCP); irrigation canal at Lopo, rather fast current, 9. XII. 1993, N9378, leg. N. Nieser, 1♀ macr. Apterous unless otherwise indicated.

Distribution. – Only known from Luzon and Mindanao.

Genus ***Xiphovelia*** Lundblad

Xiphovelia was erected by Lundblad (1933) to accommodate his *X. ensis* from Jawa. In addition there are a few species known from the Far East (Esaki & Miyamoto 1959) and one from Sri Lanka (Polhemus 1979). As these belong to the smaller Microveliinae, the paucity of described species is probably due to poor collecting. In specialisation of male genital segments they show some affinity to *Pseudovelia* (small with small parameres) although the genital segments are much smaller. On the other hand the structure of antenna with a short stout first segment, slightly narrower second and distinctly narrower third and fourth and the thoracical structure are quite different. In this genus the middle tarsus has a blade like ventral arolium and meso- meta- notum and first abdominal tergite are fused medially, in the description medial length of mesonotal area refers to the median length of these three tergites together. As stated by Andersen (1982) character states of genera of Microveliinae have not yet sufficiently been studied to get a clear picture about their relationship.

Xiphovelia skoteina sp. n.
(figs. 51-55)

Type material. – Holotype apterous ♂ INDONESIA: Sulawesi Utara, Lakes I, Quellbereich (source area), PPA Bungalow, Nov. 1985, leg. G. Zimmermann (RMNH). (The PPA bungalow is just N of the W tip of Danau Mooat). Paratypes, 51♂ 16♀ all apterous, same data as holotype, distributed as follows: 2♂ 1♀ (allotype) RMNH; 2♂ BPUH; 2♂ 2♀ PCHC; 2♂ 1♀ JTPC; 2♂ 1♀ MBBJ; 15♂ 2♀ NC; 20♂ 7♀ ZC; 3♂ 1♀ ZMAN; 2♂ 1♀ ZMUC. Dumoga Bone N. P. Tumpah River Beach, 19. Oct. 1985, leg. G. Zimmermann, 4♂ (2♂ NC, 2♂ ZC).

Description. – Apterous specimens. Dimensions. Length ♂ 1.80-1.90, ♀ 2.00-2.18, width (across metanotum/first abdominal tergite) ♂ 0.73-0.78, ♀ 0.90-0.99. Colour and pilosity. Generally dull dark ash-grey (anthracite), eyes shining, base of first antennal segment, segments 2 and 3 of rostrum , coxae, trochanters and basal part of femurs yellowish, remainder of appendages castaneous. Pronotum with an uninterrupted lighter band, about as wide as head, in most specimens only slightly contrasting with background. Body covered with well developed pilosity, yellowish, appressed, relatively fine and short on body, longer, more erect and somewhat darker on appendages, eyes bare.

Head slightly less than twice as wide as its median length (0.5/0.3). Length of antennal segments I-IV, 0.19: 0.19: 0.22: 0.31. Width of third antennal segment two third that of fourth (0.02/0.03). Body wall with shallow punctures, posteriorly more shallow and hence less distinct than anteriorly. Pronotum short, about five times as wide as long. median length of mesonotal area one fourth the median length of body (♂ 0.45, ♀ 0.52). Ventral arolia of fore and hind tarsus bristle like. Ventral arolium of middle tarsus leaflike (fig. 52). Middle and hind trochanter of subequal length. Middle tibia with about seven long hairs (apart from normal pilosity) in apical half of inner side, their length compared to the width of tibia (which is stout in both sexes) varying from slightly longer more distally to slightly shorter apically.

Male. General shape elongate oval, greatest width at posterior margin of metanotum, connexiva more or less horizontal, their lateral margins only slightly convergent posteriorly. Apical part of genital segments in dorsal view visible as a small caudal button (in most alcohol specimens genital segments expanded). Length of antenna slightly less than half the length of body (0.89/1.86). Measurements of leg segments, table 1. Anterior trochanter with an ventroapical knob (fig. 51). Dorsal margin of fore femur straight in apical three fourth. Dorsal ('outer') margin of fore tibia convex, grasping comb about half as long as tibia, more distinct in expanded apical part. Genital segments (figs. 53-55) in caudal view with comparatively low lateral 'ears'.

Female. General shape broadly oval, connexiva nearly vertical in most specimens, especially in posterior half where they are distinctly converging. Legs generally more slender than male, measurements of leg segments table 1. Anterior trochanter rounded, anterior tibia with an apical tuft os bristles, mimicking the apex of tibial comb of male. Abdominal tergite 7 somewhat longer than tergite 6, tergite 8 horizontal. Sternite 7 large, its median length one third the median length of abdominal venter. Genital segments retracted into abdomen.

Etymology. – *Skoteinos*, a Greek adjective meaning dark, sombre, refers to the general colour of the species.

Comparative notes. – In the key to *Xiphovelia* by Esaki & Miyamoto (1959) this species runs to *X. boninensis* Esaki & Miyamoto, due to the lack of shiny ('silvery') pilosity. Males of *X. skoteina* differ from all species described so far by the ventroapical tubercle of fore trochanter. Females of *X. boninensis* have the connexiva reflexed over the abdomen in caudal half, whereas in *X. skoteina* these are at most vertical. Moreover in *X. skoteina* the length of middle and hind trochanter is subequal while in other species the middle trochanter is distinctly longer than hind trochanter.

Discussion

Andersen (1983) deals with ten species of *Pseudovelia* from the Oriental Region (in addition seven taxa from the E. Palaearctic are listed). So in this paper the number of Oriental species is nearly doubled. In addition Dr. Zettel (NHMW) writes me that he has several apparently undescribed species from the Philippines. Apparently this is a, still undercollected, species rich genus in the area. They are usually found in shaded places (including overhanging banks or rocks) at the edges of streams or, more rarely, lakes. They are quite often found at places where some foam is assembled (probably because food is trapped in the foam).

Considering primarily the development of the male genital segments the genus *Pseudovelia* seems to split into two groups. The first group is the *hypodonta*-group of Andersen (1983), which is primarily characterized by 4-5 spine-like processes along the margin of the ventral impression of the first genital segment of male. On closer examination, these processes consist of a basal chitinous stump on which a small, acute narrowly packed tuft of bristles is placed. They also agree more or less in general colour pattern and body shape. The *hypodonta*-group consists of *P. aflia, P. borneensis, P. buccula, P. epimekta, P. hypodonta* and *P. sangihe.* Associated with this group is *P. koutali* whereas *P. lundbladi* which has anteriorly a broad ventral process which, although much shorter, reminds somewhat of the process in *P. koutali* and caudally three processes of the same type as found in the *hypodonta*-group may be considered a link between *P. koutali* and the *hypodonta* group. The second group which could be named *feuerborni*-group has the ventral impression on first genital segment of male bordered by a more or less distinct chitinous rim which can be fringed with hairs whereas the impression itself may also be clothed with hairs. This group contains: *P. afrofila, P. argyropardala, P. feuerborni, P. gnoma, P. longitarsa, P. mystax, P. pyrokrene, P. reiseni, P. sexualis* and according to Andersen (1983) *P. tjurpensis.* Whereas the *hypodonta*-group is comparatively homogeneous, the *feuerborni*-group can be divided in four pairs of similar species with *P. mystax* with its rather simple first genital segment and whiskers on the second as the odd one out. The first pair is formed by *P. longitarsa* and *P. sexualis* which have in common blade-like ventral arolia and strongly hairy eyes. The second pair consists of *P. argyropardala* and *P. reiseni,* which have in common a ventral impression of first genital segment without strong rim and sublateral patches of hairs inside the impression. In addition the males have the 'swimming hairs' on first segment of hind tarsi more strongly developed than in other species and both are dark grey with very contrasting patches of silvery hairs which are arranged in roughly the same pattern. These two are also geographically more restricted than the other pairs, P. Karakelong is closer to the Philippines than to the main islands of Indonesia. *P. feuerborni* and *P. pyrokrene* have the ventral impression on first genital segment somewhat similar to *P.argyropardala/reiseni* (although the chitinous rim is somewhat better developed) but have the brick red colour of most *Pseudovelia* and distinctly less developed 'swimming hairs' on first segment of hind tarsi of male. Finally *P. afrofila* and *P. gnoma* are both smaller and more oval than the others and are generally of a dark grey colour with a contrasting transverse rectangular orange mark anteriorly on pronotum. *P. kalami* finally is quite aberrant, apart from the fore tibia the antennal structure and the large depression in male venter are different from other species. This species might turn out to represent a distinct subgenus or closely related genus.

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REFERENCES

Andersen, N. M., 1982. The semiaquatic bugs (Hemiptera, Gerromorpha). – Entomonograph 3: 1-455.

Andersen, N. M., 1983. The Old World Microveliinae (Hemiptera: Veliidae) I. The status of *Pseudovelia* Hoberlandt and *Perivelia* Poisson, with a review of Oriental species. – Entomologica Scandinavica 14: 253-268.

Arnett, jr., R. H., Samuelson, G. A., & Nishida, G. M., 1993. The insect and spider collections of the world. – Flora & Fauna Handbook 11: i-v, 1-308.

Esaki, T., & Miyamoto, S., 1959. Veliidae of Japan and its adjacent territory (Hemiptera-Heteroptera) II. *Xiphovelia* Lundblad. – Sieboldia 2: 91-108, pls.10-13.

Lundblad, O., 1933. Zur Kenntnis der aquatilen und semiaquatilen Hemipteren von Sumatra, Java und Bali. – Archiv für Hydrobiologie Supplement 12: 1-195, 263-488.

Nieser, N. & Chen, P. P., 1991. Naucoridae, Nepidae and Notonectidae, mainly from Sulawesi and Pulau Buton (Indonesia). – Tijdschrift voor Entomologie 134: 47-67.

Nieser, N. & Chen, P. P., 1993. The *Rhagovelia* (Heteroptera: Veliidae) of Sulawesi (Indonesia). – Tijdschrift voor Entomologie 136: 259-281.

Polhemus, J. T., *Pseudovelia reiseni* Polhemus n. sp. p. 272-273, fig. 2. – In J. T. Polhemus & W. K. Reisen, 1976. Aquatic Hemiptera of the Philippines. – Kalikasan, Philippine Journal of Biology 5: 259-294.

Polhemus, J. T., 1979. Results of the Austrian-Ceylonese Hydrobiological Mission 1970. XIX: Aquatic and semiaquatic Hemiptera of Sri Lanka from the Austrian Indo-Pacific Expedition, 1970-71. – Bulletin of the Fisheries Research Station, Sri Lanka 29: 89-113.

Zimmermann, G., 1984. Heteroptera aus dem Nepal-Himalaya. *Geovelia* n. gen. eine Gattung terrestrischer Microveliinae (Insecta: Gerromorpha: Veliinae). – Senckenbergiana Biologia 65: 65-74.

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REVISION OF THE SOUTHEAST ASIAN SILKY LACEWING GENUS *BALMES* (NEUROPTERA: PSYCHOPSIDAE)

Oswald, J. D., 1995. Revision of the southeast Asian silky lacewing genus *Balmes* (Neuroptera: Psychopsidae). – Tijdschrift voor Entomologie 138: 89-101, figs. 1-28, tab. 1. [ISSN 0040-7496]. Published 15 June 1995.

The southeast Asian psychopsid genus *Balmes* is comprehensively revised for the first time. Four species are recognized: *birmanus, formosus, notabilis,* and *terissinus.* Each species is redescribed, illustrated, and keyed. *Balmes notabilis* is removed from the synonymy of *birmanus* and re-established as a valid species. The four species are phylogenetically (cladistically) related as follows: (*formosus* + (*terissinus* + (*notabilis* + *birmanus*))).

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Key words. – Oriental region, phylogeny, taxonomy, key.

The family Psychopsidae, silky lacewings, is a monophyletic (=holophyletic) clade containing five genera and 26 extant species (Oswald 1993). The distribution of extant psychopsids is relictual, being restricted to southern Africa, Australia, and southeast Asia. Fossil taxa attributed to this family are currently known from North America, Europe, Asia, and Australia. Psychopsids are of special interest because of their highly disjunct present geographic distribution, their unusual female ovipositional habits, and their phylogenetic position as the basalmost clade of the neuropterous superfamily Myrmeleontoidea, i.e., as the sister-group to the Nymphidae + Nemopteridae + Myrmeleontidae + Ascalaphidae (Mansell 1992; Oswald, unpublished data).

Since the publication of my earlier monograph of this family (Oswald 1993), I have had the opportunity to examine additional material of the little-known Oriental genus *Balmes* Navás. The recent taxonomic history of this genus can be summarized as follows. Kimmins (1939) recognized three *Balmes* species: *birmanus* (as '*birmana*' [sic], with *terissinus* and *notabilis* as synonyms), *formosus* (as '*formosana*' [sic]), and *gallardi.* New ([1989]) demoted *Balmes* to a junior subjective synonym of the otherwise Australian endemic genus *Psychopsis,* and treated *birmanus, formosus,* and *gallardi* as valid species of *Psychopsis.* Oswald (1993) (1) re-erected the genus *Balmes* on the basis of evidence supporting its monophyly and the existence of a sister-group relationship between *Balmes* and *Psychopsis,* (2) established the validity of *B. terissinus* and removed it from the synonymy of *birmanus,* and (3) noted the existence of a fourth, at that time apparently undescribed, *Balmes* species in China (the 'bns1' of Oswald 1993).

The species 'bns1' has since proven to be conspecific with *notabilis,* which is herein recognized as a valid species and removed from synonymy with *birmanus.* Thus, four valid species of *Balmes* are treated here: *B. birmanus* (McLachlan), *B. formosus* (Kuwayama), *B. notabilis* Navás and *B. terissinus* Navás. The current revision contains redescriptions and illustrations of each species, a key to distinguish among the species, and a phylogenetic (cladistic) analysis of interspecific relationships within *Balmes.* The latter extends the prior analysis of Oswald (1993) through the incorporation of new data for the Taiwanese species *B. formosus.*

MATERIALS AND METHODS

Material and collection acronyms. – This study is based upon approximately 40 adult *Balmes* specimens in the following collections: BMNH, The Natural History Museum, London, England; CUIC, Cornell University Insect Collection, Ithaca, NY, U.S.A.; EIHU, Insect Collection, Hokkaido University, Sapporo, Japan; MCZC, Museum of Comparative Zoology, Cambridge, MA, U.S.A.; MNHP, Muséum National d'Histoire Naturelle, Paris, France; USNM, National Museum of Natural History, Washington, DC, U.S.A.

Illustrations. – Line drawings were executed with the aid of a drawing tube attached to a dissecting microscope. Terminalic illustrations were made from cleared, and generally stained, preparations temporarily mounted in glycerin. Setae are not shown. In illustrations of the gonarcus/mediuncus/9th gonocoxite complex, membranes attached along the antextragonarcal commissure and the venter of the 9th gonocoxites are shown stretched in a manner calculated to best convey their lines of attachment, not necessarily as *in situ*.

Terminology. – General entomological terminology follows Nichols (1989). Terms for terminalic structures follow Oswald (1993).

Annotations. – The following annotations are used in the synonymical listings: Dst, distribution; FT, female terminalia; FW, forewing; H, habitus; Lst, list or listed; MT, male terminalia; Nom, nomenclature; OD, original publication/description; RD, redescription; Tax, taxonomy; W, wing. An asterisk (*) following an annotation indicates a figure (e.g., FW*, forewing figure).

Miscellaneous. – Species are treated in alphabetical order. Forewing lengths were measured from the proximal margin of the tegula to the wing apex (±.1 mm). Unless otherwise cited, reported flight periods are the earliest and latest dates of collection of adults as indicated by label data. Bracketed collection locality names and latitude and longitude coordinates found in the material examined sections have been taken principally from the Official Standard Names Gazetteers of individual southeast Asian countries, which were compiled by the U.S. Defense Mapping Agency Topographic Center for the U.S. Board on Geographic Names.

Systematic part

Genus *Balmes* Navás

Balmes Navás, 1910: 85 (Type species: *Balmes terissinus* Navás, 1910: 85, by monotypy): Navás 1917 (Tax); Kimmins 1939 (Tax); New [1989] (Nom); Oswald 1993 (RD, Tax).

Diagnosis. – The only extant genus of psychopsids known from southeastern Asia. Distinguished from the Australian genus *Psychopsis* (except *P. gallardi*) by the absence in *Balmes* of a prominent dark macula situated distally on each hind wing (fig. 3). Based on illustrations contained in New ([1989]), males of *P.*

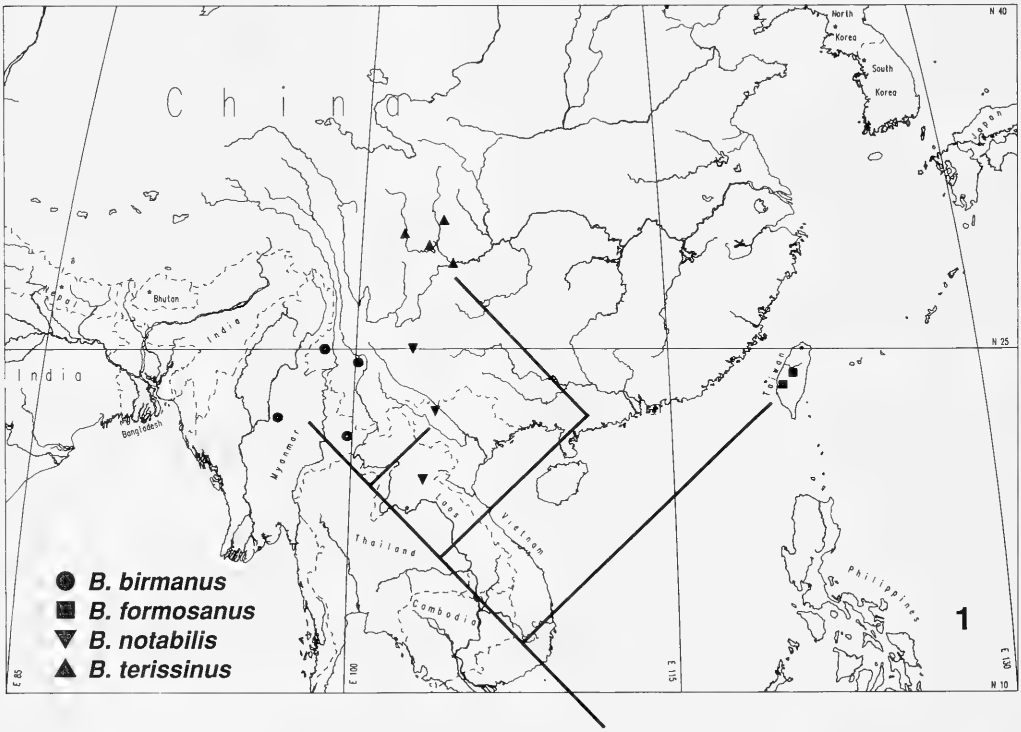


Fig. 1. Geographic distributions of *Balmes* species and cladogram of interspecific relationships. Only accurately located records have been plotted.

gallardi (unique holotype in BMNH, not examined) may be distinguished from males of *Balmes* species by (1) the presence in *gallardi* of an elongate [not short] 9th gonocoxite costa, and (2) the absence in *gallardi* of the male 9th gonocoxite superprocesses modified into a transverse tumulus.

Description. – Head: Ocelli absent, but vertex bearing 2 well-developed ocellar/cranial pulvinae. Forewing: length: 10.8 - ca. 21 mm; coloration: brown mottling on a hyaline ground; forewing costal gradate series absent or reduced (i.e., <6 crossveins), except in *formosus* where it is well developed (>20 crossveins).

Hind wing: hyaline, without a dark distal macula.

Male terminalia: 8th sternite (fig. 6): without a posteromedian lobe; 9th tergite (fig. 6): without free posteroventral processes; 9th sternite (figs. 6, 7): apex rounded (fig. 7) or emarginate (fig. 13), not narrow and parallel-sided in ventral view; gonarcus (figs. 9, 10): intragonarcus present but narrow relative to extragonarcus; extragonarcus composed of a posteriorly protruded dorsal plate, the extragonopons (egps), and a pair of lateral narrow to broad extrahemigonarcus (ehgs); mediuncus (med) weakly decurved, not recurved; 9th gonocoxites (figs. 10, 11): fused medially into a transverse sclerite which articulates with posteroventral angles of hemigonarcus; ventral costae (vc) absent or reduced to short thickenings; superprocesses (spp) present but fused into a transverse elevation on dorsal surface of conjoined gonocoxites (elevation produced as an attenuate process in *notabilis*); ventrolateral lobes (vll) sometimes present; miscellaneous: gonosaccal membrane bearing one (fig. 8) or two (figs. 21, 22) sets of bilaterally paired spiculate lobes; subanale (sa) present (figs. 9, 10).

Female terminalia: Posterior margin of 7th sternite medially depressed and emarginate (figs. 26, 27); 7th and 8th sternites fused, but path of fusion marked by a suture; copulatory fovea approximately hemispherical, overhung posteriorly by anteromedian margin of 8th sternite (figs. 26, 27); 9th gonocoxites: without a longitudinal row of stiff setae below each gonocoxal costa, without a compact aggregation of setae borne adjacent to insertion of stylus, suprastylar setae >50% cochleariform; bursa without lateral corniform diverticulae; spermatheca sigmoid in lateral view, lacking distinct hollow ventrolateral lobes; two bursal accessory glands present, but form and insertion of ducts on bursa varies interspecifically.

Distribution (fig. 1). – Southeast Asia (reported here from Taiwan, southern China, northeastern Burma, northern Laos, and northern Vietnam). The three southeast Asian species of *Balmes* appear to form a complex of allopatric or parapatric species. The few elevation records available for *Balmes* species (all for mainland species) range between 600 and 1825 meters, suggesting that *Balmes* species are montane. This conclusion is also supported by the apparent geographic restriction of mainland *Balmes* species to the upland areas of the countries in which they occur.

Biology and immature stages. – Unknown.

Species (4). – *birmanus*: Burma, China [Yunnan Prov.]; *formosus*: Taiwan; *notabilis*: China [Yunnan Prov.], Laos, Vietnam; *terissinus*: China [Sichuan Prov.].

Classification. – The following sequenced classification is recommended for this genus:

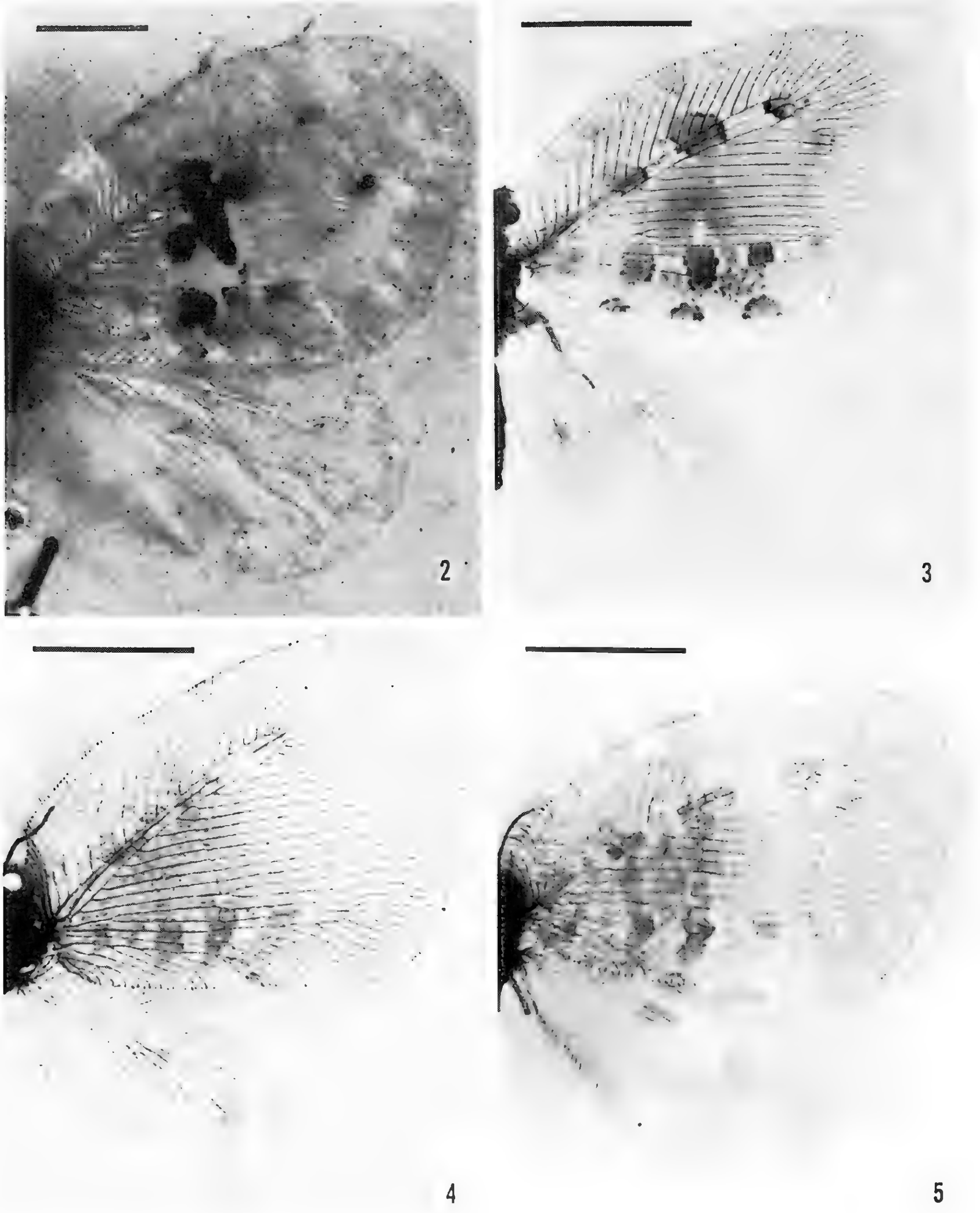
Genus *Balmes* Navás
B. formosus (Kuwayama, 1927)
B. terissinus Navás, 1910
B. notabilis Navás, 1912
B. birmanus (McLachlan, 1891)

Etymology. – From the surname of Catalan philosopher Jaime Luciano Balmes [1810-1848], see Navás 1910: 85. Gender: Masculine, implied from the original combination *Balmes terissinus*, Art. 30d.

Key to adult *Balmes* species

Notes: The male of *formosus* and the female of *notabilis* are unknown.

1. Forewing (fig. 3): costal gradate series absent (<6 crossveins/wing), intraradial area crossed by 2 gradate series, innermost series not bordered by fuscous maculae (light brown shading or mottling may be present) [continental southeast Asia].......2
– Forewing (fig. 2); costal gradate series present (>20 crossveins/wing), intraradial area crossed by 3 well-developed gradate series, innermost series bordered by fuscous maculae [Taiwan and continental southeast Asia] ....*B. formosus*
2. Forewing (figs. 4, 5): membrane immaculate or evenly patterned with light brown mottling, strongly contrasting darker brown maculae absent; Male Terminalia: ventrolateral lobes of male 9th gonocoxites present (figs. 11, 18) [continental southeast Asia] 3
– Forewing (fig. 3): membrane marked with 2 prominent rows of brown maculae (one centered on the 'vena triplica', the other on the mediocubital and intracubital spaces), each row with 2 or 3 maculae that strongly contrast with the light brown to hyaline ground colour of the membrane (fig. 3); hind margin of wing also often with a row of contrasting maculae; Male Terminalia: ventrolateral lobes of male 9th gonocoxites absent (figs. 24, 25) [China: Sichuan Province] .... *B. terissinus*
3. Male 9th sternite: apex rounded (fig. 7); Male 9th gonocoxites: ventrolateral lobes digitate and bluntly pointed distally, apices not membrane



Figs. 2-5. *Balmes* spp., wings. 2, *B. formosus* (paratype); 3, *B. terissinus*; 4, *B. notabilis*; 5, *B. birmanus*. Scale bars = 5 mm.

margined (fig. 11); superprocesses fused into a broad transverse prominence (fig. 11) [Burma, China: Yunnan Province] .... *B. birmanus*

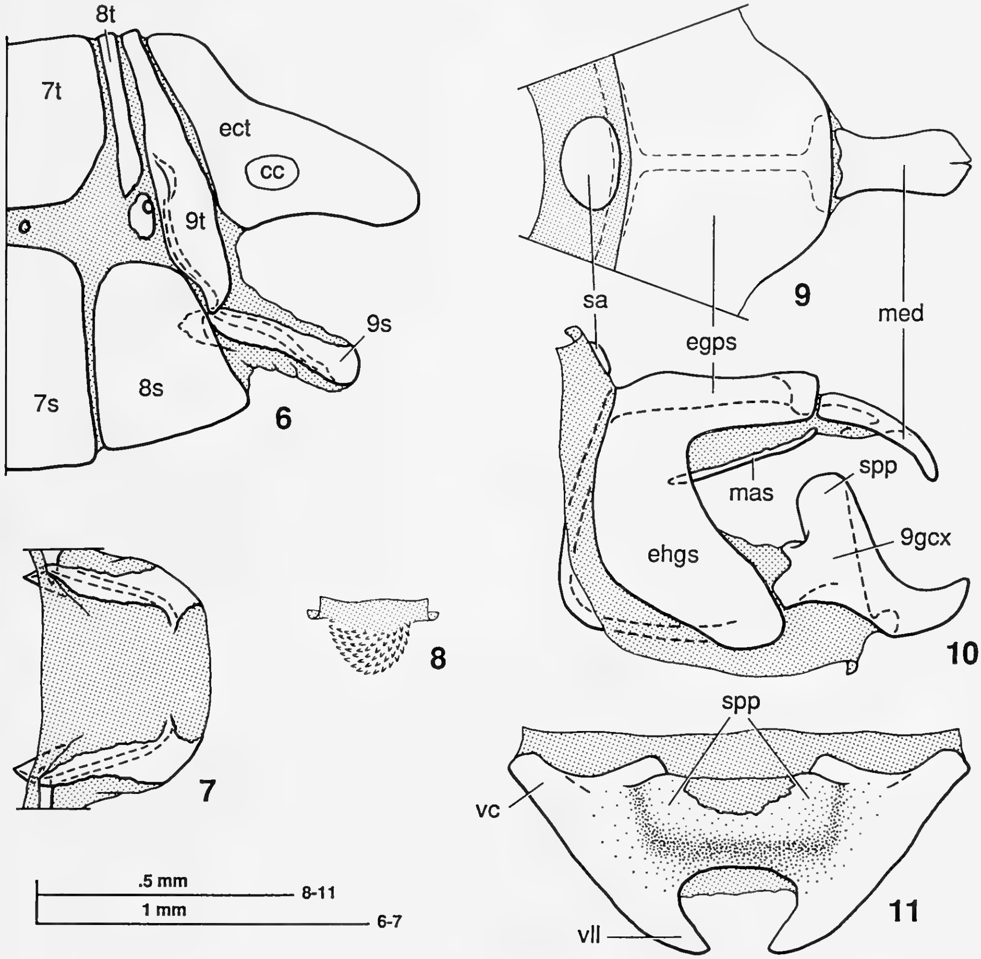
– Male 9th sternite: apex conspicuously emarginate (fig. 13); Male 9th gonocoxites: ventrolateral lobes plate like and broadly rounded distally, apices membrane margined (fig. 18); superprocesses fused and projecting medially as a short process (figs. 16, 17) [China: Yunnan Province, Laos, Vietnam] .... *B. notabilis*

Balmes birmanus (McLachlan)
(figs. 5-11)

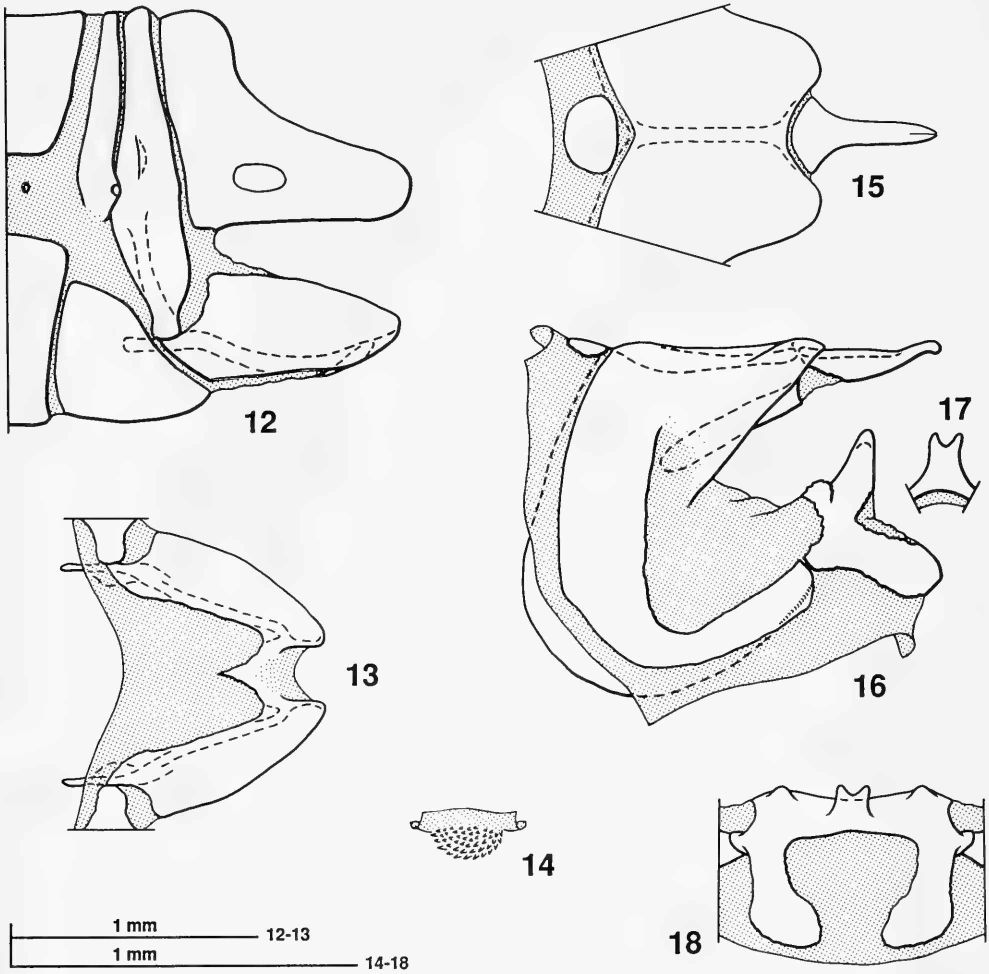
Psychopsis birmana McLachlan, 1891: 320 (OD). – Krüger 1922 (Lst); New [1989] (RD, Dst, MT*, FT*, W*).
Balmes birmanus (*-a* [sic]). – Navás 1930 (Lst, Dst); Kimmins 1939 (Lst, Dst); Oswald 1993 (Lst).

Diagnosis. – Distinguished from all other *Balmes* species by the following combination of characters: (1) forewing intraradial area traversed by two [not three] gradate series (fig. 5), (2) apex of male 9th sternite rounded [not conspicuously emarginate] (fig. 7), and (3) ventrolateral lobes of male 9th gonocoxites present [not absent] (fig. 11).

Description. – Forewing (fig. 5): length: 11.2 - 15.7 mm (mean = 12.5 mm, n = 9 wings); markings: light brown mottling on a hyaline ground, markings somewhat darker along 'vena triplica' and along cubital and mediocubital spaces, distal margin often with small brown patches bounded by narrow hyaline arcs



Figs. 6-11. *Balmes birmanus*, male terminalia. 6, abdominal apex, lateral; 7, 9th sternite, ventral; 8, ventral spiculate lobe of gonosaccus, lateral; 9, medial portion of gonarcus, dorsal; 10, gonarcus / 9th gonocoxite complex, lateral; 11, fused 9th gonocoxites, posterodorsal. Abbreviations: 7s, 8s, 9s, sternites; 7t, 8t, 9t, tergites; 9gcx, 9th gonocoxite(s); cc, cercal callus; ect, ectoproct; ehgs, extrahemigonarcus; egps, extragonopons; mas, mediuncal accessory sclerite; med, mediuncus; sa, subanale; spp, superprocessus; vc, ventral costa; vll, ventrolateral lobe.



Figs. 12-18. *Balmes notabilis*, male terminalia. 12, abdominal apex, lateral; 13, 9th sternite, ventral; 14, ventral spiculate lobe of gonosaccus, lateral; 15, medial portion of gonarcus, dorsal; 16, gonarcus / 9th gonocoxite complex, lateral; 17, medial process of 9th gonocoxites, posterior; 18, fused 9th gonocoxites, posterodorsal.

(these lacking or inconspicuous in rubbed wings); costal gradate series absent (1-2 adventitious costal crossveins occasionally present); intraradial area traversed by two gradate series.

Male terminalia (figs. 6-11): 9th sternite: posterior margin rounded, not sagittally emarginate; gonarcus: intragonarcus narrow dorsally, broadened toward anteroventral angles, anterior and ventral margins marked internally by thickened costae; extrahemigonarcus broad; midline and posterior margin of extragonopons marked by a T-shaped costa internally, posterior margin transverse; mediuncus: length approximately twice average width, slightly constricted basally; apex rounded or obtusely angulate with a narrow sagittal emargination; 9th gonocoxites: superprocesses united sagittally to form a low transverse elevation; elevation bilobed in posterior view due to a shallow median emargination; ventrolateral lobes present as a pair of free, attenuated, and medially convergent lobes; spiculate gonosaccal lobes: one pair present on ventral surface of bursa.

Female terminalia: 7th sternite: parafoveal lobes weakly developed, not prominently projecting; 8th sternite: reduced, transverse, expanded medially, attenuate laterally, anterior margin not emarginate sagittally; bursal accessory gland ducts: fused proximally, attached to sagittodorsal surface of bursa as a single common duct.

Distribution (fig. 1). – Mainland southeast Asia (reported here from northeastern Burma and the adjacent portions of Yunnan Province, China).

Flight period. – 14 March - April (no day recorded).

Primary type. – *Psychopsis birmana.* Holotype ♀ (BMNH), examined. Type locality: 'Birmah' [=BURMA, precise locality unknown]. Verbatim label data: 'Type.' [pink rectangle], 'Type' [white circle with red border], 'Birmah' [script, white rectangle], 'McLachlan Coll. / B.M. 1938-674' [blue rectangle], 'Psychopsis / birmana ML.' [McLachlan script, white rectangle], 'Holotype / Psychopsis / birmana det. / J.D. Oswald 1994' [red rectangle]. Condition: parts of the following missing – both antennae, left fore- and hind legs and right foreleg. Minor insect pest damage. Pinned through thorax, wings spread. Terminalia macerated in KOH by Oswald in 1994, stained with Chlorazol Black, and placed in a glycerin-filled microvial pinned below specimen. This is the single specimen upon which the description of *birmana* was based (McLachlan 1891: 321).

Other material examined (6♂, 3♀ = 9). – BURMA: *Mandalay division*: 1♂, 2♀, Maymyo [22°02'N 96°28'E], iv.1912, Mackwood; 14.iii.[19]01, Barrow; no date, Scott (BMNH). *Shan state*: 2♂, Kolaw, S. Shan States, iv.1916, 1215m (4000'), Mackwood (BMNH); 1♀, Loimwe [Loi Mwe, 21°11'N 99°46'E], iv, 1520-1825m (5000-6000'), Kingford (MCZC). CHINA: *Yunnan province*: 1♂, bet[ween]. Tengyueh [=Tengchong, 25°02'N 98°28'E] and Nan Tien, '1909-10', Brown (CUIC); 2♂, Yun Hsien [=Yunxian, 24°25'N 100°06'E], iv.1942, Jellison (USNM).

Etymology. – Unexplained, probably derived from the type locality 'Birmah' [=Burma].

Balmes formosus (Kuwayama)
(figs. 2, 27)

Psychopsis (*Orientichopsis*) *formosa* Kuwayama, 1927: 123 (OD, H*).
Balmes formosana [sic]. – Kimmins 1939 (Lst, Dst).
Psychopsis formosa. – New [1989] (RD, Dst, FT*, W*).
Balmes formosa [sic]. – Oswald 1993 (Lst).

Diagnosis. – Distinguished from all other *Balmes* species by the presence of three [not two] gradate series traversing the intraradial area of the forewing (fig. 2).

Description. – Forewing (fig. 2): length: ca. 21 mm (n = 1 wing); markings: predominantly hyaline, center of disk with two fuscous maculae, one (proximal) nearly circular and one (distal) elongate and continued anteriorly across 'vena triplica', an additional small fuscous dot in middle of intraradial space just beyond middle gradate series, also with scattered paler brown markings, particularly along cubital and mediocubital spaces; costal gradate series with more than 20 crossveins; intraradial area traversed by three gradate series.

Male: Unknown.

Female terminalia (fig. 27): 7th sternite: parafoveal lobes strongly developed, prominently projecting; 8th sternite: a small cordate plate, anterior margin sagittally emarginate; bursal accessory gland ducts: two free ducts inserted bilaterally symmetrically on dorsal surface of bursa at a pair of widely separated (more than two duct diameters) points.

Distribution (fig. 1). – Taiwan.

Flight period. – August.

Primary type. – Holotype ♀ [not ♂] (EIHU), not examined. Type locality: TAIWAN: 'Rengechi, near Horisha, Taichiu-district, Formosa' [Horisha = TAIWAN: *Nan-t'ou hsien*: Pu-li, 23°58'N 120°57'E].

Material examined (1♀ paratype). – TAIWAN: *Chia-i hsien*: 1♀, 'Kagi' [=Chia-i, 23°29'N 120°27'E], viii.1921, Hirayama (EIHU).

Etymology. – Unexplained, probably derived either from Latin *formosus*, beautiful, or the island name Formosa (=Taiwan). Name incorrectly treated by Oswald (1993) as a noun in apposition, based on the island name Formosa. Since 'formosa' is a valid Latin adjective, the termination of a species-group name based on this word must match the gender of the genus-group name with which it is combined, Art. 31b.

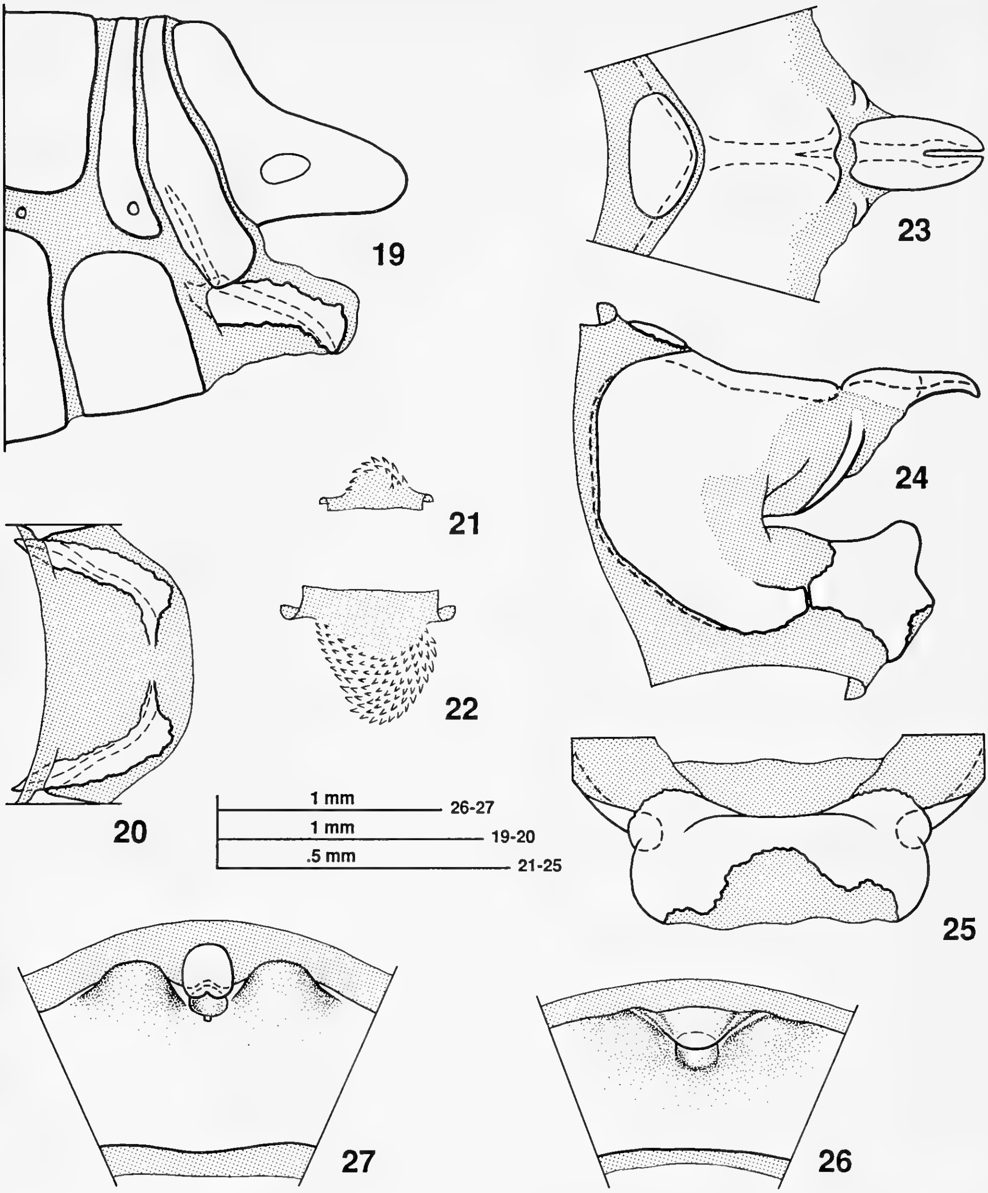
Comments. – *Balmes formosus* is known only from the two females (not males as stated by Kuwayama) of the type series.

Balmes notabilis Navás, **stat. n.**
(figs. 4, 12-18)

Balmes notabilis Navás, 1912: 197 (OD). – Navás 1917 (RD).
'bns1'. – Oswald 1993 (Lst).

Diagnosis. – Distinguished from all other *Balmes* species by the following combination of characters: (1) forewing intraradial area traversed by two [not three] gradate series (fig. 4), (2) apex of male 9th sternite conspicuously emarginate [not rounded] (fig. 13).

Description. – Forewing (fig. 4): length 12.5 - 14.0 mm (mean = 13.2 mm, n = 4 wings); markings: very similar to *birmanus*, light brown mottling on a hyaline ground, markings somewhat darker along 'vena triplica' and along cubital and mediocubital spaces, hyaline-bounded brown patches of distal margin (see *birmanus* description) obscure to absent; costal gradate series absent; intraradial area traversed by two gradate series.



Figs. 19-27. *Balmes terissinus*, male terminalia. 19, abdominal apex, lateral; 20, 9th sternite, ventral; 21, dorsal spiculate lobe of gonosaccus, lateral; 22, ventral spiculate lobe of gonosaccus, lateral; 23, medial portion of gonarcus, dorsal; 24, gonarcus / 9th gonocoxite complex, lateral; 25, fused 9th gonocoxites, posterodorsal. 26-27, *Balmes* spp., female 7th (medial portion) and 8th sternites, ventral. 26, *B. terissinus*; 27, *B. formosus*.

Male terminalia (figs. 12-18): 9th sternite: posterior margin prominently emarginate medially; gonarcus: intragonarcus narrow throughout, broadest at anteroventral angle; extragonopons with a strong sagittal costa internally, posterior margin with a pair of rounded lobes divided by a broad medial excavation; extrahemigonarcus composed of a broad proximal region and a narrower distal region, the two regions being continuous anteroventrally but separated distal to this region by an approximately 60° angle in the posterior margin of the hemigonarcus; mediuncus: apical 2/3 to 3/4 slender and nearly parallel sided, base flared and broader; apex bifid (condition usually not obvious because paired apical lobes usually lie parallel with their medial margins adpressed); 9th gonocoxites: superprocesses united and produced medially to form a short digitate process; apex of process distinctly forked (as shown in fig. 17) to only slightly emarginate; anterior margin of transverse gonocoxal bar lateral to median process usually with a pair of low, setose, convexities; ventrolateral lobes present as a pair of shallowly concavo-convex, membrane-margined, spathulate lobes; spiculate gonosaccal lobes: one pair present on ventral surface of bursa.

Female: Unknown.

Distribution (fig. 1). – Mainland southeast Asia (reported here from southern China [Yunnan Province], northern Laos and northern Vietnam).

Flight period. – 22 April - 2 June.

Primary type. – Lectotype ♂ (BMNH), designated by New ([1989]) by inference of holotype, examined. Type locality: PEOPLE'S REPUBLIC OF CHINA: probably Yunnan Province, see discussion below. Verbatim label data: 'Type' [white circle with red border], 'mamun[?], yuman [=? Yunnan] / H. E. Hobson / 1900-192' [white rectangle, text in somewhat illegible script], '*Balmes / notabilis* / Nav[ás].' [blue-lined white notebook paper, rectangle with corners clipped, in Navás'(?) script], 'Lectotype / *Balmes / notabilis* det. / J.D. Oswald 1994' [red rectangle]. Condition: parts of left fore- and midlegs and right midleg missing, wings somewhat tattered. Stage mounted, wings spread, probably formerly extracted from alcohol. Terminalia macerated in KOH and placed in a glycerin-filled microvial pinned below specimen.

Navás (1912) cited two specimens in the type series of *notabilis*, one in the British Museum and one in his personal collection. The BMNH specimen cited by New ([1989]:845) as the 'holotype' must, consequently, be considered a lectotype, Art. 74b. The specimen stated to have been in Navás' collection has not been traced. The precise type locality of *notabilis* is uncertain. In the original description Navás cited a single locality, 'China, Junam' (referred to by Navás 1917 as 'China: Yu-nam'), but this site does not match the text of the lectotype's locality label. It is possible that this locality was taken from the unseen specimen retained in Navás' collection. Attempts to identify 'Junam' or 'Yu-nam' in several Chinese gazetteers have failed. In the present work I interpret the word 'yuman' on the lectotype locality label to be a variant or erroneous spelling of 'Yunnan', in reference to the Chinese province of Yunnan, where *notabilis* has been confirmed to occur. The significance of the word 'mamun[?]' is unknown. It could not be traced in the available gazetteers.

Other material examined (3♂). – CHINA (Mainland): *Yunnan Prov.*: 1♂, Kunming [25°04'N 102°41'E], 2.vi.1941 (USNM). LAOS: *Xieng khouang*: 1♂, Xieng Khouang [19°20'N 103°22'E], 22.iv.1919, Salvaza (BMNH). VIETNAM: *Hoang lien son*: 1♂, 'Chapa' [=Sa Pa, 22°21'N 103°50'E], Tonkin, v.-vi.1916, Salvaza (BMNH).

Etymology. – Unexplained, probably derived from Latin, *notabilis*, noteworthy.

Comments. – Based on its distinctive male terminalia, *B. notabilis* is here recognized as a valid species and is resurrected from the synonymy of *birmanus*, where it was placed by Kimmins (1939) and subsequent authors.

Balmes terissinus Navás
(figs. 3, 19-26)

Balmes terissinus Navás, 1910: 85 (OD, FW*). – Navás 1917 (RD); Oswald 1993 (Lst).

Diagnosis. – Distinguished from all other *Balmes* species by the following combination of characters: (1) forewing intraradial area traversed by two [not three] gradate series (fig. 3), (2) apex of male 9th sternite rounded [not conspicuously emarginate] (fig. 20), and (3) ventrolateral lobes of male 9th gonocoxites absent [not present] (fig. 25).

Description. – Forewing (fig. 3): length 10.8 - 15.7 mm (mean = 13.1 mm, n = 22 wings); markings: pattern similar to *birmanus* with brown mottling on a hyaline ground, but markings along 'vena triplica' and cubital and mediocubital spaces usually strongly contrasting with adjacent membrane, hyaline-bounded brown patches of distal margin (see *birmanus* description) obscure to absent; costal gradate series absent (1 or 2 adventitious costal crossveins occasionally present); intraradial area traversed by two gradate series.

Male terminalia (figs. 19-25): 9th sternite: posterior margin rounded, not sagittally emarginate; gonarcus: intragonarcus expressed as a narrow internal costa following course of antextragonarcal commissure; extragonopons not prominently produced, midline marked internally by a thickened costa which divides posteriorly, distomedial margin of extragonopons narrowly emarginate; extrahemigonarcus broad dorsally, tapering toward articulation with 9th gonocoxites; postextragonarcal commissure often poorly defined; mediuncus: length 1 1/2 to 2 times width, nearly parallel-sided proximally, attenuated distally; apex bifid with a narrow but distinct separation between the tines; 9th gonocoxites: superprocesses united sagittally to form a low transverse elevation; ventrolateral lobes absent; spiculate gonosaccal lobes: two pairs present – an inconspicuous pair on dorsal surface of bursa adjacent to ventral margin of fused 9th gonocoxites, and a second larger pair on ventral surface.

Female terminalia (fig. 26): 7th sternite: parafoveal lobes weakly developed, not prominently projecting; 8th sternite: reduced, transverse, expanded medially, attenuate laterally, anterior margin not emarginate sagittally; bursal accessory gland ducts: two free ducts inserted bilaterally symmetrically on dorsal surface of bursa at a pair of closely adjacent (less than two duct diameters) points.

Distribution (fig. 1). – Mainland southeast Asia (reported here only from Sichuan Province, China [some imprecise records may also refer to far northern Yunnan Province]).

Flight period. – April (no date) - 21 July.

Primary type. – Holotype ♂? (MNHP?), not examined. Type locality: 'Tibet, Ta-Tsien-lou' [=CHINA: *Sichuan province*: Lucheng (=Tatsienlu, Tatsientu, Kangting, and Kangding, 30°03'N 102°02'E)].

The presumptive holotype of *terissinus*, stated by Navás to reside in the Paris Museum, was not available for examination. The forewing maculation patterns of the material attributed here to this species closely match the maculation pattern shown in Navás' (1910:86, fig. 24) figure of the forewing of *terissinus*. Particularly apparent are: (1) the strong contrast between the wing's dark macula and its light ground colour, and (2) the well-developed row of macula along the hind margin of the forewing. The identification of this material is also supported by distributional evidence. All of the specimens attributed here to *terissinus* were collected in China in either Sichuan province or, possibly for some specimens, far northern Yunnan province. The combined distribution of this material and the type locality of *terissinus* (from Sichuan province) form a compact range which is allopatric relative to the ranges of other *Balmes* species.

Material examined (18♂, 3♀, 5?). – CHINA: *Sichuan* [=Szechwan] *province*: 1?, Suifu [=Yibin, 28°46'N 104°34'E], 30.v.1925, 610m (2000'), Graham (MCZC); 17♂, 4?, Yunnan border S of Suifu, iv.[19]29, Graham (MCZC, USNM); 1♀, Chengtu [=Chengdu, 30°40'N 104°04'E], 21.v.1929, Parish? (CUIC); 1♂, 1♀, Chengtu, v.1934, Graham (MCZC, USNM); 1♀, Mt. Omei [=Emei Shan, 29°32'N 103°21'E], 21.vii.[19]35, 1215m (4000'), Graham (USNM).

Etymology. – Derived from the surname of J. Terisse, collector of the holotype (see Navás 1910:85).

PHYLOGENETIC ANALYSIS

Overview. – A cladistic analysis was used to estimate relative interspecific relationships within the genus *Balmes* and the position of *Balmes* within the family Psychopsidae.

Computational methods. – Cladograms were generated by application of the 'ie' (implicit enumeration) tree calculation option of HENNIG86 (Farris 1988) to the input data file described under *Data* below. The 'ie' tree calculation option guarantees identification of the minimal length tree(s) for a given input matrix.

Characters. – The characters and character states used in the present analysis are identical to those used in the earlier analysis of Oswald (1993), except for the addition of a fifth state to character 44, see below. See Oswald (1993) for detailed definitions and discussions of characters and their states.

Character 44. Female 8th sternite. (state 4 [new state]) present, a small cordate plate, emarginate anteromedially. Oswald (1993) attributed four unordered states to this character. Because the female 8th sternite state found in *formosus* does not fit well into any of those states, the preceding state is added here to accommodate *formosus* into the present analysis. This state is an autapomorphy of *formosus*.

Data. – The input data matrix contained numerically-coded morphological character data derived from: (1) Oswald (1993: Appendix 2), for 21 previously character-scored psychopsid species and the hypothetical ancestor used to root the tree, and (2) a row of newly coded data (Table 1) for *B. formosus*. Characters 10-39 in table 1 pertain to the unknown male of *formosus* and were coded as unknown data ('?'). The following two additional *formosus* characters were coded as unknown: [1] Shape of forewing humeral plate (character 7) – the humeral plates of the

Table 1. Coded character state data for *Balmes formosus*. Characters (left numbers) and states (right numbers) are identical to those given by Oswald (1993:28-40), except as noted in the text under 'Phylogenetic Analysis: Characters'. Matrix symbols: 0, 1, 2, 4 character state numbers; ?, missing data (i.e., missing female data [characters 7 and 49] and unknown male data [characters 10-39]).

1	1	16	?	31	?	46	1
2	0	17	?	32	?	47	1
3	0	18	?	33	?	48	1
4	0	19	?	34	?	49	?
5	1	20	?	35	?	50	1
6	1	21	?	36	?	51	1
7	?	22	?	37	?	52	0
8	1	23	?	38	?	53	0
9	0	24	?	39	?	54	2
10	?	25	?	40	1	55	1
11	?	26	?	41	0	56	1
12	?	27	?	42	1	57	0
13	?	28	?	43	1	58	0
14	?	29	?	44	4	59	0
15	?	30	?	45	0	60	1

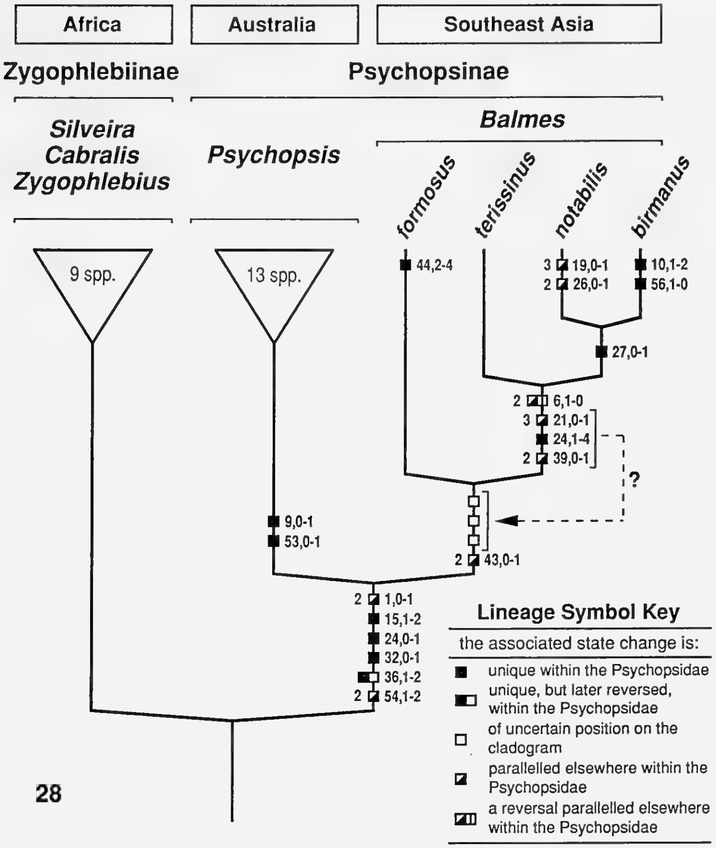


Fig. 28. Cladogram showing relative interspecific relationships within *Balmes*, and the position of *Balmes* relative to the other higher taxa of extant psychopsids. Character data are mapped only for *Balmes* and immediately adjacent lineages. Character state changes are shown in the following format [left to right]: (1) number of occurrences on the cladogram, including those on lineages not fully illustrated (see *Phylogenetic Analysis: Results*), (2) lineage symbol, (3) character number, (4) state numbers [ancestral state - derived state]. Male terminalic characters 21, 24, and 39 cannot be unambiguously mapped within *Balmes* because the male of *formosus* is unknown.

available paratype of *formosus* are obscured, consequently, this character could not be coded, and [2] Distal apodemes of female 9th tergite (character 49) – no distal apodemes could be located in *formosus*; however, because the membranous region where these apodemes are located is poorly preserved in the available paratype, the apparent absence of these structures may be an artifact, particularly since they are frequently difficult to observe even in well-preserved material. In the analysis of Oswald (1993), distal apodemes were shown to be a synapomorphy of the Psychopsidae, and it is strongly suspected that they will subsequently be found to be present in *formosus*. To indicate the present unreliability of the coding of this character in *formosus*, it has been coded as an unknown datum in the present analysis.

Results. – A single most parsimonious tree (length = 105, c.i. = 0.83, r.i. = 0.91) was found. This tree is shown in fig. 28 in a reduced form that illustrates character data only for lineages within *Balmes* and those that immediately surround its attachment site to the more general tree. The branching patterns and character distributions of species within *Psychopsis* and the Zygophlebiinae are identical to those presented by Oswald (1993: 43, fig. 53). The tree shown in fig. 28 places *Balmes* as the sister-group to the genus *Psychopsis* and resolves relative interspecific relationships within *Balmes* as follows: (*formosus* + (*terissinus* + (*notabilis* + *birmanus*))).

General discussion. – Oswald (1993) depicted the southeast Asian species clade *terissinus* + *notabilis* [as 'bns1'] + *birmanus* as the monophyletic sister-group of the Australian genus *Psychopsis*, and advocated taxonomic recognition of *Balmes* at generic rank. Additionally, the Taiwanese species *formosus* (not examined for that analysis) was tentatively attributed to *Balmes*. The finding here that *formosus* represents the sister-group to the clade *terissinus* + *notabilis* + *birmanus* confirms the appropriateness of placing *formosus* within *Balmes*.

The monophyly of *Balmes* is supported in the current analysis by a single character: the fusion of the female 7th and 8th sternites (character 43; independently derived in *Psychopsis illidgei*). However, because the male of *formosus* is currently unknown, this weak level of support may be misleading. Three male terminalic characters (21, 24, 39) contain state transformations that are synapomorphic for the three non-*formosus Balmes* species; any or all of the derived states of these transformations could be subsequently identified in the male of *formosus* and lead to more robust support for the *Balmes* clade.

Character discussions. – [Character 6] Forewing, crossveins of costal gradate series: (0) absent or few [mean ≤ 5 crossveins/wing]; (1) numerous [mean > 5 crossveins/wing]. The previous analysis of Oswald (1993) identified two equally parsimonious three-step optimizations of this character, either (1) the presence of a well-developed gradate series is plesiomorphic within the Psychopsidae and secondarily reduced in *Zygophlebius pseudosilveira* Oswald ['zns1' of Oswald 1993] and *Balmes*, or (2) the absence of well-developed gradate series is plesiomorphic within the Psychopsidae and developed independently in *Psychopsis* and the Zygophlebiinae, but subsequently lost in the zygophlebiine species *Zygophlebius pseudosilveira*. The presence of a well-developed gradate series in *Balmes formosus*, and its inferred position here as the sister-group to the three *Balmes* species treated by Oswald (1993), now renders the first optimization more parsimonious than the second. The current cladogram unambiguously supports the first optimization as the better interpretation of costal gradate series evolution within the Psychopsidae, with the minor modification that the loss of the costal gradate series in *Balmes* is now seen as a synapomorphy of only the three Indochinese *Balmes* species, rather than as a synapomorphy of the entire genus.

[Character 39] Male gonosaccal membrane, rounded spiculate lobes: (0) absent; (1) present. The presence of a pair of spiculate lobes on the venter of the eversible male gonosaccus is an interesting feature of the male terminalia of the Indochinese species of *Balmes*. A similar pair of lobes has been developed independently in *Psychopsis insolens*. These lobes probably function during copulation and insemination to anchor the everted male gonosaccus within the female bursa (Oswald 1993). Because the male of *B. formosus* is unknown, it is currently uncertain whether the presence of these lobes constitutes a synapomorphy of *Balmes* in its entirety, or only of its mainland species. A second, smaller, pair of lobes is present on the dorsal surface of the gonosaccus in *B. terissinus*. Because *terissinus* is the sister-group of the one-pair-lobed clade *notabilis* + *birmanus*, and the male of *formosus* is unknown, it is presently impossible to infer the proper cladogram positions of, and polarities among, the three states (a) no lobes, (b) one pair of lobes, and (c) two pairs of lobes. Discovery of the male of *formosus* should resolve these questions.

[Character 56] Female bursa, number of inserted bursal accessory gland ducts: (0) 1 unpaired duct; (1) 1 pair of ducts; (2) 2 pairs of ducts. One pair of bursal accessory glands with ducts that insert at a pair a widely separated, bilaterally symmetrical, points on the dorsal/dorsolateral surface(s) of the female bursa is plesiomorphic in the Psychopsidae (Oswald 1993; state (1) above). This plesiomorphic condition undergoes significant alteration in the Indochinese species of *Balmes*. *Balmes formosus* exhibits the plesiomorphic condition of two widely separated [>>2 times single duct diameter] ducts. In *B. terissinus* two separate ducts are present, but they are inserted very close together [<2 times single duct diameter]. In *B. birmanus* the ducts are partially fused distally, resulting in only one, common, duct being inserted on the dorsum of the bursa. The intermediate state of *terissinus* was not treated separately here, to maintain consistency with the analysis of Oswald (1933); however, were it to be considered as a separate state, the narrowing of the interduct insertion distance would map on fig. 28 as another synapomorphy of the clade *terissinus* + *notabilis* + *birmanus*. Since the female of *notabilis* is unknown, it is uncertain whether the fusion of the bursal accessory gland ducts should be considered a synapomorphy of *notabilis* + *birmanus*, or simply an autapomorphy of *birmanus*. The distal fusion of bursal accessory gland ducts is an unusual condition, which, to my knowledge, has not been reported in any other neuropteran.

Biogeography

The placement of *formosus* within *Balmes* is consistent with the biogeographic hypothesis advanced by Oswald (1993), which suggested that southeast Asian psychopsids constituted a monophyletic group that could be traced to a common ancestor that reached Asia either by active dispersal from Australia or by transport on an ancient rift fragment derived from the northern margin of Gondwanaland in the vicinity of present-day Australia. Additionally, the basal position of *formosus* within *Balmes* correlates with the marked disjunction between the known distributions of *formosus* (Taiwan) and the mainland *Balmes* clade composed of *terissinus*, *notabilis*, and *birmanus* (upland areas in Burma, Laos, Vietnam, and south central China). Although the precise significance of this disjunction is unclear, its explanation is probably rooted in the historical biogeography of southeastern Asia.

FUTURE RESEARCH

The genus *Balmes* is the most poorly known of the five extant genera of the family Psychopsidae. Distributional records for this genus are sparse and additional collecting is needed to more fully document the ranges of its species. It will be especially interesting to see if the apparent allopatry of the Indochinese species is corroborated by future collections. The adult female of *notabilis* and the adult male of *formosus*, remain unknown. The discovery of the male of *formosus* is particularly desirable.

The immature stages of *Balmes* species are completely unknown. Their discovery would be of considerable interest because it would make possible comparisons among the larvae of psychopsids from southern Africa, Australia, and southeast Asia, the three disjunct regions of the world in which living silky lacewings are currently found.

Because the neuropterid fauna of southeast Asia is poorly known, additional undescribed psychopsid species may exist in this region. Any new living species discovered in this region would be expected to fall within, or as sister-groups to, the *Balmes* clade.

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REFERENCES

Farris, J. S, 1988. Hennig86 Reference. Version 1.5. – Privately published.

Kimmins, D. E, 1939. A review of the genera of the Psychopsidae (Neuroptera), with a description of a new species. – Annals and Magazine of Natural History (11)4: 144-153.

Krüger, L, 1922. Psychopsidae. Beiträge zu einer Monographie der Neuropteren-Familie der Psychopsiden. – Stettiner Entomologische Zeitung 83: 17-48.

Kuwayama, S, 1927. On a new species of Psychopsidae from Formosa. – Insecta Matsumurana 1: 123-126.

Mansell, M. W, 1992. The systematic position of Nemopteridae (Insecta: Neuroptera: Myrmeleontoidea). – In: Canard, M., H. Aspöck & M. W. Mansell, eds., Current Research in Neuropterology. – Proceedings of the Fourth International Symposium on Neuropterology, pp. 233-241.

McLachlan, R, 1891. An Asiatic *Psychopsis* (*Ps. birmana*, n. sp.). – Entomologist's Monthly Magazine 27: 320-321.

Navás, L, 1910. Hemeróbidos (Ins. Neur.) nuevos con la clave de las tribus y géneros de la familia. – Brotéria (Zoologica) 9: 69-90.

Navás, L, 1912. Insectos neurópteros nuevos o poco conocidos. – Memorias de la Real Academia de Ciencias y Artes de Barcelona (3)10: 135-202.

Navás, L, 1917. Ensayo monográfico de la familia de los Sicópsidos (Ins. Neur.). – In: Asociación Española para el Progreso de las Ciencias, Congreso de Valladolid (5th, held October 1915) 6: 181-210.

Navás, L, 1930. Névroptères et insectes voisins. Chine et pays environnants. Première [I] série. – Notes d'Entomologie Chinoise 1(6): 1-12.

New, T. R, 1989. The Psychopsidae (Insecta: Neuroptera) of Australia and the Oriental Region. – Invertebrate Taxonomy 2 (1988): 841-883.

Nichols, S. W, 1989. The Torre-Bueno glossary of entomology. Revised Edition, compiled by Stephen W. Nichols. – New York Entomological Society, New York, 840 pp.

Oswald, J. D, 1993. Phylogeny, taxonomy and biogeography of extant silky lacewings (Insecta: Neuroptera: Psychopsidae). – Memoirs of the American Entomological Society 40: 1-65.

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REVISION OF THE COCKROACH GENUS *HOMOPTEROIDEA* SHELFORD (BLATTARIA, POLYPHAGIDAE)

Roth, L.M., 1995. Revision of the cockroach genus *Homopteroidea* Shelford (Blattaria, Polyphagidae). – Tijdschrift voor Entomologie 138: 103-116, figs. 1-55. [ISSN 0040-7496]. Published 15 June 1995.

Eight species of *Homopteroidea* occur in Malaysia, Mentawai I., Philippines, Sabah, Sarawak, Sulawesi, and Sumatra. Five species are redescribed, one is transferred from *Ctenoneura*, another is resurrected from synonymy, and two new taxa are described. Diagnostic characters are given for the genus and a key is presented to distinguish the adults.

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Key words. – *Homopteroidea*; Blattaria, Polyphagidae; cockroaches; taxonomy; redescriptions, new species.

Princis (1963: 104) listed four species of *Homopteroidea* from Malaysia and Indonesia. In the present paper eight taxa are considered to be valid: one species is transferred from *Ctenoneura*, another is resurrected from synonymy, five are redescribed, and two new taxa are described.

The following museums and their curators or collection managers kindly loaned me specimens: HECO – Hope Entomological Collections, University of Oxford, England; Dr. George C. McGavin & Mr. I. Lansbury; MZZB – Museum Zoologi Bogoriense, Bogor, Indonesia; MCZC – Museum of Comparative Zoology, Harvard University, Cambridge, MA, U.S.A.; RMNH – National Museum of Natural History (Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands; Mr. J. van Tol; ZILS – Zoological Institute, Lund, Sweden; Dr. Roy Danielsson.

SYSTEMATIC PART

Genus ***Homopteroidea*** Shelford

Homopteroidea Shelford, 1906: 274. – Type species: *Homopteroidea nigra* Shelford, by monotypy.

Fulmekia Karny, 1926: 152. – Type species: *Homopteroidea nodipennis* (Karny) = *Fulmekia nodipennis* Karny, by monotypy.

Diagnosis. – Eyes reduced, wide apart, lateral, located behind the antennal sockets (fig. 19). Tegmina and wings usually fully developed extending beyond end of abdomen, or tegmina reduced and hind wings vestigial (one species, fig. 53); venation and pigmentation of right and left tegmina usually differ in fully developed winged forms, the major veins thickened or raised, the region of the presutural vein (Hanitsch's terminology) branches of the right tegmen colourless hyaline (fig. 3, right, a; except in *aberrans).* Hind wing without an intercalary vein between the radius and media, cubitus vein with two (fig. 34) or three (fig. 11), branches whose distal regions usually are connected by cross veins (fig. 4; except in *aberrans*). Front femur Type C_1, the piliform spinules are practically contiguous and appear as a dense fringe (fig. 22); pulvilli absent, tarsal claws symmetrical, distinctly toothed on their proximal halves, arolia usually absent (fig. 5), or if present small and 'fleshy' whitish (fig. 6). Male: Abdomen unspecialized; the supraanal plate usually with a large white or yellowish medial nonsetose macula (fig. 13; absent in male *aberrans* and all females; I do not consider this a tergal gland). I have examined a pair of *Homopteroidea nodipennis* that were collected joined end to end *in copula* with the distal half of the male's supraanal plate bent anteriorly and the female's terminalia were inserted and held by the male's phallomeres in his genital chamber. Apparently the unsclerotized membranous zone on the male's supraanal plate is more flexible than the heavily sclerotized areas and allows the plate to be bent so that the female's genital segments can be inserted and grasped properly; some pinned specimens have the distal half of the supraanal plate bent upwards even though they are not in copula. Subgenital plate symmetrical with a pair of similar widely spaced styli (fig. 14); the anterior margin of the plate often is straight and usually lacks lateral apodemes (fig. 30).

Female subgenital plate incised longitudinally (fig. 50).

Distribution checklist by species of *Homopteroidea*

(Records for specimens from localities which I have not seen are taken from the literature and are shown in brackets.)

aberrans Hanitsch: Mentawai; Sabah; Sumatra .. 115
biramiata sp. n.: Sumatra 112
brachyptera sp. n.: Sumatra 114
maculata Hanitsch: Mentawai; Philippines; Sabah. [Java; Sumatra] 112
minor Hanitsch: Sabah; Sumatra 114
nigra Shelford: [Java]; Malaysia; Mentawai; Sabah; Sarawak; Sulawesi; [Sumatra] 109
nodipennis Karny: Malay Peninsula; Sabah; Sarawak; Sumatra 106
shelfordi Hanitsch: Sabah; Sarawak. [Borneo; Malacca; Sumatra] 104

Geographical distribution checklist of *Homopteroidea* species

(Specimens from localities I have not seen are taken from the literature and are shown in brackets.)

Borneo: *shelfordi.* – Java: [*maculata; nigra*]. – Malacca: [*shelfordi*]. – Malayasia: *nigra.* – Malay Peninsula: *nodipennis.* – Mentawai I.: *aberrans; maculata; nigra.* – Philippine I.: *maculata.* – Sabah: *aberrans; maculata; minor; nigra; nodipennis; shelfordi.* – Sarawak: *nigra; nodipennis; shelfordi.* – Sulawesi: *nigra.* – Sumatra: *aberrans; biramiata; brachyptera; minor; nodipennis;* [*maculata; nigra; shelfordi*]

Key to species of *Homopteroidea*

1. Tegmina and wings fully developed extending beyond end of abdomen 2
– Tegmina reduced, not reaching end of abdomen, hind wings vestigial (fig. 53) .... *brachyptera*
2. Left and right tegmina similar in colour and sclerotization. Hind wing branches of the cubitus vein not connected by cross veins (fig. 1E in Roth 1993) .... *aberrans*
– Right tegmen with a clear hyaline presutural zone which is coloured in the left one (fig. 3). Hind wing branches of the cubitus vein connected by cross veins (fig. 4) 3
3. Tegmina with a pale hyaline macula on their proximal halves (fig. 28) .... *maculata*
– Tegmina without pale maculae 4
4. Hind wing with two cubitus branches (fig. 34) 5
– Hind wing with three cubitus branches (fig. 4) 6
5. Hyaline presutural zone with four or five oblique branches (fig. 43). Arolia absent .... *minor*
– Hyaline presutural zone with more than five branches (fig. 34). Arolia present (fig. 33) .... *biramiata*
6. Pronotum dark reddish brown with the lateral border regions lighter (fig. 20). Antennae brownish or black with as many as 15 white terminal antennomeres. Male genitalia as in fig. 25.......... .... *nigra*
– Pronotum with the distal lateral border regions whitish or pale (figs. 1, 7). Antennae without white terminal segments 7
7. Arolia absent (fig. 5). Male genitalia as in fig. 2 .... *shelfordi*
– Arolia present (fig. 6). Male genitalia as in fig. 8 .... *nodipennis*

REDESCRIPTIONS, AND DESCRIPTIONS OF NEW SPECIES

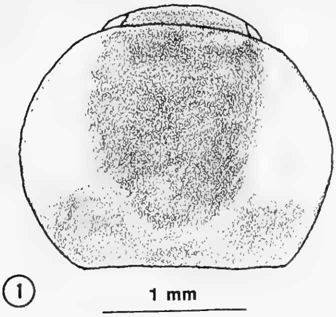
Homopteroidea shelfordi Hanitsch
(figs. 1-5)

Homopteroidea shelfordi Hanitsch 1925: 99, fig. 12 (♂ & ♀) (in part, 2♂ from Mt. Murud only); 1929: 266, fig. 6; 1932a: 52; 1932b: 6; 1933a: 328; 1933b: 235; Bruijning 1948: 146; Princis 1963: 104.
Fulmekia nodipennis (nec Karny). Princis, 1963: 105.

Type material. – Lectotype ♂ (terminalia slide 276) (here designated; Princis labelled this specimen lectotype, 1963 but apparently never published the designation), Mt. Murud, Sarawak, 6500 ft., Dr. E. Mjöberg, Sarawak Museum dd 1925; Type Orth. $206^{1}/_{4}$ in HECO. Paralectotypes. Sarawak. HECO: same data as lectotype 1♂ (fragmented), Type Orth. $206^{2}/_{4}$. Additional material. – SABAH. HECO: ♀ paralectotype of *Homopteroidea minor* Hanitsch, Type Orth. $389^{2}/_{2}$, B.N. Borneo, Mt. Kinabalu, Kenokok, 3300 ft., 22.iv.1929.

Two other paralectotypes in HECO with the following data are not *shelfordi*: one with the same data as the lectotype, Type Orth. $206^{3}/_{4}$, has on the back of the type label '*Homopteroidea hanitschi* sp. n., K. Princis, 1963', but the description was never publis-

Figs. 1-11. *Homopteroidea* spp. – 1-4. *H. shelfordi* Hanitsch, male lectotype: 1, pronotum; 2, genitalia (dorsal); 3, left and right tegmina (a = presutural vein in right tegmen); 4, left hind wing; 5, tarsal claws. – 6-11. *H. nodipennis* (Karny) males: 6, tarsal claws; 7, pronotum; 8, genitalia (dorsal); 9, left tegmen; 10, right tegmen; 11, right wing. (6, 9-11, from Singgalang, Sumatra; 7, 8, from Sipitang, Sabah).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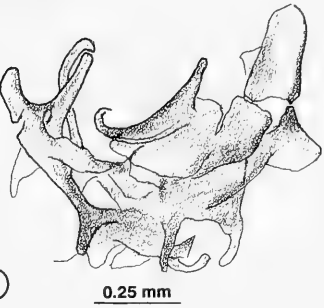
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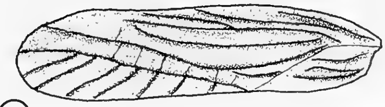
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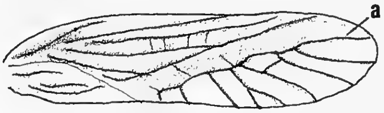

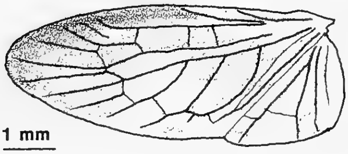
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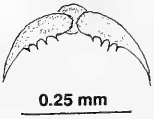
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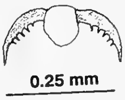
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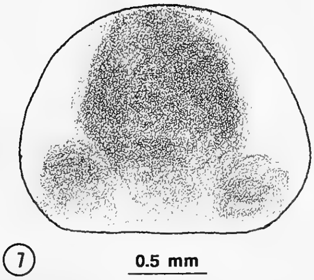
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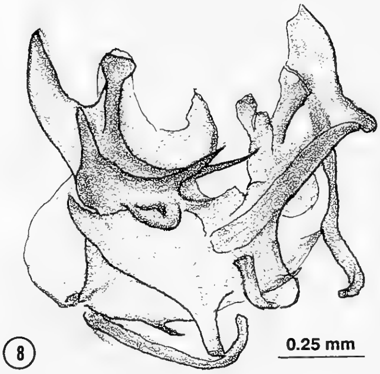
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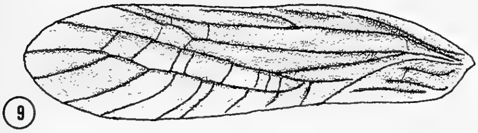
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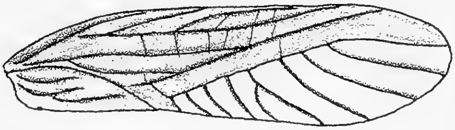
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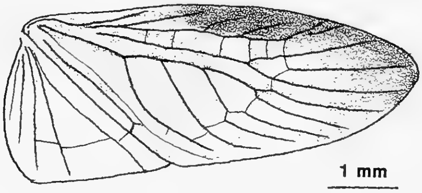
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hed. It is a new species, namely *biramiata*, described below. The other specimen (Type Orth. $206^4/_4$) is *Homopteroidea nodipennis* (Karny) a species which Princis incorrectly synonymized with *shelfordi*.

Redescription. – Male: Head slightly exposed, eyes reduced, lateral, widely separated, interocular space greater than the distance between antennal sockets, ocellar spots well developed, elliptical. Pronotum suboval, hind margin straight (fig. 1). Tegmina and wings fully developed, extending beyond end of abdomen, left tegmen with seven oblique branches in the presutural zone, the right one with seven or eight branches (fig. 3). Hind wing cubitus vein with three branches distally connected by cross veins (fig. 4). Front femur Type C_1, pulvilli and arolia absent, tarsal claws symmetrical, serrated on their proximal halves (fig. 5). Abdominal terga unspecialized, supraanal plate hind margin convexly rounded, right and left paraprocts similar simple plates. Genitalia as in fig. 2.

Female (based on the paralectotype of *Homopteroidea minor* Hanitsch): Left tegmen damaged, right tegmen presutural vein with seven oblique branches. Cubitus vein of hind wing with three curved branches distally connected by cross veins. Front femur Type C_1, pulvilli and arolia absent, tarsal claws serrated. Supraanal plate trigonal, apex broadly, shallowly concave.

Colour. – Head blackish, clypeus, labrum, and mandibles pale, ocellar spots white, maxillary palpi black. Pronotum dark brown with about two thirds of the lateral borders pale, hyaline (fig. 1). Tegmina reddish brown, presutural area of the right one clear hyaline (fig. 3). Hind wing infuscated (fig. 4). Adomen brown, male supraanal plate with a medial pale macula.

Measurements (mm) (♀ in parentheses). – Length, 4.7 (4.0); pronotum length × width, 1.6 × 2.0 (1.3 × 1.7); tegmen length, 6.4 (4.7); interocular width, 0.9 (0.7).

Comments. – So far *shelfordi* is found only on Mt. Murud [3°52'N 115°30'E], and Mt. Kinabalu [6°05'N 116°33'E]. Most of the other records (Hanitsch's and Bruijning's) apparently are *nodipennis*. The two species are very close and are distinguished by the presence or absence of arolia, and differences in their male genitalia.

The female specimen from Mt. Kinabalu is smaller than the male and is similar in size to specimens of *Homopteroidea minor* which probably led Hanitsch to designate it a syntype of that species.

Homopteroidea nodipennis (Karny)
(figs. 6-11)

Fulmekia nodipennis Karny, 1926: 158, figs. 151-155. Syntypes 1♂, 2♀, 'Maryland' in Sumatra, O.K., Lichtfang, v.1925, leg. Dr. L. Fulmek, No. 2; in MZZB [not examined].

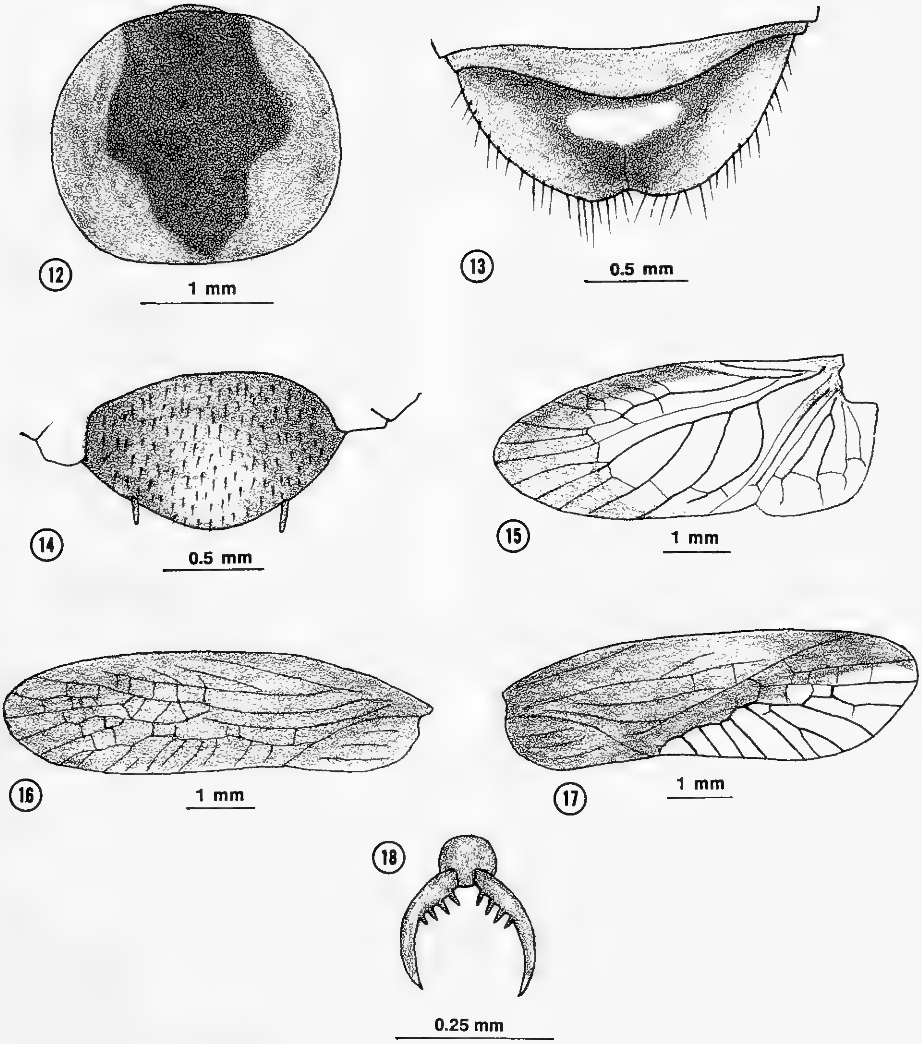
Homopteoidea nodipennis (Karny). – Princis 1963: 105 (incorrectly listed as a synonym of *Homopteroidea shelfordi* Hanitsch).

Material examined. – SABAH. ZILS: The following were collected by S. Adebratt: Malaysia, Sabah, Sipitang, Mendolong, T5/R, 1 (abdomen missing), 11.v.1988; 1♂ (terminalia slide 426), 1♀, 28.iv.1988, 1♂, 2.iii.1989, T1B/W4, 1♀, 10.iii.1988, T6/R, 1♀, 14.iii.1989, T3/W5, 1♂, 20.iii.1989, 1♀, 24.ii.1989. One specimen retained in MCZC. RMNH: Malaysia, Sabah, Long Pa Sia airstrip along S. Pa Sia, 115°43'E 4°25'N, 1090 m, 1♀, 14.x.1986, J. Huisman; Beaufort, 105 km S. of Long Pa Sia area, Sg. Ritan, 115°42'E 4°24'N, 1160 m, undisturbed evergreen tropical rainforest, 1♂, 7.iv.1987, J. van Tol & J. Huisman. – SARAWAK. RMNH: Borneo, Sarawak, 16km N. of Bario, Long Rapun, Sg. Dapur, ML, 115°35'E 3°53'N, 1200 m, 1♂, 19-20.ii.1987, J. Huisman. – [Indonesian] BORNEO. HECO: O. Borneo, Pajau R., 1♀, Mjöberg. – SUMATRA. RMNH: The following were collected by E. Jacobson: Fort de Kock (Sumatra), 920 m, 2♂, 2♀, 1925; Air Njuruk Dempu, 1400 m, 1♂, 4♀, viii.1916; Gun. Teleman, Sum., 1♂, 1♀, 1917; Sungai Kumbang, Sum., 1♂ (terminalia slide 208), viii.1915. Two retained in MCZC. HECO: Gunung Singgalang (Sumatra's Westkust), 1800 m, ♂ & ♀ in copula, 5♂, 1♀, 1925, E. Jacobson. MALAY PENINSULA. HECO: paralectotype of *Homopteroidea shelfordi* Hanitsch (Type Orth. $206^4/_4$), Perak, Larut Hills, 4000-5000 ft., capt. ii.-iii.1905, & pres. by R. Shelford.

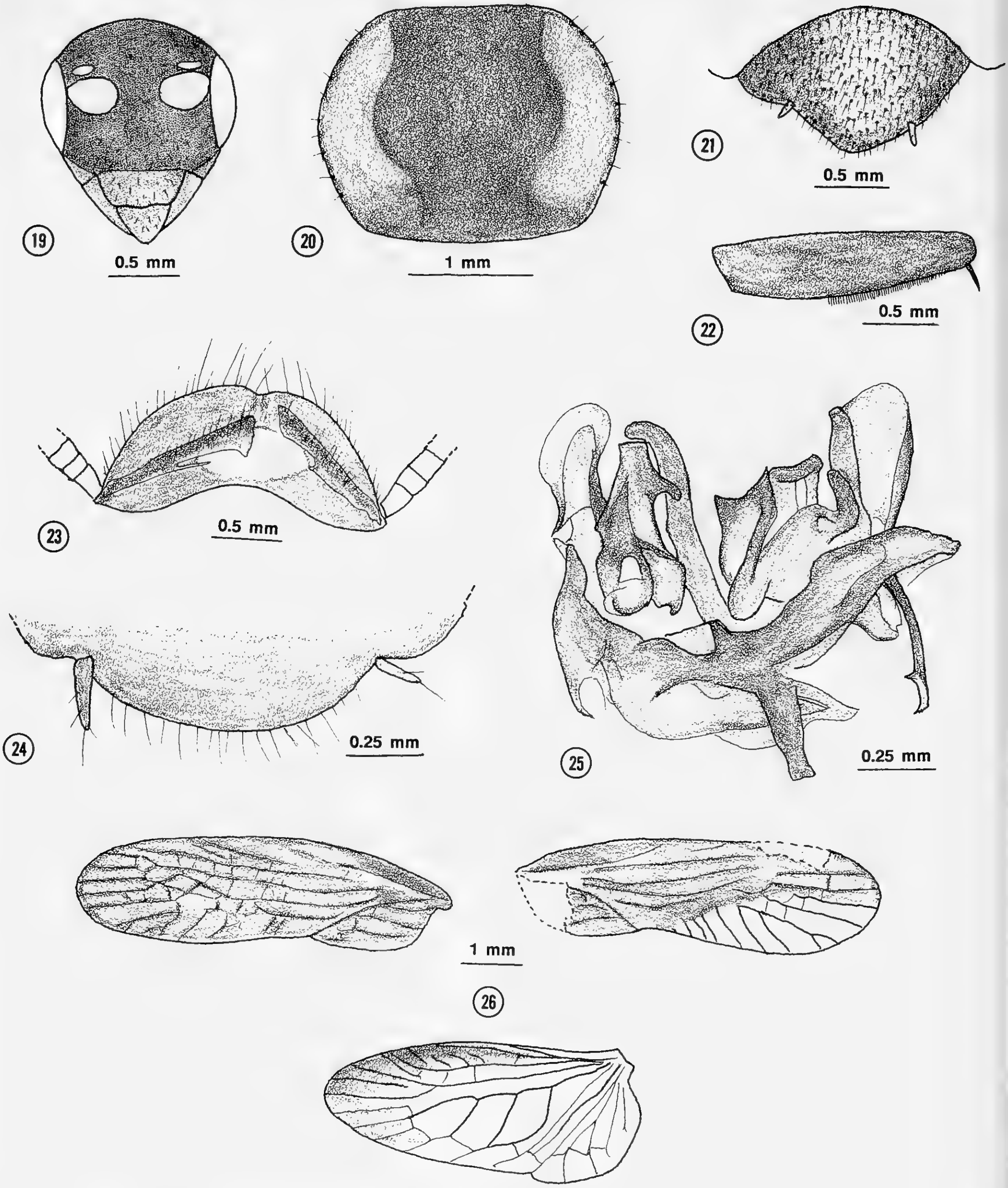
Redescription. – Male: Head globose, exposed, eyes wide apart, lateral, behind the antennal sockets. Pronotum subparabolic the dark portions slightly raised (fig. 7). Tegmina and wings fully developed extending beyond end of abdomen; right and left tegmina with six to eight oblique presutural branches (fig. 9-10). Hind wing with three subcostal veins, cubitus vein with three branches distally connected by cross veins (fig. 11). Front femur Type C_1; pulvilli absent, tarsal claws symmetrical, serrated on proximal halves, very small arolia present (fig. 6). Abdominal terga unspecialized; supraanal plate with a large hyaline whitish median macula, hind margin convexly rounded, right and left paraprocts similar simple plates. Subgenital plate symmetrical with small, similar, cylindical widely separated styli, interstylar margin rounded. Cerci with a long terminal spine. Genitalia as in fig. 8.

Female: Left tegmen presutural zone with four to six oblique branches, right one with seven (one branched) or eight. Supraanal plate hind margin trigonal, apex rounded. Subgenital plate divided mediolongitudinally, distal margin in lateral view truncate.

Colour. – Head dark reddish brown, ocellar spots whitish, distal part of clypeus yellowish, palpi dark reddish brown to blackish; proximal segments of antennae brown, remainder blackish. Pronotum with

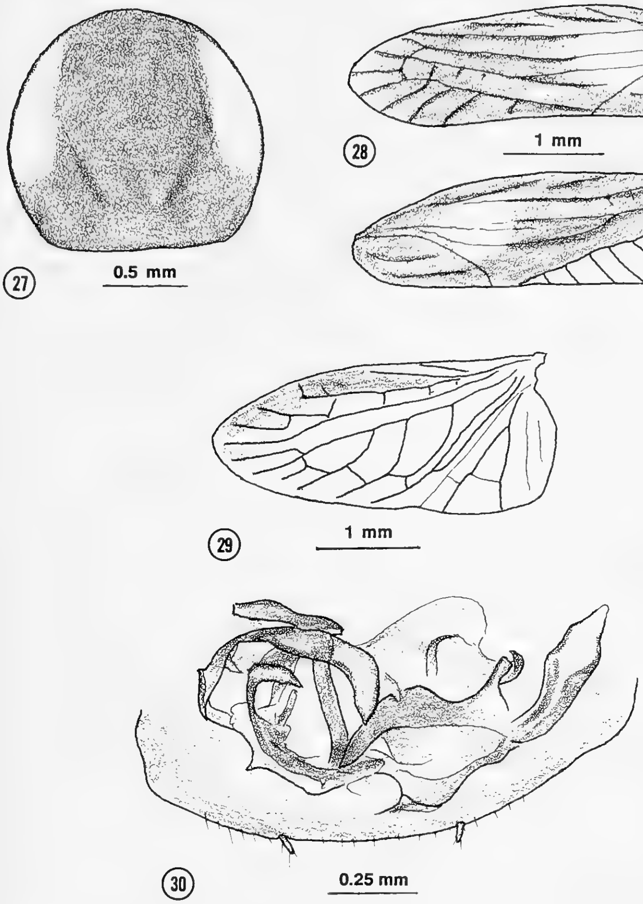


Figs. 12-18. *Homopteroidea nigra* Shelford, males from Sipitang, Sabah. – 12, pronotum; 13, supraanal plate (dorsal); 14, subgenital plate (ventral); 15, left hind wing; 16, left tegmen; 17, right tegmen; 18, tarsal claws.



Figs. 19-26. *Homopteroidea nigra* Shelford, male from Perak. – 19, head; 20, pronotum; 21, subgenital plate (ventral); 22, front femur (anterior surface); 23, supraanal plate and paraprocts (ventral); 24, styli and interstylar margin of subgenital plate (dorsal); 25, genitalia (dorsal). 26, left and right tegmina, and left hind wing.

raised portions dark brown, about two thirds of the distal lateral zones yellowish white (in some females, white) (fig. 7). Tegmina brown, raised veins on dorsal surface dull yellowish, on ventral surface white, presutural zone on left tegmen brown, on right tegmen clear hyaline. Hind wing with subcostal and apical areas darkened, some veins distally white. Abdomen brown, supraanal plate with a clear hyaline macula.



Figs. 27-30. *Homopteroidea maculata* Hanitsch: 27, male pronotum; 28-29, female left and right tegmina, and left hind wing; 30, subgenital plate and genitalia (dorsal). (27, 30, from Sipora; 28, 29, from holotype).

Cerci brown. Legs brown, tarsi lighter.

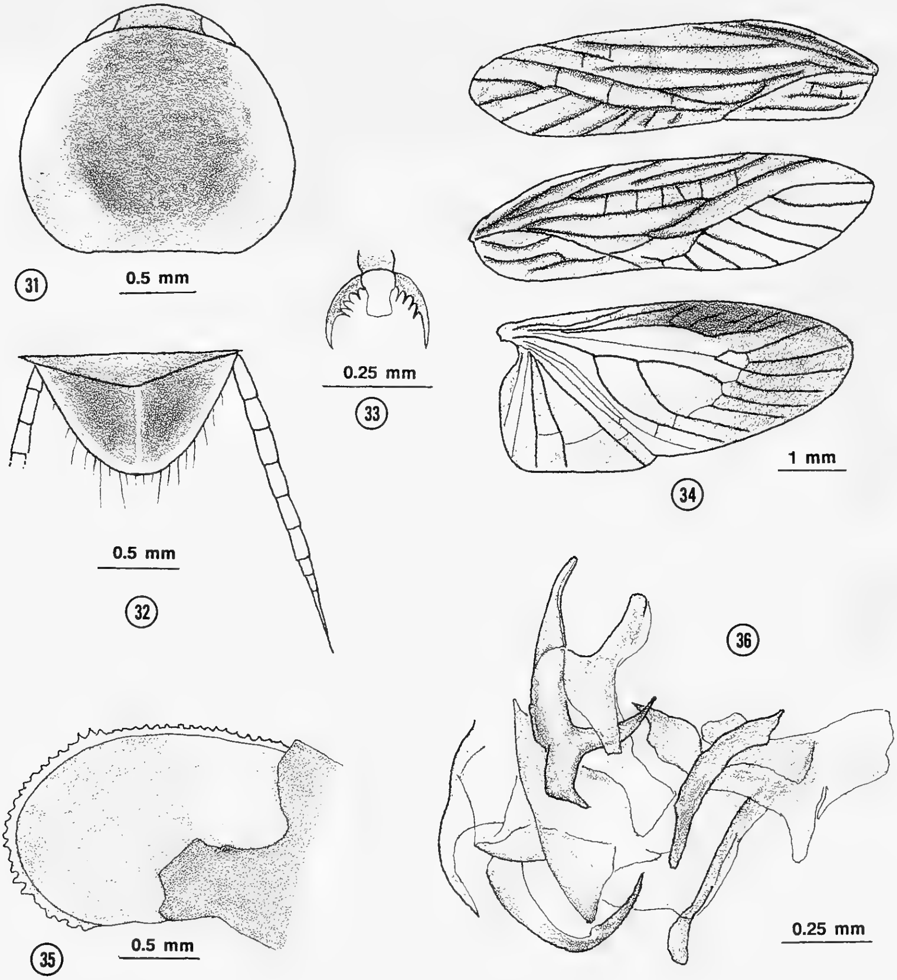
Measurements (mm) (♀ in parentheses). – Length, 4.6-5.5 (4.5-5.3); pronotum length × width, 1.4-1.6 × 1.6-1.9 (1.3-1.6 × 1.6-1.8; tegmen length, 5.3-6.5 (5.0-6.7); interocular width, 0.7 (0.7-0.8).

Comments. – This species is very similar to *shelfordi* and Princis incorrectly synonymized it with that taxon. Karny's description of *nodipennis* is very complete and the specimens I have identified as this species agree closely with his description. One of the critical characters he mentioned (p. 160) was the presence of 'verkümmerten Haftläppchen' (rudimentary arolia), a structure absent in *shelfordi.*

Homopteroidea nigra Shelford
(figs. 12-26)

Homopteroidea nigra Shelford, 1906: 274, pl. 16, figs. 13, 14 (♀); Hanitsch 1915: 127; 1923: 466; 1928: 37, 43; 1932a: 52, 80; 1932b: 6; 1933a: 303, 328; 1933b: 235; Hebard 1929: 96; Bruijning 1948: 44, 146; Princis 1950: 162.

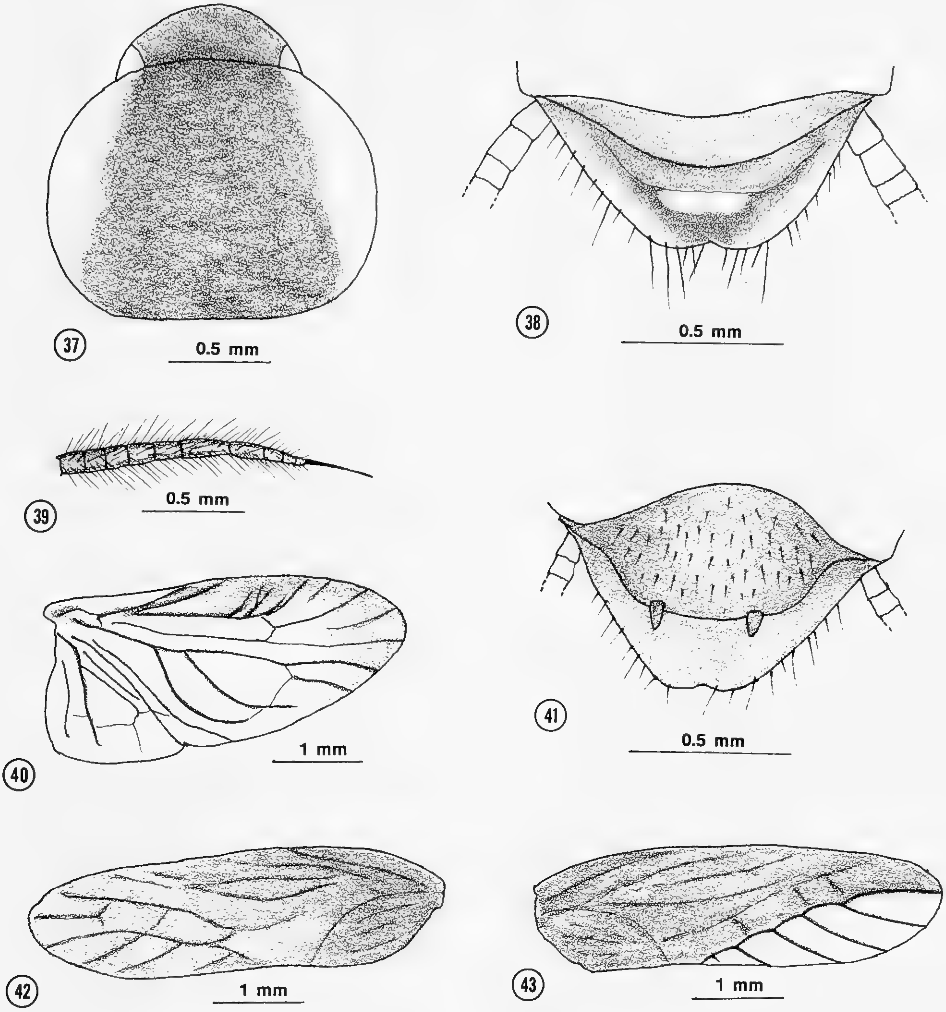
Type material. – Holotype ♀, Kuching, N.W. Borneo [SARAWAK], 9.x.1899, pres. 1905 by the Sarawak Museum; Type Orth. 205 in HECO [the specimen is fragmented with parts mounted on cards]. – Additional material: MENTAWE[A]I. HECO: Sipora, 1♂, 1♀, 1 (abdomen missing), v.-vi.1894, E. Modigliani, Mus. Civico Genova. MALAYSIA. HECO: Perak, F.M.S., Batang Padang, Jor Camp, 1800 ft., 1♂ (wing slide 272, terminalia slide 273,), 31.v.1923, H.M. Pendlebury. – SULAWESI (Celebes). HECO: Macassar, 1♂, 1896, Doherty, M. Burr Collection, pres. 1903 by M.B. – SABAH. ZILS: Malaysia, Sipitang, Mendolong, T2A/W4, 1♂, 1 (abdomen missing), 8.xii.1987, T1B/W4, 1♂ (terminalia slide 425), 15.iv. 1988, 1♀, 1 (abdomen missing), 20.iii.1988, 1 (abdomen missing), 8.iii.1989, T4/R, 1♂. 13.v.1988, T5/R, 2♂, 28.iv.1988, 1♂,



Figs. 31-36. *Homopteroidea biramiata* sp. n.. – 31-34. female: 31, pronotum; 32, supraanal plate (dorsal); 33, tarsal claws and arolium; 34, left and right tegmina, and right hind wing; 35, ootheca (lateral); 36, male genitalia (dorsal). (31-33, from holotype; 34, 35, paratype from Fort de Kock, Sumatra; 36, paralectotype of *Homopteroidea shelfordi* from Mt. Murud, Sumatra).

3.v. 1988, 2 (abdomens missing), 11.v.1988. Two retained in MCZC.

Description. – Male (previously undescribed): Head globose, eyes reduced, widely separated, lateral, interocular space greater than the distance between antennal sockets, ocellar spots transverse (fig. 19); fifth maxillary palpomere swollen, about as long as the fourth, each shorter than the third. Pronotum suboval (figs. 12, 20). Tegmina and wings fully developed extending beyond end of abdomen; right tegmen with seven or eight oblique branches in the clear hyaline presutural zone (figs. 17, 26, top). Hind wing cubitus vein with three branches that are distally joined by cross veins (figs. 15, 26, bottom). Front femur Type C_1, with a dense row of almost contiguous piliform spinuli (fig. 22); pulvilli and arolia absent, tarsal claws symmetrical basal half serrated (fig. 18). Abdominal terga unspecialized, supraanal plate hind margin convexly rounded, apex weakly indented (fig. 13), right and left paraprocts similar simple plates (fig. 23). Subgenital plate with a pair of small, similar, cylindrical widely separated styli, interstylar margin convexly rounded (figs. 14, 24). Cerci with a large terminal spine. Genitalia with complex phallomeres as in fig. 25.



Figs. 37-43. *Homopteroidea minor* Hanitsch, male from Sipitang, Sabah. – 37, pronotum; 38, supraanal plate (dorsal); 39, cercus; 40, right hind wing; 41, subgenital plate (ventral); 42, 43. left and right tegmina.

Female: Similar to male except for the subgenital plate which is deeply, longitudinally incised, the margins of the incision contiguous, the distal margin in profile truncate (as in figs. 50, 51).

Colour. – Head shiny black, clypeus, labrum, and mandibles light brown, ocellar spots yellowish white or white (fig. 19); antennae dark brownish or black with about 15 terminal white segments (Shelford described the antenna as being fuscous; the fragmented holotype lacks antennae and they probably lacked the distal antennomeres when it was originally described; several specimens from Sabah had some white antennomeres and one which appeared to have undamaged antennae had 15 white segments but in most specimens segments are missing and these have fewer or no white antennomeres.); maxillary and labial palpi black. Pronotum with raised portion black or dark brown, broad lateral zones lighter reddish brown (figs. 12, 20). Tegmina dark reddish brown except for the clear zone in the presutural area of the right wing cover (figs. 16, 17, 26 top). Hind wing with costal veins and apical region infuscated (figs. 15, 26 bottom). Abdomen dark brown, supraanal plate with a large clear hyaline area (figs. 13, 23; absent in female). Legs with femora brownish, tibiae and tarsi pale.

Measurements (mm) (♀ in parentheses). – Length, 5.2-6.1 (6.3); pronotum length × width, 1.8-2.0 × 2.1-2.3 (1.9-2.0 × 2.3); tegmen length, 5.6-6.3 (5.5-5.8); interocular width, 0.9 (0.9-1.0).

Homopteroidea maculata Hanitsch
(figs. 27-30)

Homopteroidea maculata Hanitsch, 1929: 266, figs. 7-9 (♀); 1932a: 81; Bruijning 1948: 147; Princis 1963: 105.

Material examined. – Holotype, ♀, Lubuksikaping (SUMATRA's Westkust), 450 m, 1926, E, Jacobson; Type Orth. 363 in HECO. – Additional material: SABAH. ZILS: Malaysia, Sabah, Sipitang, Mendolong, T5/R, 1♀, 28.iv.1988, 1♀ (abdomen missing), 11.v.1988, S. Adebratt. – PHILIPPINE ISLANDS. HECO: Mt. Makiling, Luzon, 1♀, Baker. – MENTAWE[A]I Islands. HECO: Sipora, 1♂ (terminalia slide 275), v.-vi.1894, Modigliani, Mus. Civ. Genova.

Redescription. – Female: Head slightly exposed, eyes wide apart, reduced, lateral, interocular space greater than the distance between antennal sockets. Pronotum suboval, the midregion shallowly cucullate, hind margin straight. Tegmina and wings fully developed extending well beyond end of abdomen, left tegmen with four or five branches of the presutural vein, the right one with six or seven rami (fig. 28). Hind wing cubitus vein with three branches connected distally by cross veins (fig. 29). Front femur Type C_1, pulvilli and arolia absent, tarsal claws symmetrical, their proximal halves serrated. Supraanal plate with hind margin convexly rounded, entire. Subgenital plate divided medially, hind margin in profile truncate.

Male (previously undescribed). – Pronotum (fig. 27), tegmina and wings as in female (fig. 28, 29). Abdominal terga unspecialized. Supraanal plate with a hyaline area medially, hind margin convexly rounded, entire, right and left paraprocts similar plates. Subgenital plate with hind margin rounded, styli similar, small, widely separated, interstylar margin weakly curved (fig. 30). Genitalia as in fig. 30.

Colour. – Head dark brown, labrum and lower half of clypeus lighter; antennae dark brown; maxillary palpomeres grayish. Pronotal disk with cucullate portion dark brown, about two thirds of the lateral regions lighter or whitish (fig. 27). Left tegmen brown with a brownish yellow hyaline macula on anterior half; right tegmen similarly coloured except that the presutural vein area is colourless-hyaline (fig. 28). Abdomen brown. Legs brown, tarsi lighter.

Measurements (mm). – Length, 4.5 (5.0-5.2); pronotum length × width, 1.5 × 1.6 (1.4-1.6 × 1.6-2.0); tegmen length, 4.5 (4.0-5.6); interocular width, 0.8 (0.7-0.8).

Comments. – The species is readily recognized by the hyaline mark on the proximal half of each tegmen.

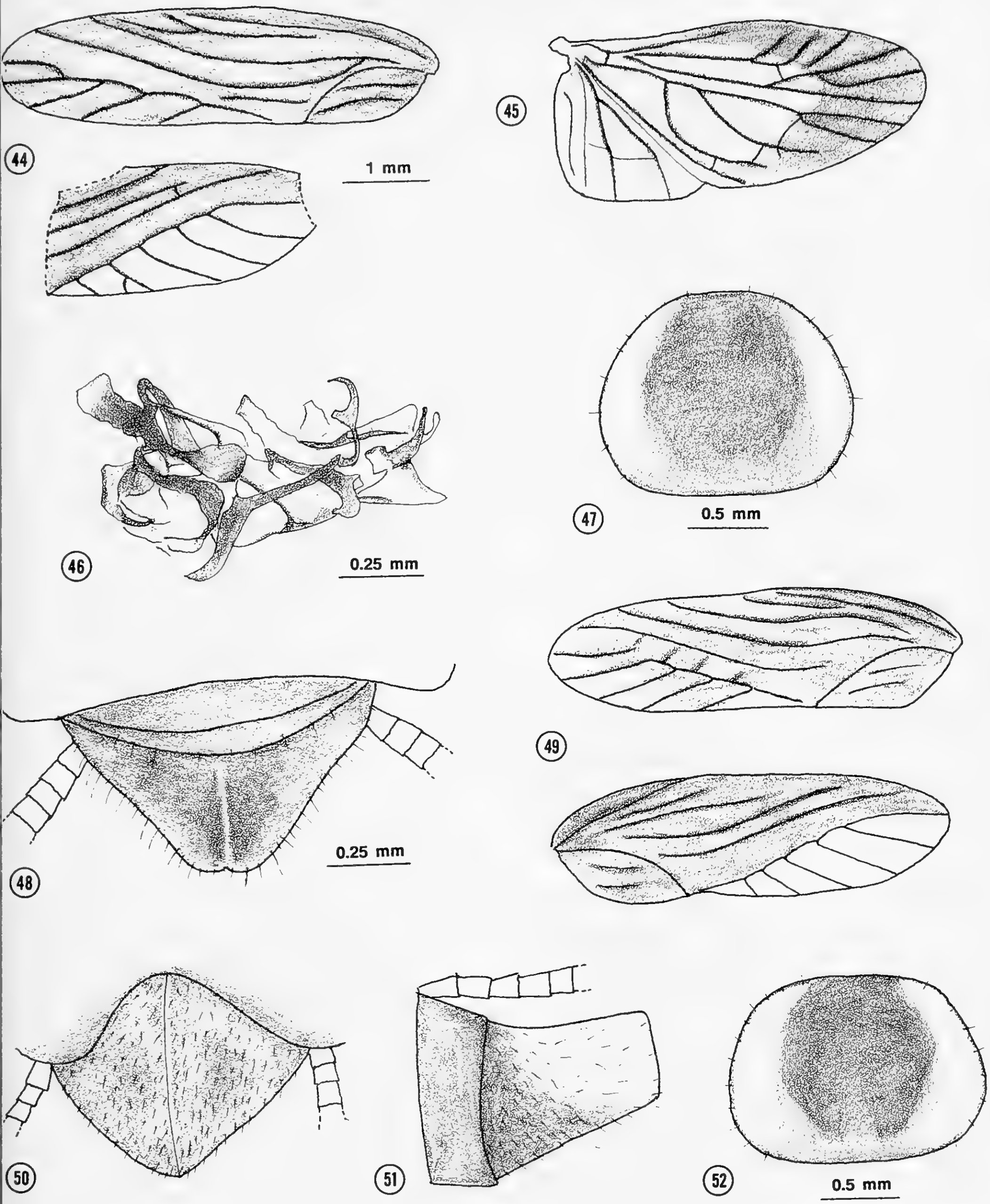
Homopteroidea biramiata sp. n.
(figs. 31-36)

Type material. – Holotype, ♀, Fort de Kock (SUMATRA), 920 m, E. Jacobson (det. by Bruijning as *Homopteroidea shelfordi* Hanitsch); in RMNH. [I selected a female as the holotype because the one male is in very poor condition]. – Paratypes. SARAWAK. HECO: Mt. Murud, Sarawak, 6500 ft., 1♂ (terminalia slide 277) paralectotype of *Homopteroidea shelfordi* Hanitsch (Type Orth., $206^3/_4$). – SUMATRA. HECO: Fort de Kock (Sumatra), 920 m, 1♀ (carrying an ootheca in the vertical position), 1925, E. Jacobson.

Description. – Male: Head hidden, eyes reduced, wide apart, lateral, ocellar spots very small, interocular width greater than the distance between antennal sockets. Pronotum suboval, hind margin weakly curved. Tegmina and wings fully developed extending beyond end of abdomen, the left tegmen with about seven oblique branches in the presutural zone, a similar number in the clear presutural zone of the right wing cover. Hind wing with two curved branches of the cubitus vein, distally joined by cross veins. Front femur Type C_1, pulvilli absent, tarsal claws symmetrical, serrated, arolia present. Abdominal terga unspecialized. Supraanal plate with hind margin convexly rounded, apex very shallowly indented, right and left paraprocts similar plates. Subgenital plate with a pair of widely separated styli, interstylar margin convex. Genitalia as in fig. 36.

Female: Head slightly exposed, eyes reduced, lateral, wide apart, interocular width greater than the distance between antennal sockets, ocellar spots absent. Pronotum suboval, hind margin straight, (fig. 31). Tegmina and wings fully developed extending beyond end of abdomen both with seven or eight oblique branches in the presutural zones (fig. 34 top & middle). Hind wing with two branches of the cubitus vein, distally connected by cross veins (fig. 34 bottom). Front femur Type C_1, pulvilli absent, tarsal claws symmetrical, serrated on their proximal halves, arolia present (fig. 33). Supraanal plate subtrigonal, apex rounded (fig. 32). Subgenital plate divided longitudinally the distal margin truncate in profile. Cerci with a terminal spine (fig. 32).

Colour. – Head reddish brown, clypeus, labrum, and mandibles yellowish brown, maxillary palpi blackish; antennae brown. Pronotum dark reddish brown, the lateral proximal two thirds whitish (fig. 31). Tegmina brownish hyaline, the presutural zone of the right one clear hyaline (fig. 34 middle). Hind wing infuscated darkest in the costal and apical zones (fig. 34 bottom; ♂ wing darker than the ♀). Abdomen brown, male supraanal plate with a hyaline macula. Cerci and legs brown, tarsi lighter.



Figs. 44-52. *Homopteroidea minor* Hanitsch. 44-47, male lectotype. – 44, left and right (damaged) tegmina; 45, right hind wing; 46, genitalia (dorsal); 47, pronotum. – 48-52, female from Sipitang, Sabah: 48, supraanal plate (dorsal); 49, left and right tegmina; 50, subgenital plate (ventral); 51, subgenital plate (lateral); 52, pronotum.

Ootheca. – The ootheca carried by the female (fig. 35) measures 1.3 mm high and 2 mm long. It is white and has about 40 variably shaped serrations in the keel. The serrations contain respiratory tubes that allow air to reach the eggs. There is a yellowish (yolk-like) swelling internally that distends part of the lateral walls of the egg case but there are no longitudinal lines demarking the egg cells. The shape of the serrations resemble those of the polyphagid *Latindia* sp. but in that species the teeth are more uniform (Roth 1971: figs. 12, 13). In most cockroach oothecae that have toothed or serrated keels, each serration leads to a single egg but this is not true in *Homopteroidea* or *Latindia* spp.; the latter has about 60 serrations but there are usually only eight eggs (Roth 1971: 128).

Measurements (mm) (♀ in parentheses). – Length, ? (4.7-5.4); pronotum length × width, 1.6 × 1.9 (1.5 × 1.8); tegmen length, ca 7 (5.7-5.8); interocular width, 0.8 (0.7-0.8).

Etymology. – The specific name refers to the two branches of the cubitus vein of the hind wing.

Comments. – The hind wings of *Homopteroidea biramiata* (fig. 34, bottom), and *minor* (fig. 40) have two cubitus branches (other species have three), but their tegmina differ in the number of oblique branches in the clear presutural zones (seven in *biramiata*, fig. 34, middle; five in *minor*, fig. 43).

Homopteroidea minor Hanitsch
(figs. 37-52)

Homopteroidea minor Hanitsch, 1933a: 303, 328 (♂ lectotype only; ♀ paralectotype = *Homopteroidea shelfordi*).

Material examined. – Lectotype (here designated), ♂ (terminalia slide 274), Mt. Kinabalu, B.N. Borneo [SABAH], Kenokok, 3300 ft., 22.iv.1929; Type Orth. 389$^1/_2$, in HECO. – Additional material: SABAH. ZILS: The following were collected by S. Adebratt: Malaysia, Sipatang, Mendolong, 1♂, T4/R, 1♀, T6/R, 14. iii.1989, T3/W5, 1♂, 1♀, 17.iii.1989, T5/R, 1♀, 1 (abdomen missing), 28.iv. 1988, 1♀, 1.v.1988. One retained in MCZC. – SUMATRA. HECO: Si-Rambé (Sumatra's Westkust), 1♂, xii.90-iii.91, E. Modigliani, Mus. Civ. Genova.

Redescription. – Male: Head largely exposed, eyes lateral, very far apart, interocular space greater than the distance between the ocellar spots or antennal sockets. Pronotum suboval (figs. 37, 47). Tegmina and wings fully developed extending beyond end of abdomen; left tegmen with three or four oblique branches in the presutural zone (figs. 42, 44 top), the right tegmen with four or five rami in that area (figs. 43, 44 bottom). Hind wings with about three costal veins (only their bases distinct), median vein with a branch that reaches the anterior margin, cubitus vein with two branches distally joined by cross veins (figs. 40, 45). Front femur Type C_1; pulvilli and arolia absent, tarsal claws symmetrical, distinctly toothed. Abdominal terga unspecialized. Supraanal plate ample, the distal region turned upwards its apex weakly indented (fig. 38). Subgenital plate symmetrical with a pair of small, similar, widely separated styli, interstylar margin not produced (fig. 41). Cerci with a long terminal spine (fig. 39). Complex genital phallomeres as in fig. 46.

Female: Pronotum as in fig. 52. Tegmina (fig. 49) and hind wing are similar to the male. The supraanal plate lacks a medial hyaline spot (fig. 48) and the astylar subgenital plate is longitudinally divided with its distal margin truncate in lateral view (figs. 50, 51).

Colour. – Brown. Head dark brown, clypeus and labrum lighter, maxillary palpi grayish. Pronotum with broad lateral regions whitish subhyaline (darker in lectotype), the remainder dark brown (figs. 37, 47, 52). Left tegmen entirely dark brown or reddish brown (figs. 42, 44 top, 49 top), right tegmen with the presutural region clear hyaline, the remainder dark brown or reddish brown (figs. 43, 44 bottom, 49 bottom). Hind wing with the apical region, and the costal vein zone infuscated (figs. 40, 45). Abdomen brown, supraanal plate with a white or yellowish macula across the middle (fig. 38). Legs and cerci lighter brown.

Measurements (mm) (♀ in parentheses). – Length, 3.8-4.5 (3.8-4.6); pronotum length × width, 1.3-1.4 × 1.6-1.7 (1.3-1.4 × 1.7); tegmen length, 3.5-4.2 (4.1-4.4); interocular width, 0.7 (0.7).

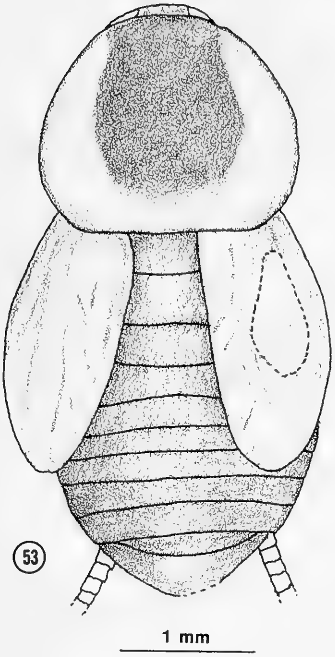
Comments. – Hanitsch's 'description' of this species was as follows: 'The two specimens [♂ and ♀] quite agree in colouring and structure with *H. nigra* Shelford, but measure only 5 mm. in total length, as against 7 mm. of the type of *nigra.* In the absence of more material I must leave it uncertain as to whether or not they represent a new species.' The differences in male genitalia, tegmen and wing structure (fewer cubitus branches in *minor*) and size, leave no doubt that both taxa are valid.

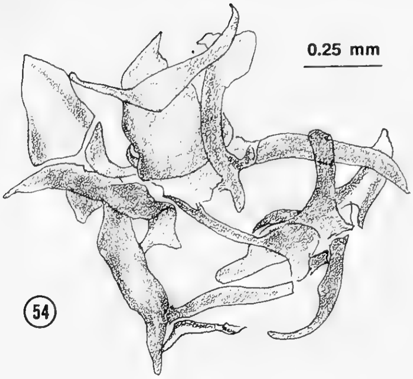
Homopteroidea brachyptera sp. n.
(figs. 53, 54)

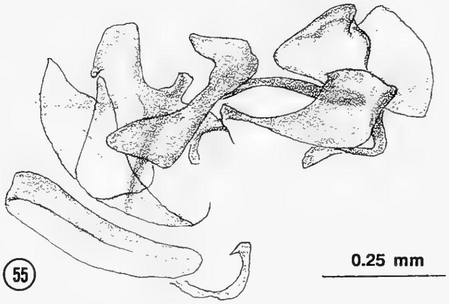
Type material. – Holotype, ♂ (right tegmen on slide 271, genitalia on slide 278), SUMATRA, Si-Rambé, xii.1890-iii.1891, E. Modigliani; in HECO. – Paratype. SUMATRA. HECO: Wai Lima, 1♀.

Description. – Male: Head globose, slightly exposed, eyes reduced, wide apart, interocular space greater than distance between antennal sockets. Pronotum suboval, widest behind the middle (fig. 53). All but one hind leg missing: pulvilli absent, tarsal claws symmetrical, proximal half of ventral margin serrated, arolia absent. Tegmina reduced, widely separated reaching to about the sixth segment, venation indistinct; hind wing vestigial (fig. 53). Supranal plate hind margin convexly rounded (fig. 53), right and left paraprocts similar simple plates. Genitalia as in fig. 54.

Female: The specimen is in very poor condition and mounted on a card. Tegmina are reduced and hind wings are vestigial. Only one hind leg is present







Figs. 53-55. *Homopteroidea* spp. – 53-54. *Homopteroidea brachyptera* sp. n., holotype male: 53, habitus (dotted line on the right tegmen shows the outline of the underlying vestigial wing); 54, genitalia (dorsal). – 55. *Homopteroide aberrans* (Hanitsch), male genitalia (dorsal), from Wai Lima, Sumatra.

and it lacks pulvilli and an arolium and the tarsal claws are serrated. Supraanal plate trigonal, apex rounded.

Colour. – Head reddish brown. Pronotum with raised portion dark brown, lateral regions pale (fig. 53). Both tegmina similar, light brown hyaline, veins indistinct, right tegmen without a clear hyaline presutural zone (fig. 53). Abdominal terga and sterna brown, male supraanal plate with a medial clear zone (fig. 53).

Measurements (mm) (♀ in parentheses). – Length, 4.1; pronotum length × width, 1.5 × 1.8 (1.2 × 1.8); tegmen length, 1.9 (2.1).

Etymology. – The specific name refers to the reduced tegmina and wings.

Comments. – This is the only species of *Homopteroidea* whose tegmina are reduced and wings are vestigial.

Homopteroidea aberrans (Hanitsch) **comb. n.**
(fig. 55)

Ctenoneura aberrans Hanitsch. – Roth 1993: 86, fig. 1 (redescribed ♀ and described ♂).

Material examined. – SABAH. ZILS: Malaysia, Sabah, Sipitang, Mendolong, T5/R, 1♂, 6.v.1988, T4/R. 1♂, 14.iii.1989, A1L, 1♂, 8.iv.1988, 1♂, 25.iv.1988, 1♂, 26.iv.1988, 1♂, 5.v. 1988, S. Adebratt. One specimen retained in MCZC. – SUMATRA. HECO: Wai Lima, Z. Sumatra, Lampongs, 2♂, 2♀, xi.-xii.1921, Karny & Siebers; Sumatra Binjei, Deli Hoa, Kapala Roessu, 1♀, viii.1922, Toxopeus. MCZC: Wai Lima, Sumatra, 1♂ (terminalia slide 275).

Measurements (mm) (♀ in parentheses). – Length, 4.0-4.3 (4.7); pronotum length × width, 1.0-1.2 × 1.6-1.8 (1.2 × 1.6); tegmen length, 4.0-4.5 (4.4); interocular width, 0.7 (0.8).

Comments. – This species was originally in *Ctenoneura*, and I considered it to be atypical from other members of that genus because its tarsal claws are serrated and its subgenital plate is symmetrical with two small similar styles. These are diagnostic characters of *Homopteroidea* and I am therefore transferring *aberrans* to that genus. However, it may be considered 'aberrant' in this genus because the presutural zone of the right tegmen is not clear hyaline, the curved branches of the cubitus vein are not connected by cross veins, and the male supraanal plate lacks a hyaline macula (Roth 1993: figs. 1C, E). The male genital phallomeres are shown in fig. 55.

Acknowledgements

I thank the Australian Biological Resources Survey (ABRS) for partial support, and the museums, curators, and collection managers indicated in the introduction, who loaned me specimens.

References

Bruijning, C. F. A., 1948. Studies on Malayan Blattidae. – Zoologische Mededelingen Leiden 29: 1-174.

Hanitsch, R., 1915. Malayan Blattidae. – Journal of the Straits Branch Royal Asiatic Society 69: 17-178.

Hanitsch, R., 1923. Malayan Blattidae. Part II. – Journal of the Malayan Branch of the Royal Asiatic Society 1: 393-474.

Hanitsch, R., 1925. On a collection of Blattidae from northern Sarawak, chiefly Mt. Murud and Mt. Dulit. – Sarawak Museum Journal 3(1): 75-106.

Hanitsch, R., 1928. Spolia Mentawiensia. Blattidae. – Bulletin of the Raffles Museum Singapore, Straits Settlements 1: 1-44.

Hanitsch, R., 1929. Fauna Sumatrensis. Blattidae. – Tijdschrift voor Entomologie 72: 263-302.

Hanitsch, R., 1932a. Beccari and Modigliani's collection of Sumatran Blattidae in the Museo Civico, Genoa. – Annali del Museo civico di Storia naturale di Genova 56: 48-92.

Hanitsch, R., 1932b. On a collection of blattids from the east coast of Sumatra. – Miscellanea Zoologica Sumatrana 62: 1-8.

Hanitsch, R., 1933a. The Blattidae of Mt. Kinabalu, British North Borneo. – Journal of the Federated Malay States Museums, Singapore 17: 297-337.

Hanitsch, R., 1933b. On a collection of Bornean and other oriental Blattidae from the Stockholm Museum. – Entomologisk Tidskrift 54: 230-245.

Hebard, M., 1929. Studies in Malayan Blattidae (Orthoptera). – Proceedings of the Academy of Natural Sciences of Philadelphia 81: 1-109.

Karny, H. H., 1926. Beiträge zur Malayischen Orthopterenfauna. – Treubia 9: 11-291.

Princis, K., 1950. Indomalaiische und australische Blattarien aus dem Entomologischen Museum der Universität in Lund. – Opuscula Entomologica 15: 161-188.

Princis, K., 1963. Blattariae: Subordo Polyphagoidea, Fam. Polyphagidae. *In* Beier (ed.): Orthopterorum Catalogus 4: 77-172. 's-Gravenhage.

Princis, K., 1971. Blattariae: Subordo Epilamproidea, Fam. Ectobiidae. *In* Beier (ed.): Orthopterorum Catalogus 14: 1039- 1224. 's-Gravenhage.

Roth, L. M., 1971. Additions to the oothecae, uricose glands, ovarioles, and tergal glands of Blattaria. – Annals of the Entomological Society of America 64: 127-141.

Roth, L. M., 1993. Revision of the cockroach genus *Ctenoneura* Hanitsch (Blattaria, Polyphagidae). – Tijdschrift voor Entomologie 136: 83-109.

Shelford, R., 1906. Studies of the Blattidae. – Transactions of the Entomological Society of London 1906 (Part II): 231-280.

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DESCRIPTION OF A NEW SPECIES OF *CTENONEURA* HANITSCH FROM SABAH (BLATTARIA, POLYPHAGIDAE)

Roth, L. M., 1995. Description of a new species of *Ctenoneura* from Sabah (Blattaria, Polyphagidae). – Tijdschrift voor Entomologie 138: 117-119, figs. 1-8, table 1. [ISSN 0040-7496]. Published 15 June 1995.

A new species of *Ctenoneura* Hanitsch from Sabah is described. New collection records are given for two known species.

Dr. L. M. Roth, 81 Brush Hill Road, P.O. Box 540, Sherborn, MA 01770, U.S.A.

Key words. – *Ctenoneura*; Blattaria, Polyphagidae; cockroaches; new species.

Princis (1963: 101; 1971: 1138) listed 15 species of *Ctenoneura*. I (Roth 1993: 83) added 12 new taxa in revising the genus and also provided a key to distinguish the adults; in a recent paper (Roth 1995), I transferred *Ctenoneura aberrans* Hanitsch to *Homopteroidea*. The genus is principally Malaysian, Indonesian, and Asian.

While my 1993 revision was in press, Dr. Roy Danielsson sent me a number of specimens of *Ctenoneura* from the Zoological Institute, Lund, Sweden (ZILS), of which at least one is new and is described below. Mr. Willem Hogenes of the Zoologisch Museum, Universiteit van Amsterdam, The Netherlands (ZMAN) sent me some material. New records of two known species are also presented below.

SYSTEMATIC PART

Genus ***Ctenoneura*** Hanitsch

Ctenoneura Hanitsch, 1925: 100. – Roth 1993: 83 (revision).

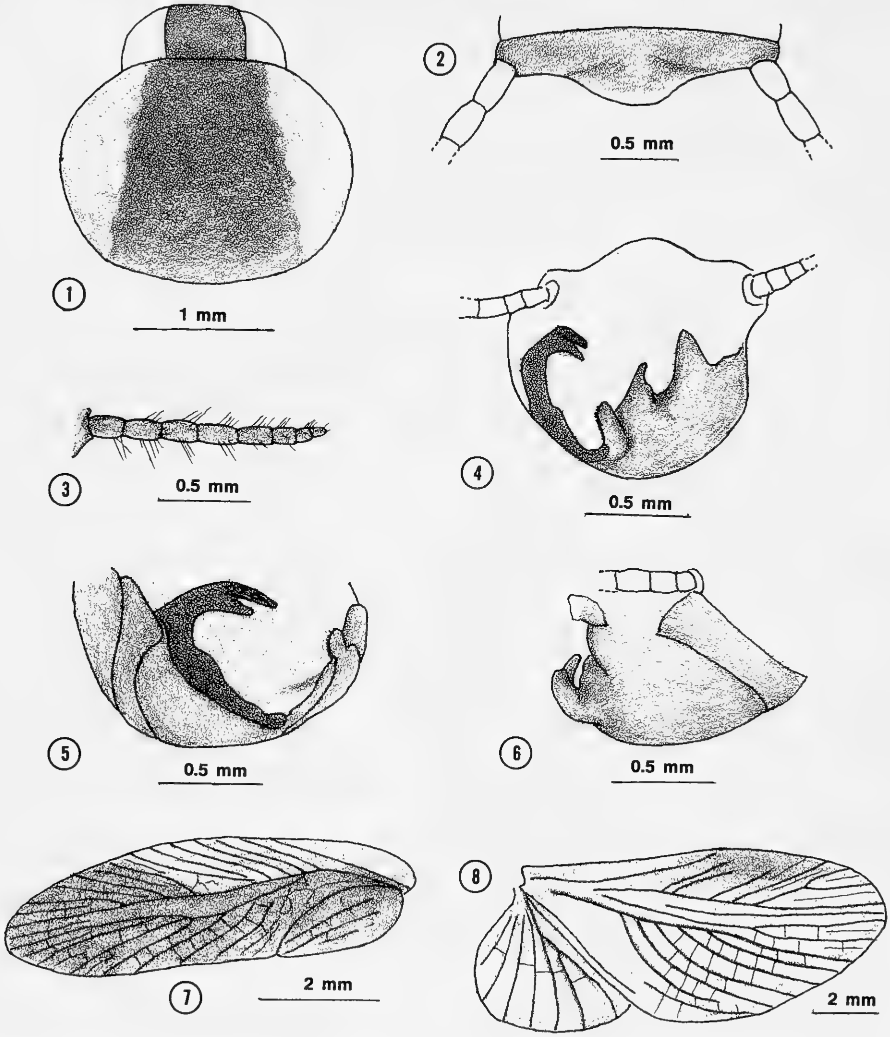
Rediagnosis. – Tegmina and wings fully developed extending beyond end of abdomen. Right and left tegmina generally similar in venation and sclerotization, major veins not thickened, often densely reticulate with numerous cross veins, discoidal sector oblique (fig. 7). Hind wing usually with an intercalary vein (between the radial and media veins), cubitus vein with three to eight branches (usually more than three) that generally are parallel and reach, or almost reach the wing margin, and with numerous small cross veins connecting them (fig. 8). Front femur Type C_1, pulvilli absent, tarsal claws symmetrical, simple, arolia present (small or subobsolete) or absent. Male: Abdominal terga unspecialized. Subgenital plate asymmetrical, usually with one stylus, or none. Female: subgenital plate valvular.

Ctenoneura Hanitsch is very close to *Homopteroidea*. The two genera can be separated by differences shown in table 1.

Ctenoneura sipitanga sp. n.
(figs. 1-8)

Type material. – Holotype ♂, Malaysia, SABAH, Sipitang, Mendolong, T1B/W4, 15.iv.1988, S. Adebratt; in ZILS. – Paratypes. Sabah. ZILS: same locality and collector as holotype, T6/R, 1♂, 8.iii.1989, T1B/W4, 1♂, 15.iv.1988 (retained in the Museum of Comparative Zoology, Harvard University), T4/R, 1♂, 3.v.1988.

Description. – Male: Head well exposed, eyes large, bulbous, (fig. 1), interocular width slightly less than the distance between antennal sockets, ocellar spots very small. Pronotum suboval (fig. 1). Tegmina and wings fully developed extending well beyond end of the abdomen, the former with nonthickened veins and oblique discoidal sectors (fig. 7). Hind wing with an elongated subcostal vein that terminates, along with about four costal veins, in a swelling; intercalary vein present, simple, media vein bifurcate distad, cubitus vein with five curved, about equally spaced, parallel, simple branches (fig. 8). Front femur Type C_1; pulvilli absent from all legs, tarsal claws simple, symmetrical, arolia minute. Abdominal terga unspecialized. Supraanal plate transverse, short, with midregion of the hind margin convexly rounded, entire



Figs. 1-8. *Ctenoneura sipitanga* sp. n., males from Sipitang, Sabah: 1. pronotum; 2. supraanal plate (dorsal); 3. cercus; 4. subgenital plate (end view); 5. subgenital plate (left lateral); 6. subgenital plate (right lateral); 7. left tegmen; 8. right hind wing.

(fig. 2). Subgenital plate asymmetrical, strongly convex, hind margin on the left side curved dorsad and forming an apically bifurcate spicular process; the right side has three dissimilar processes, two of them contiguous at the mid margin, and the third closer to the cercus; styli absent (figs. 4-6). Cerci without a terminal spine (fig. 3).

Colour. – Head reddish brown; antennae light brown. Pronotum with a dark reddish brown macula that extends from the anterior to the posterior margins, the wide lateral regions yellowish subopaque or opaque (fig. 1). Right and left tegmina similar, their humeral and proximal part of the costal vein zones yellowish, the remainder reddish brown, hyaline (fig. 7). Hind wings with a yellowish tinge. Abdomen, cerci, and legs light brown, subgenital plate yellow its hind margin that forms the bifurcate process on the left side very dark brown (figs. 4, 5).

Female: Unknown.

Measurements (mm). – Length, 5.0-6.5; pronotum length × width, 1.6-1.7 × 2.1-2.2; tegmen length, 6.1-6.5; interocular width, 0.5.

Etymology. – The species is named after the locality, Sipitang [5°05'N 115°33'E].

Comments. – Most of the males of *Ctenoneura* are determined by differences in the shapes of their sub-

Table 1. Generic differences between *Ctenoneura* and *Homopteroidea*

Character	*Ctenoneura*	*Homopteroidea*
Tegmina	Right tegmen without a clear presutural zone.	Right tegmen with a clear presutural zone.
Hind wing	Intercalary vein present; cubitus vein with 3 to 8 branches.	Intercalary vein absent; cubitus vein with 2 or 3 branches.
Tarsal claws	symmetrical, simple.	symmetrical, serrated.
Subgenital plate (♂)	Asymmetrical; with one left stylus or none.	Symmetrical; with a pair of small, similar styli.

genital plates (key, *in* Roth, 1993: 84). The very dark apically bifurcate process on the left hind margin of the subgenital plate (figs. 4, 5) distinguishes *sipitanga* from all other known *Ctenoneura*.

Ctenoneura scutica Roth

Ctenoneura scutica Roth, 1993: 102, fig. 16 (♂).

Material examined.- SABAH. ZILS: Malaysia, Sabah, Sipitang, Mendolong, P1l, 1♂, 10.iii.1989, S. Adebratt.

Comments. – The species is known only from Sabah.

Ctenoneura major Hanitsch

Ctenoneura major Hanitsch: Roth, 1993: 96, fig. 9 (♀ & ♀).

Material examined. – SABAH. ZMAN: Borneo, Sabah, Kinabalu Nat. Park, sample Sab. 37, montane forest, understory at light, headquarters area Kiau View trail, 1560 m, 1♂, 18.xi.1989, M.J. & J. P. Duffels.

Comments. – This male is slightly smaller than the holotype which is from Mt. Murud, Sarawak. Its measurements (mm) are as follows: Length, 7.7; pronotum length × width, 2.1 × 2.8; tegmen length, 10.2; interocular width, 0.6.

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I thank the Australian Biological Resources Survey (ABRS) for partial support, and Dr. Roy Danielsson, and Mr. Willem Hogenes who sent me the specimens.

REFERENCES

Hanitsch, R., 1925. On a collection of Blattidae from northern Sarawak, chiefly Mt. Murud and Mt. Dulit. – Sarawak Museum Journal 3(1): 75-106.

Princis, K., 1963. Blattariae: Subordo Polyphagoidea, Fam. Polyphagidae. *In* Beier (ed.): Orthopterorum Catalogus 4: 77- 172. 's-Gravenhage.

Princis, K., 1971. Blattariae: Subordo Epilamproidea, Fam. Ectobiidae. *In* Beier (ed.): Orthopterorum Catalogus 14: 1039-1224. 's-Gravenhage.

Roth, L. M., 1993. Revision of the cockroach genus *Ctenoneura* Hanitsch (Blattaria, Polyphagidae). – Tijdschrift voor Entomologie 136: 83-109.

Roth, L. M., 1995. Revision of the cockroach genus *Homopteroidea* Shelford, with redescriptions, and descriptions of two new species (Blattaria, Polyphagidae). – Tijdschrift voor Entomologie 138: 103-116.

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NEW AND RARE SPHECIDAE (HYMENOPTERA) FROM WEST AFRICA

Simon Thomas, R. T., 1995. New and rare Sphecidae (Hymenoptera) from West Africa. – Tijdschrift voor Entomologie 138: 121-130, figs. 1-14, tabs. 1-3. [ISSN 0040-7496]. Published 15 June 1995.

Eight new species of Sphecidae from Senegal, Côte d'Ivoire, Nigeria, and Niger are described: *Liris (Leptolarra) rufula* sp. n., *L. (Leptolarra) senegalensis* sp. n., *Nitela (s.s.) miekae* sp. n., *Miscophus rufigaster* sp. n., *M. senegalensis* sp. n., *M. wieringi* sp. n., *M. eburneus* sp. n., and *M. pseudochrysis* sp. n. In addition a description is presented of the unknown female *Miscophus sallitus* Andrade.

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Key words. – Hymenoptera, Sphecidae, West Africa, new species.

The Sphecidae were obtained during a research program in northern Senegal on the effects of chemical locust and grasshopper control on other insects. The area in which the research was executed was homogenous savannah with sparse trees and shrubs (Everts 1990). Collecting was carried out on seven plots (A-G), each with five malaise traps (1-5). The plots, 2 x 2 and 2 x 3 km, were situated 25-35 km south east of Richard Toll (fig. 1). The insects in the malaise traps were collected once a week, five times before and five times after spraying. Plot C, for reference, was not sprayed.

By counting the number of different insect species or groups before and after spraying the effect of the insecticides could be measured (Evers 1990). This paper describes new species of Sphecidae found in the material.

Through the courtesy of J. W. Evers and K. W. R. Zwart (LUW) I also had the opportunity of studying other Sphecidae from Côte d'Ivoire, Nigeria, and Niger, which are described here too.

Abbreviations of depositories

ZMAN, Institute for Systematics and Population Biology (Zoological Museum), University of Amsterdam, The Netherlands ; LUW, Laboratory of Entomology, University of Wageningen, The Netherlands; RMNH, National Museum of Natural History (formerly: Rijksmuseum van Natuurlijke Historie), Leiden, The Netherlands.

Abbreviations and symbols

Ocellar measurements (after Andrade 1960): POL - Distance between the posterior ocelli; OOL -Distance between a posterior ocellus and the corresponding eye; SOL -Distance between the anterior ocellus and a posterior one; VOL -Distance between a posterior ocellus and an imaginary line interconnecting the posterior corners of the eyes (fig. 2). The microsculpture terms used in this paper are after Eady (1968).

SYSTEMATIC PART

Liris Fabricius, 1804

This is a large cosmopolitan genus comprising over 260 species, for the greater part found in the tropics. About 70 species are found in the Ethiopian Region. Both described species can be assigned to the subgenus *Leptolarra* Cameron, 1900, by having a transverse row of stout setae on the apex of the pygidial plate, the surface of pygidium covered with appressed hairs, and claws untoothed.

Liris (Leptolarra) rufula sp. n.
(fig. 3)

Type material. – Holotype female: Senegal, 25-35 km sud de Richard Toll, piège malaise E1, 10. viii.1989, leg. H. v. d. Valk c.s. (LUW). – Paratypes: same locality and collector as holotype, piège malaise F2, 1♀ 23.ix.1989, piège malaise A3, 1♂ 19.-viii.1989 (LUW); piège malaise C2, 1♀ 8.viii.1989, piège malaise C3, 1♂ 20.ix.1989 (ZMAN); piège malaise C3, 1♀ 13.ix.1989 (RMNH).

Description

Female 17 mm. Black; shining apical part of clypeus ferruginous. Palpi yellow ferruginous. Mandible

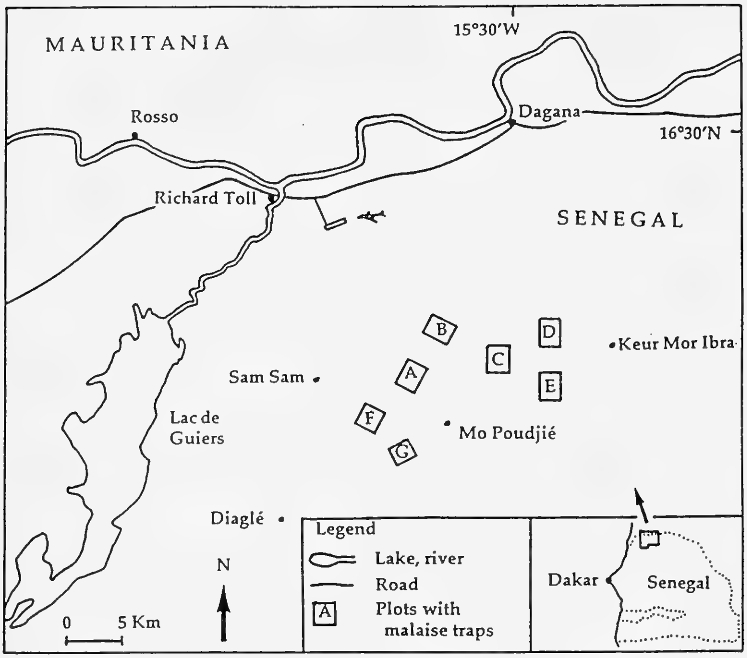


Fig. 1. Map of Senegal, the plots in the research area are indicated.

ferruginous with dark brown apex. Scape, pronotal lobe, tegula, and propodeal spiracle ferruginous. Pedicel and flagellomeres I-VIII blackish brown with ferruginous apical ring. Gaster bright ferruginous.

Apical margin of clypeus faintly undulated. Mandible monodont with broad, deep emargination on externoventral margin. Clypeus with central longitudinal shining spot and shining rim along apex. Clypeus two and a half times wider than long. All flagellomeres three times as long as wide at apex. Flagellomere X not flattened. Vertex dull with fine points. Frons and genae with silvery pubescence. Eyes with scattered erect hairs. Inner eye margins converge to vertex (from 40 to 17). Midocellus round.

Pronotum with scarce silvery pubescence, sides of pronotum faintly obliquely striated. Mesonotum, scutellum, and metanotum shining with very fine points. Propodeum wider at the base than long (53 : 43). Dorsum and posterior face of propodeum with strong transversal striation. Propodeum with some pubescence along lateral sides. Side of propodeum with oblique striation.

Gaster with very short silvery pubescence. Pygidium narrow, shining, with large points, points separated from each other by twice their own diameter. Pygidial plate a little more than twice as long as wide, ending

Table 1. Differences in colour and characteristics of the females of the species *Liris (Leptolarra) rufula* sp. n., *L. (Leptolarra) senegalensis* sp. n. and *L.* (*Leptolarra*) *croesus* (F. Smith).

	L. (L.) rufula sp. n.	*L.* (*L.*) *senegalensis* sp. n.	*L. (L.) croesus* (F. Smith)
Scape	ferruginous	ferruginous	black
Antennae	blackish brown	partly black, partly ferruginous	black
Flagellomere X	round	flat	round
Pronotal lobe	brown, no pubescence	brown with silver pubescence	black, no pubescence
Mesonotum	dull and finely punctulated	with goldish pubescence	with goldish pubescence
Lateral part of propodeum	strigose with silvery pubescence	strigose with silvery pubescence	punctulated without pubescence, short ridges along edges
Gaster	bright ferruginous	dark ferruginous	black
Pygidial plate	narrow (38 : 17)	broad (37 : 26)	broad (38 : 28)
Apex of pygidium	6 satae in one row	10 satae in 2 rows	6 satae in one row
Body	slender	slender	robust

blunt with a row of five stout setae at apex (fig. 3), with some short reclining hairs and a few upright thin hairs.

Wings hyaline with ferruginous veins. Apex of forewing beyond the nervation softly fumigated. Hindwing hyaline.

Legs including coxae ferruginous. Spines of tibiae II and III black.

Claws untoothed; spines of tarses I dark brown and pointed at top. Metatarse I with five spines, last spine not longer than next tarsus. Largest spine of tibia III 0.6 length of metatarse III.

No difference in structure or colour of holotype and paratypes was found; the sizes of the paratypes are 15 and 10 mm. The number of setae at apex of pygidium varies from 5 to 3.

Male 8-9 mm. Colour and structure largely the same as in holotype. On exterior side of flagellum a low carina runs from flagellomeres III-X. No difference in structure or colour in second male.

Etymology. – The name of the species refers to its remarkable reddish coloration of gaster and legs.

Comparative notes. – See under *L. (Leptolarra) senegalensis* sp. n.

Liris (Leptotarra) senegalensis sp. n.
(fig. 4)

Type material. – Holotype female, Senegal, 25-35 km sud de Richard Toll, piège malaise E1, 2.ix.1989, leg. H. v. d. Valk c.s. (LUW). – Paratypes: same locality and collector as holotype; piège malaise C3, 1 ♀ 28.viii.1989 (LUW); piège malaise G1, 1 ♀ 16.ix.1989, piège malaise G2, 1 ♀ 16.ix.1989 (ZMAN); piège malaise G3, 1 ♀ 23.ix.1989 (RMNH).

Description

Female 17 mm. Black; mandibles ferruginous with apical 0.4 black. Palpi, clypeus, scape, pedicel, and flagellomere I ferruginous. Flagellomere II ferruginous with black stripe externally. Flagellomeres III-X internally ferruginous, externally blackish. Genae and vertex with short silvery pubescence. Gaster dark ferruginous, apical halves of tergites with very short silvery pubescence.

Apical margin of median lobe of clypeus shining and broadly arched. Clypeus nearly two and a half times as wide as long (48 : 19). Head dull with tiny points and some depressed white hairs. Frons and genae with silvery pubescence covering the underlying structure. Flagellomere I three times as long as wide at apex. Flagellomeres III-IV two times as long as wide at apex. Flagellomeres V-IX one and a half times as long as wide at apex. Flagellomere X externally flattened. Eyes with scattered erect hairs. Inner eye margins converge to vertex (from 43 to 16). Mandible monodont with broad deep emargination on externoventral margin.

Pronotum with scarce silvery pubescence, apical half of pronotal lobe ferruginous with rounded top. Thorax with light yellow pubescence, shining, with tiny points. Propodeum dull with fine granulation. Side of propodeum with oblique striation.

Sternites II-V with a few long apical setae. Pygidium wide, 1.3 times as long as wide at the base (fig. 4). Dorsal side of pygidium punctulated covered with short depressed goldish hairs. Apical rim rounded with ten setae in two rows.

Forewing yellowish with yellow veins. Apical part beyond first transverse submarginal vein grey with brown veins. Hindwing yellowish with yellow veins.

All legs including coxae ferruginous. Claws untoothed, apical half black. Spines of tibiae II and III black. Largest spine of tibia III as long as metatarse III. Spines of frontleg ferruginous. Metatarse I with five spatulated spines; apical spine nearly 0.4 longer than next tarsus. All pecten of the tarsi longer than next tarsus.

The paratypes do not differ in structure or colour. Their sizes are between 14 and 15 mm. The apical setae of the pygidium range from 7-12.

Male unknown.

Etymology. – The species is named after the country in which the material was found (Senegal).

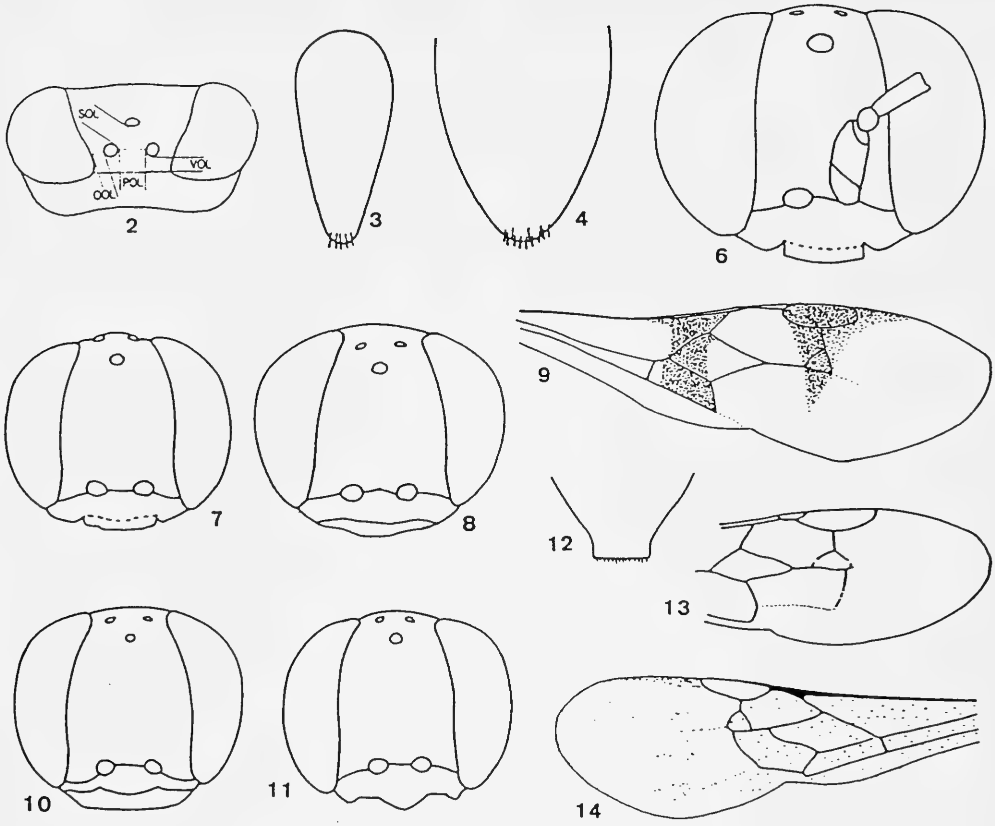
Comparative notes. – Although *Liris (Leptolarra) rufula* sp. n. and *L. (Leptolarra) senegalensis* sp. n. are much alike. *L. senegalensis* resembles in structure and colour *L. (Leptolarra) croesus* (F. Smith), the first species being slender in general appearance and the second species more robust. *L. rufula* differs from all the other species of *Liris (Leptolarra)* in having a bright ferruginous gaster and legs. The light coloration could be an adaption to strong solar radiation and reflection from the sandy soil (Lomholdt 1985). The differences of the three species are summarized in table 1.

Nitela Latreille, 1809

Nitela is a cosmopolitian genus. The Ethiopian Region has the largest share of the 43 species. The subgenus *Nitela* is mostly found in the Old World and Australia. The described species belong to the subgenus *Nitela* Latreille in having bare eyes and frontoclypeal carine absent or if present not lamelliform.

Nitela (s.s.) miekae sp. n.

Type material. – Holotype female, Senegal,



Figs. 2-4, 6-14: 2, dorsal view of head of *Myscophus*, showing the ocellar measurements; 3, *Liris rufula* sp. n., female, pygidium; 4, *Liris senegalensis* sp. n., female, pygidium; 6, *Miscophus rufigaster* sp. n., female, head, anterior view; 7, *Miscophus senegalensis* sp. n., female, head, anterior view; 8-9, *Miscophus wieringi* sp. n., female - 8, head, anterior view; 9, forewing; 10-12, *Miscophus eburneus* sp. n. – 10, female, head, anterior view; 11, male, head anterior view; 12, sternite VII, ventral view; 13, *Miscophus pseudochrysis* sp. n., female forewing; 14, *Miscophus sallitus* Andrade, female, forewing.

Ziguinchor, 13.v.1983, mangrove, J. W. Everts (ZMAN). – Paratypes 1 ♂ 1♀, same data as in holotype (ZMAN).

Description

Female 4 mm. Black; tegula dark ferruginous. First and basal half of second segment of labial palpi dark brown, apical half of second segment and the next two segments light brown. First two and basal half of the third segment of the maxillary palpi dark brown, apical half of third segment and the next three segments light brown. Mandibles basal third black, apical two third ferruginous. Antennae black, flagellomeres III-X ventrally with dense short bluish white pubescence.

All segments of the palpi with some hairs at the apical end of the segments. Clypeus wider than high (17 : 7), bulging in the middle with narrow and high midcarina. Clypeus and ventral half of frons with dense silvery pubescence covering underlying structure. Dorsal part of frons and vertex finely rugose. Interocular distance across base of clypeus nearly twice as wide as across vertex. POL : OOL = 3.5, SOL : OOL = 2.5, VOL : OOL = 2.0. Along interocular rim of the compound eyes a line of white scales. Pedicel length 0.6 of width. Flagellomeres I and II 1.6 times as long as wide. Flagellomeres III-VI 1.4 times as long as wide. Flagellomeres VII-X 1.2 times as long as wide. Flagellomeres X somewhat dorso-ventrally flattened.

Dorsal side of pronotum separated from front side by a transversal carina showing a triangle in the middle. Mesonotum transversally finely strigose, punctulated in between. Mesonotum separated from scutel-

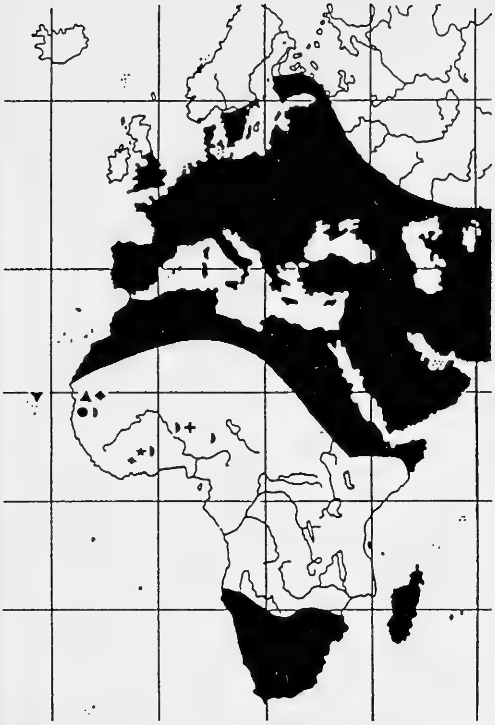


Fig. 5. Distribution of the *Miscophus bicolor* species group in the Ethiopian and west Eurasian regions (Lomholdt 1985) and the species described in this paper. – ★ *M. rufigaster* sp. n., ● *M. senegalensis* sp. n., ▲ *M. wieringi* sp. n., ■ *M. eburneus* sp. n., ◆ *M. pseudochrysis* sp. n., ▼ *M. sallitus* Andrade, + *M. funebris* Honoré.

lum by a crenulated furrow. Scutellum and metanotum finely reticulated. Mesopleura strongly rugose with a glabre, shining hypoepimeral area. Episternal sulcus and hypersternaulus strongly developed. Metapleura and sides of propodeum with longitudinal strigose. Dorsal side of propodeum strongly reticulate rugose, propodeal enclosure separated from vertical sides by a carina. Ventral side of thorax with scattered white hairs.

Tergites and sternites I-V black with apical ferruginous rim, tergite VI black without pygidium. Tergite I nearly twice as wide as long on the dorsal surface. Apex of sternites with some white hairs.

Wings hyaline with light brown veins and stigma.

All tibiae black with apical and basal brown rings. All femurs black with apical brown rings. All tarsi brown.

Male 4 mm. Colour and most of the structure as in holotype. Apex of scutellum five longitudinal crenulate.

Etymology. – I am pleased to name this species after my wife Miek, who has helpfully assisted me in the field and in preparing the manuscript.

Comparative notes. – *Nitela (s.s.) miekae* sp. n. is the first species of this genus collected in West Africa, resembling very much *N.* (s.s.) *mochii* Arnold (1940), which was collected at Wadi Hoff, 60 km south of Cairo, Egypt. The differences in characteristics of both species are given in table 2.

Miscophus Jurine, 1807
(fig. 5)

Miscophus is represented by about 150 species in all regions except Australia. Most species are found in the Old World, especially the Mediterranean area. Up till now no *Miscophus* species were found in West Africa south of Spanish Sahara (20° N) (Lomholdt 1985). All species described below belong to the *bicolor* species group. The *bicolor* species group holds small species, rarely more than 6 mm long; genae mostly without erect whitish pilosity; apex of fifth sternite in the females without a complex of very shallow large rough puncturation (Andrade 1960).

Fig. 5 shows the known distribution of the *bicolor* species group (after Lomholdt 1985) as well as the collecting places of the new species in West Africa.

The *Miscophus* species are distinctive sanddwellers (Honoré 1944). They are found along the desert, but also around 'wadis'. Mostly found in spring (March–June) on the hottest part of the day on the sand or around the stems of desert plants. Nest in the soil. Spider catchers.

Table 2. Differences in characteristics of the species *Nitela (s.s.) mochii* Arnold and *N. (s.s.) miekae* sp. n.

	Nitela (s.s.) mochii Arnold	*Nitela (s.s.) miekae* sp. n.
Clypeus and lower part of face	pubescence scarce and silvery	pubescence dense and silvery covering underlying structure
Frons	closely punctulated	finely rugose
Mesonotum	punctulated	transversal finely strigose
Proportinal length of pedicel and flagello-meres I and II	4 : 5 : 5	4 : 4 : 5
Tergite I	nearly three times as wide as long	twice as wide as long

Miscophus rufigaster sp. n.
(fig. 6)

Type material. – Holotype female, Côte d'Ivoire, 30-35 km N.Korghogo, mal. tr. 38, 10.iii.1980, J. W. Everts (ZMAN). – Paratypes 1♀, same data as holotype (ZMAN); 1♀, same place and collector, mal. tr. 25, 17.iv.1980 (LUW).

Additional specimens. – 1♀, Côte d'Ivoire, Katiola-Coton, 13.xi.1980, mal. tr., J. W. Everts (RMNH); 1♀, same place and collector, malaise, 20.iii.1981 (ZMAN).

Description

Female 7 mm. Black; mandibles ferruginous with red brown apex after a black ring. Apex of subbasal notch of mandible red brown. Scape, pedicel, and gaster light ferruginous. Palpi dark greyish.

All segments of palpi with outstanding hairs. Inner margins of compound eyes mostly parallel, at vertex somewhat converging and near clypeus diverging (fig. 6). Median lobe of clypeus bulged, convex with smooth and shining rim, rest of clypeus with long silvery hairs and punctulated. Frons with scarce silvery pubescence. Apex of scape ending in sloping top; the 0.6 distal internal part of the scape with a shining translucent area (fig. 6). Pedicel somewhat wider than long. Flagellomeres I-III three times as long as wide at apex, flagellomeres IV-X twice as long as wide at base. Vertex finely and closely punctulated, bulging between the ocelli. POL : OOL = 1.5, SOL : OOL = 1.9, VOL : OOL = 1.3.

Pronotum, mesonotum, scutellum, and metanotum finely and closely punctulated. Metanotum with lateral oblique silver pubescens, directed outwards. Dorsal part of propodeum somewhat longer than wide (15 : 20) with minute, oblique strigose and clear longitudinal midcarina. Posterior face of propodeum rather abruptly cut, forming an angle of about 100 degrees with its dorsum, horizontal striated.

Sixth tergite sharply pointed apically, without pygidium. Sternites II-VI each with two apical outstanding hairs.

Forewing hyaline, somewhat clouded beyond the nervation. First recurrent vein received by the first submarginal cell, close to submarginal II, second recurrent vein received by submarginal cell II near the apical end. Hindwing hyaline, media diverging beyond cu-a. Jugal lobe round and small with a very deep incision.

Legs ferruginous; external side of the femora somewhat darker; coxae black. Tarsi apically brown. Metatarsus I with two lateral spines. The apical spines of metatarsus and first tarsus twice as long as the next tarsus. The apical spine of second tarsus one third longer than the third tarsus.

Male unknown.

Etymology. – From Latin rufo, meaning red, and gaster, referring to all segments behind the propodeum.

Variation. – One female, Côte d'Ivoire, Katiola-Coton, malaise, 20.iii.1981, leg. J. W. Everts, differs somewhat from the type in having the last three tergites and sternites dark brown and the forewing tip white.

Comparative notes. – *Miscophus rufigaster* sp. n. and *M. funebris* Honoré (1944) are much alike. The differences in colour and characteristics of both species are given in table 3.

Miscophus senegalensis sp. n.
(fig. 7)

Type material. – Holotype female, Senegal, Ziguinchor, 13.v.1983, malaise, mangrove, J. W. Everts (ZMAN).

Description

Female 4.5 mm. Black; palpi ferruginous; mandibles dark ferruginous, black ring before amber red ap-

Table 3. Differences in colour and characteristics of the females of the species *Miscophus rufigaster* sp. n. and *M. funebris* Honoré.

	M. rufigaster sp. n.	*M. funebris* Honoré
Legs	excluding coxae ferruginous	black
Last three gastral segments	light ferruginous	dark brown
Clypeus	mostly shining without pubescence	silvery pubescence
Pedicel	somewhat wider than long	somewhat longer than wide
Flagellomeres I-III	3 times as long as wide	2.1 times as long as wide
SOL : OOL	1.9	2.0
VOL : OOL	1.3	1.0
Dorsal part of propodeum	obliquely strigose	closely punctulated
Forewing	hyaline, clouded beyond nervation	basal part somewhat clouded; hyaline over discoidal and submarginal cell, clouded beyond nervation with white wing tip

ex, black base; apex of median lobe of clypeus brown; pedicel and first three flagellomeres light ferruginous. Scape ventrally ferruginous and dorsally dark brown.

Palpi with scarce short pubescence. Clypeus and lower part of frons with scarce white pubescence directed apically. Medium lobe of clypeus smooth and slightly bulging with a few large points. Apical rim of medium lobe of clypeus smooth, no punctation, separated from basal part by a crenulated furrow (fig. 7). Head with close and very fine punctulation. Inner margins of compound eyes curved, near clypeus and at vertex converging (17 : 20 : 13). Pedicel 0.9 of the length of flagellomere I and as long as flagellomere II. Flagellomeres II-VIII twice as long as wide. Flagellomeres IX and X somewhat shorter. Flagellomere X conical. POL : OOL = 3.0, SOL : OOL = 2.0, VOL : OOL = 0.4.

Pronotal collar rather developed, transition to the anterior declinity relatively sharp and well defined. Mesonotum, scutellum, and metanotum very closely and finely punctulated. Propodeum equally long and wide at the base, very finely and obliquely strigose and with longitudinal midcarina. Propodeum with short silvery forwardly depressed pubescence. Side of propodeum obliquely strigose. Mesopleuron and metapleuron shining and finely punctulated. Posterior face of propodeum rather abruptly cut, forming an angle of about 100 degrees with its dorsum.

Apical rim of tergites dark brown. Tergites and sternites very finely punctulated. Tergite VI rounded apically without pygidium.

Wings hyaline. Veins along front edge of forewing dark brown. Other veins light ferruginous. 1m-cu entering submarginal cell I at a distance from submarginal cell II equal to the length of M2. Cu1 and 2m-cu not reduced. Jugal lobe round and small equally long and wide with very deep incision.

Inner side of tibia I, whole tibia II, and tarsi brown. Other parts of the legs black. Hind tibia with two apical spines, one spine as long as 0.7 of metatarse III.

Male unknown.

Etymology. – The species is named after the country in which the type was collected (Senegal).

Comparative notes. – *M. senegalensis* belongs to the *aenigma* species subgroup within the *bicolor* species group. The species resembles *M. nevesi* Andrade, 1952 from Portugal. The differences are found in the size of the body and the structure of the head. The clypeus of *M. senegalensis* is more pointed; the dorsal view of the head shows a much wider size behind the eyes; POL : OOL = 3.0 and SOL : OOL = 2.0 in *M. senegalensis* and POL : OOL = 1.8 and SOL : OOL = 1.4 in *M. nevesi* . The inner corners of the compound eyes at the vertex are nearly right-angled in *M. senegalensis* and rounded in *M. nevesi* . The ocelli are placed more posteriorly, VOL : OOL = 0.4 in *M. senegalensis* and 1.0 in *M. nevesi.* Posterior face of propodeum has a different cut, forming an angle with its dorsum of about 130° in *M. nevesi* and 100° in *M. senegalensis* .

Miscophus wieringi sp. n.

(figs. 8, 9)

Type material. – Holotype female, Senegal, 25-35 km sud de Richard Toll, piège malaise D3, 31. viii.1989, leg. H. v. d. Valk (LUW). – Paratype 1♀, same place and collector as holotype, piège malaise C3, 13.ix.1989 (ZMAN).

Description

Female 7 mm. Head black; palpi creamy white, mandibles ferruginous, apex red, apex of subbasal notch red. Scape, pedicel, and clypeus light ferruginous; flagellomeres I and II ventrally ferruginous dorsally brown, other flagellomeres ventrally brown and dorsally dark brown. Pronotum, pronotal lobe, and tegula ferruginous. Gaster light ferruginous.

External side of palpi with erect hairs. Clypeus arched with rounded middle part. Clypeus narrow (19 : 5) with broad translucent ferruginous rim with some long hairs (fig. 8). Apex of scape ending in sloping top (compare with fig. 6). Distance between compound eyes at vertex half the distance just above clypeus. POL : OOL = 3.2, SOL : OOL = 4.0, VOL : OOL = 2.5. Frons and clypeus with short and scarce goldish pubescence covering the fine punctulation. Flagellomere I two and a half times as long as wide. Flagellomeres II and III twice as long as wide; flagellomeres IV-X somewhat shorter. Flagellomere X conical.

Pronotum rather long, collar half as long as wide, lateral rounded. Collar finely and longitudinally strigose. Mesonotum, scutellum, and metanotum with short goldish pubescence and very closely punctulated. Mesopleuron strigose. Propodeum without pubescence, shining, equally long and wide at the base, lateral front part obliquely striated, middle apical part very finely almost transversally striated, with rather high midcarina. Angle between dorsum of propodeum and hindslope about 100 degrees. Upper part of mesopleuron with some goldish pubescence. Lower part of the mesopleuron and mesosternum with silvery pubescence.

Gaster shining, with few small points. Tergites II-IV translucent. Apex of tergite VI sharp, without pygidium.

Forewing (fig. 9) hyaline with two clouded bands, one just in front of submarginal cell I and the other just over the marginal cell and submarginal cell II.

Zone between the two clouded bands milky white with white veins. Other veins light brown. Forewing with petiole of submarginal cell II as long as height of this cell. Cu1 and 2m-cu reduced. Jugal lobe round and very small with deep incision.

All legs including coxa light ferruginous with brown spines. Coxa I ventrally translucent and equally long and wide at the base.

Male unknown.

Etymology. – I am very pleased to name this species after my friend H. Wiering, for his great help in preparing this manuscript.

Comparative notes. – *M. wieringi* belongs to the *bicolor* species group and resembles *M. heliophilus* Pulawski, 1968 closely. Mesonotum, scutellum, and metanotum are punctulated in *M. wieringi* and strongly shagreen in *M. heliophilus.* The mesopleuron is closely punctulated in *M. wieringi* and ridged longitudinally in *M. heliophilus.* There is a difference in the place of the ocelli: POL : OOL = 3.2 and SOL : OOL = 4.0 in *M.wieringi* and POL : OOL = 2.4 and SOL : OOL = 3.0 in *M.heliophilus.*

Miscophus eburneus sp. n.
(figs. 10-12)

Type material. – Holotype female: Côte d'Ivoire, 30-35 km N.Korghogo, mal.tr. 39, 28.iv.1980, J. W. Everts (ZMAN). – Paratypes 1♀, same data as holotype; 1♂, Côte d'Ivoire, 30-35 km N.Korghogo, mal.tr. 11, 3.i.1980, J. W. Everts (LUW); 2♀, same data as holotype; 1♂, Côte d'Ivoire, 30-35 km N.Korghogo, mal.tr. 40, 28.iv.1980, J. W. Everts (ZMAN); 1♀, Côte d'Ivoire, 30-35 km N.Korghogo, mal.tr. 35, 17.xii.1979, J. W. Everts, 1♂, Côte d'Ivoire, 30-35 km N.Korghogo, mal.tr. 40, 28.iv.1980, J. W. Everts (RMNH).

Additional specimens. – 1♀, Côte d'Ivoire, Katiola-Savanne, malaise, 20.ii.1981, leg. J. W. Everts c.s., 1♀, Senegal, 25-35 km sud de Richard Toll, piège malaise D3, 27.ix.1989, leg. H. v. d. Valk, 1♀, Niger, Niamey, Centre Aghrymet, piège malaise-mil, 26.viii-1.ix.1988, Y. Jongema, 1♀, Nigeria, savanne-zone, ii-iii.1975, leg. P. Splithof & H. de Jongh; 1♂, Côte d'Ivoire, 30-35 km N.Korghogo, mal.tr. 34, 28.iv.1980, J. W. Everts (LUW); 1♀, Côte d'Ivoire, 30-35 km N.Korghogo, mal.tr. 2, 28.ii.1980, J. W. Everts, 1♀, Côte d'Ivoire, Katiola, malaise, 20.iv.1980, leg. J. W. Everts, 1♂, Ivory Coast, Koudougou 10 km SE Bouaflé, malaise-trap, 16.ii.1981, J. W. Everts, 1♀, Senegal, 25-35 km sud de Richard Toll, piège malaise G4, 21.viii.1989 H. v. d. Valk, 1♀, Senegal, 25-35 km sud de Richard Toll, piège malaise G4, 30.ix.1989, H. v. d. Valk, 1♀, Senegal, Vélingara, malaise, 15.v.1989 , J. W. Everts, 1♀, Senegal, Ziguinchor, 13.v.1983, J. W. Everts (ZMAN).

Description

Female 5.5 mm. Black; palpi light ferruginous; mandibles ferruginous, apex of mandible and apex of subbasal notch red brown. Scape, pedicel, pronotal lobe, tegula, and apical half of clypeus ferruginous. Legs including coxae ferruginous; spines of all legs dark brown. Sternites I and II, tergites I and II, and lateral side of tergite III ferruginous.

Palpi externally hairy. Clypeus rather low (19 : 5) with shining translucent apical rim (fig. 10). Clypeus and frons just above antennal sockets with scarce silvery pubescence. Head very finely punctulated. Frontal line shining. Inner margins of compound eyes from clypeus up to halfway frons parallel, upper half converging to apex (fig. 10). POL : OOL = 2.0, SOL : OOL = 4.0, VOL : OOL = 2.5. Pedicel somewhat longer than wide, flagellomeres I and II four times as long as wide, flagellomeres III and IV twice as long as wide, flagellomeres V-X one and a half times as long as wide.

Pronotum, mesonotum, scutellum, and metanotum finely punctulated. Propodeum with transversal strigose and midcarina. Mesopleuron strigose. Propodeum equally long and wide at base (16 : 15). Side of propodeum obliquely strigose. Mesopleuron finely and horizontally strigose.

Sternites and tergites shining, very finely punctulated. Tergite VI apically punctulated, without pygidium. Sternite III-VI apically some long hairs.

Forewing somewhat clouded with hyaline band over submarginal cell I and discoidal cell II. Veins light brown and in hyaline band nearly hyaline. First recurrent vein received by submarginal cell I at 0.3 from submarginal cell II. Cu1 and 2m-cu strongly reduced. Hindwing hyaline. In hindwing only medial and submedial cell present. Jugal lobe small with a deep jugal excision.

Coxa I and apical half of coxa II and III ferruginous, basal part of coxa II and III black. Femurs and tibiae I-III for the greater part ferruginous, femurs I and II with an apical, external black spot, tibia III externally black; all tarsi dark brown. All coxae triangle formed, 1.3 as long as wide at the base.

Male 5 mm. Colour largely as in holotype. Clypeus trilobed, with narrow apical rim ferruginous (fig. 11). Scarce silvery pubescence on basal part of clypeus and on frons just above antennal sockets. Tarsi of all legs dark brown. Sternite II with two lateral small round dark brown spots. Tergite VII rounded apically. Sternites III -VII apically two or three outstanding long hairs. Apex of sternite VII straight with a line of short hairs (fig. 12).

Etymology. – From Latin eburneus, meaning made from ivory, so named in reference to the country in which the material was collected (Ivory Coast).

Variations. – The colour of the pronotum varies in different areas. Some females from Ivory Coast have a ferruginous spot at the lateral side of the pronotum. The females of northern Senegal have a complete ferruginous pronotum; all legs including the coxae are completely ferruginous. The females of southern Senegal, Niger, and Nigeria have a black pronotum as in the holotype. In one male from Ivory Coast the dark spots on the second sternite are missing.

Comparative notes. – The new species *M. eburneus* sp. n. is very near to *M. mineticus* Honoré. The anterior edge of the clypeus of *M. eburneus* without discontinuites is even more straight than the clypeus of *M. mineticus.* The legs of *M. eburneus* are mostly ferruginous and black in *M. mineticus. M. eburneus* has no cupreous tinge. Propodeum of *M. mineticus* is obliquely ridged with hairs directed forwards, while *M. eburneus* has a transversally ridged propodeum without hairs.

Miscophus pseudochrysis sp. n.

(fig. 13)

Type material. – Holotype female, Senegal, 25-35 km sud de Richard Toll, piège malaise C3, 13.ix.1989, H. v. d. Valk (LUW). – Paratype 1♂, 27.ix.1989, all other data as in holotype (ZMAN).

Description

Female 5 mm. Shining green; mandibles red brown with dark green base; palpi brownish; scape dark brown; pedicel and flagellum black. Tergites II and III green with cupreous tint. Clypeus with dark brown apical rim.

Ventral side of the segments of the palpi with two rows of curved hairs. Clypeus almost straight at apex, rounded towards compound eye, flat between antennal sockets. Clypeus low (20 : 5). Lower half of frons very roughly rugose. Upper half of frons with few large points on punctulated area; vertex very finely and closely punctulated. POL : OOL = 3.5, SOL : OOL = 3.5, VOL : OOL = 2.0. Pedicel a little longer than wide at apex (5 : 4). Flagellomeres I - IV three times as long as wide at apex. Flagellomeres V-VIII twice as long as wide at apex. Flagellomeres IX and X a little longer than wide. Flagellomere X flattened externally.

Pronotum, mesonotum, and scutellum very finely punctulated, the points arranged in waves, only visible when strongly magnified. Sides of pronotum horizontally strigose, pronotal lobe shining with some reclining white hairs. Dorsal part of propodeum, with strong midcarina, finely strigose obliquely in front and almost transversally apically. Propodeum at base wider than long (16 : 12). Sides of propodeum strongly and horizontally strigose. Mesopleuron reticulated. Episternum of mesonotum with short horizontal lines starting at episternal sulcus, rest of episternum punctated.

Tergites very finely punctulated. Sixth tergite apex sharp and brown, no pygidium. Sternite V with two outstanding hairs at apex; sternite VI with some outstanding hairs at apical half.

Wings hyaline with light ferruginous veins. Veins Cu1 and 2m-cu in forewing strongly reduced (fig. 13). Height of second submarginal cell 0.75 of base of the cell.

All tarsi dark brown. Coxa I almost equilaterally triangular and bulging. Metatarse I with two apical spines and one lateral spine in the middle.

Male 4.5 mm. Colour and most characteristics as in holotype. Base of mandible including basal notch black, middle part brown, apex black. Scape with brown ventral spot. Frons with two horizontal carinas just above antennal sockets. Sternites II-VI with a few setae along apex.

Etymology. – The species takes its name from its great resemblance to *M. chrysis* Kohl, 1894.

Comparative notes. – *M. pseudochrysis* resembles very much *M. chrysis* Kohl, 1894, of which only one female was collected; a comparison can only be given for the females. Reticulated part of the frons up to the midocellus in *M. chrysis* and only half way in *M. pseudochrysis.* Episternum of the mesothorax in *M. pseudochrysis* is horizontally strigose and in *M. chrysis* reticulated. Sternum of the mesothorax in *M. pseudochrysis* is finely punctulated and horizontally strigose in *M. chrysis* . The colour of *M. chrysis* is bright green-blue and of *M. pseudochrysis* bright green and the tergites II and III have a cupreous tint.

Miscophus sallitus Andrade, 1960

(fig. 14)

De Beaumont (1956) mentions a new species of *Miscophus* from the Cape Verde Island of Sal. The single male was later described by Andrade (1960) as *M. sallitus.* Three females, collected in 1988 on the island of Sal, were mentioned as belonging to the same species (Simon Thomas & Wiering 1993). A description of a female is given below.

Description

Female 5 mm. Black; apical half of mandibles amber ferruginous, apical internal side of scape light brown; pedicel with light brown apical ring. Vertex, pronotum, mesonotum, metanotum, and tergites with rather marked cupreous tint.

Clypeus arched with shining rim. Lower part of face and clypeus with silver pubescence. Upper frons very finely and closely punctulated. POL : OOL = 1.7, SOL : OOL = 2.3, VOL : OOL = 2.0. Flagellomeres IX and X are missing in all specimens, VII and VIII on external side with shallow furrow. Flagellomeres I-IV three and a half times as long as wide at apex. Flagellomeres V-VII three times as long as wide at apex. Flagellomere VIII twice as long as wide at apex.

Pronotal collar, mesonotum, scutellum, and metanotum finely punctulated. Dorsal central part of propodeum obliquely striated; side of dorsal part of propodeum striation interrupted and sides of propodeum obliquely striated.

Tergites extremely finely punctulated. Sternites with a few long black hairs at apex.

Forewing hyaline, slightly clouded beyond the nervation zone. Veins ending rather far from apex (fig. 14).

Material. – 3 ♀, Cabo Verde: Sal: Salinas Pedra da Lume, 15.xi.1988, T. & M. Simon Thomas (ZMAN).

Miscophus funebris Honoré, 1944

Material. – 1 ♀, Niger, Niamey, Centre Agrymet, piège malaise, 8.vi.1989, leg. J. Hollands (LUW), 1 ♂, same data as female (ZMAN).

This species is new for Niger. Up till now *Miscophus funebris* Honoré was only known from Egypt. In structure the specimens from Egypt and Niger are very much alike. The Niger specimens differ in extension of the ferruginous colour on legs and first two gastral segments from the Egyptian specimen. All gastral segments of the Niger specimens are light ferruginous, whereas the two first gastral segments of the Egyptian specimen are dark ferruginous. The gastral segments from III to the apex of the Egyptian specimen is also ferruginous. The legs of the Niger specimens are ferruginous with an external dark stripe on the tibiae, whereas the Egyptian specimen has dark brown legs.

Only one specimen of Egypt is known (Honoré 1944) and one female and one male from Niger. No specimens have been found in between Egypt and Niger. From these few specimens it is impossible to tell the colour variations are a constant characteristic of the specimens from Egypt and Niger or a variation in both populations.

Comparative notes. – See under *M. rufigaster* sp. n.

REFERENCES

Andrade, N. F., 1952. Sphecidae of Portugal. Genus *Miscophus* Jurine. – Memorias e Estudos do Museo zoologico da Universidade de Coimbra 211: 1-42.

Andrade, N. F., 1960. Palaearctic *Miscophis: bicolor* group and isolated species (Hymenoptera, Sphecidae). – Memorias e Estudos do Museo zoologico da Universidade de Coimbra 262: 1-136.

Arnold, [G]., 1940. New species of African Hymenoptera No. 4. – Annals of the Transvaal Museum 20: 101-143.

Beaumont, J. de, 1956. Sphecidae et Pompilidae (Hym.). – Commentationes Biologicae 15 (21): 1-7.

Eady, R. D., 1968. Some illusstrations of microsculpture in the Hymenoptera. – Proceedings of the royal Entomological Society of London (A) 43: 66-72.

Everts, J. W., 1990. Environmental effects of chemical locust and grasshopper control. – F.A.O., Rome: 1-277.

Honoré, A.-M., 1944. Materiaux pour une monographie des *Miscophus* d'Egypte. – Bulletin de la Société Fouad 1er d'Entomologie 28: 45-79.

Kohl, F. F., 1894. Zur Hymenopterenfauna Afrikas. – Annalen des naturhistorischen Museums, Wien (series 9) 3: 279-351.

Lomholdt, O. C., 1985. A reclassification of the larrine tribes with a revision of the Miscophini of Southern Africa and Madagascar (Hymenoptera: Sphecidae). – Entomologica scandinavica, supplement 24: 1-183.

Pulawski, W., 1968. *Miscophus heliophilus* sp. n. (Hym., Sphecidae). – Polskie Pismo entomologiczne 38: 285-287.

Simon Thomas, R. T. & H. Wiering, 1993. Notes on the Cape Verde Islands Fauna of Sphecidae and Apidae (Hymenoptera). – Courier Forschungs-Institut Senckenberg 159: 403-409.

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THE GENUS *EUPHAEA* RAMBUR IN BORNEO (ODONATA: EUPHAEIDAE)

Descriptions and records of Malesian Odonata, 3 *)

> *The males are the most brilliant of oriental insects, and they are exceeded by none in elegance of form.*
> Laidlaw 1924: 298

Tol, J. van & N. Norma-Rashid, 1995. The genus *Euphaea* Rambur in Borneo (Odonata: Euphaeidae). Descriptions and records of Malesian Odonata, 3. – Tijdschrift voor Entomologie 138: 131-141, figs. 1-40. [ISSN 0040-7496]. Published 15 June 1995.

The genus *Euphaea* Rambur is revised for the species occurring in Borneo. *E. laidlawi* Kimmins of the *tricolor* species group is synonymized with *E. subcostalis* Selys. *Euphaea ameeka* sp. n., a new species of the *impar* species group close to *E. impar* Selys, is described from Brunei. A key to species of *Euphaea* occurring in Borneo is provided, and the distribution of all species is illustrated.

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Key words. – Borneo, *Euphaea*, new species, revision.

*) Part 2: Tijdschrift voor Entomologie 133 (1990): 273-279.

The dragonfly fauna of Brunei was virtually unexplored when a few years ago Drs. A. G. Orr and D. J. Thompson started their studies on ecology and behaviour of these insects. A first collection identified by the senior author revealed more than 80 species (Thompson & van Tol in press), including several species new to science. One of these species is described in the present paper.

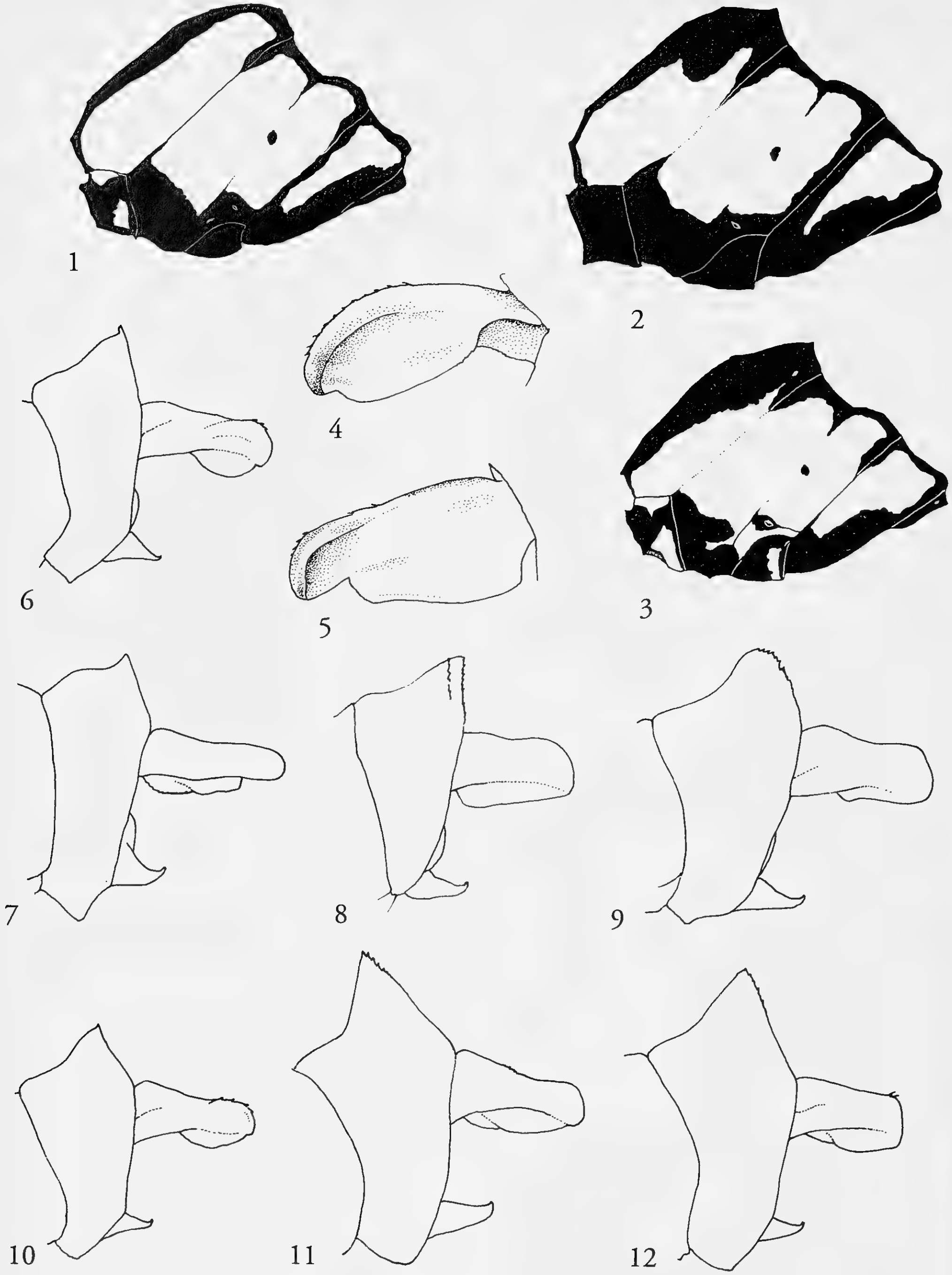
According to present knowledge there are eight species of Euphaeidae in Borneo, viz. six species of *Euphaea* and two of *Dysphaea. Euphaea inaequipar* Selys, reported from Borneo by Selys (1859: sep. 7-8) and Ris (1930), has proved to be a synonym of *Euphaea impar* Selys from Sumatra (Lieftinck 1940). The *Euphaea* species of Borneo are rather poorly known, although adequate material is available in collections worldwide, including the Leiden Museum. One of the reasons is that the species of the complex *tricolor - subcostalis - laidlawi - subnodalis* are very difficult to distinguish. Comparative overviews were first provided by Laidlaw (1920, 1924), followed by Ris (1930) who reviewed the species when he described *E. cora* from the Philippines. In his description of *E. laidlawi*, Kimmins (1936) included sketches of the characteristic seminal vesicles of the first three species mentioned, and Lieftinck (1940) provided the same for *subnodalis. Euphaea basalis* seems to be a more distantly related species.

The aim of the present paper is to provide an overview of all species indigenous to Borneo, and to describe their distribution. Since most species have been sufficiently described before, we present a full description for the newly discovered species only, and include short diagnoses for the other species.

Terminology of body parts follows Watson & O'Farrell (1992).

MATERIAL

We have examined the specimens kept in the Leiden Museum (RMNH), consisting of series of all species known from Borneo and collected in most parts of that island. From eastern Kalimantan there are large series taken by M. E. Walsh-Held, while L. Coomans de Ruiter collected extensively in the western part of the island. Both collectors were active during the 1930's. A smaller collection was made in the central part of present-day Kalimantan, mainly taken by Nieuwenhuis in the 1890's. Collections from the non-Indonesian part of Borneo are from Mt. Merapok (Dent province, former British North Borneo, collected at the end of the 19th century; this



Figs. 1-12. *Euphaea* species, males. – 1, *E. ameeka* sp. n., thorax in lateral view. Brunei (JvT 8363); 2, *E. cora*, same. Samar Is., Philippines; 3, *E. impar*, same. Kalimantan (JvT 8362); 4, *E. ameeka* sp. n., inner view of superior anal appendage (JvT 5016); 5, *E. cora*, same; 6-12, last abdominal segment and anal appendages, left lateral view, 6, *E. ameeka* (JvT 5016); 7, *E. cora*; 8, *E. subcostalis* (JvT 8737); 9, *E. basalis* (JvT 8733); 10, *E. impar* (JvT 8968); 11, *E. subnodalis*; 12, *E. tricolor* (JvT 8802).

locality can be found on map 67 of Anonymus 1905, see also Anonymus 1925/1926) (this locality is presumably identical to Gn. Lumaku; Merapok is now a village in the extreme NW corner of Sarawak, just at the border with Sabah), from Sabah (Kinabalu area, east and southern Sabah, among others collected by the senior author), from Sarawak (leg. M. A. Lieftinck), and finally recent collections from Brunei, brought together by Drs. A. G. Orr and D. J. Thompson. Apart from these series, we were also able to study single specimens of series kept in other institutions, obtained in exchange for the Leiden Museum by M. A. Lieftinck.

SYSTEMATIC PART

Key to the males of *Euphaea* of Borneo

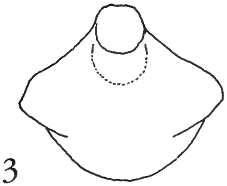
Keys to the *Euphaea* species of Borneo have been published by Laidlaw (1920, 1924) and Ris (1930). The present key includes some features not used in those keys, and the new species described in this paper. The males of all Bornean species of *Euphaea* have a hyaline fore wing. The genus *Dysphaea* is characterised by the nodus situated at the middle of the wing (basal to nodus in *Euphaea*), and a smoothly rounded dorsum of abdominal segment 10 (with dorsal projection in *Euphaea*). The superior anal appendages are stronger curved inward in *Dysphaea* than in *Euphaea*. The females are more difficult to distinguish, and are not further discussed here.

1. Brown opaque area of hind wing at least from nodus to tip of wing (in some species area basal to nodus also opaque to some extent); basal part of opaque area with distinct metallic blue shine; thorax brownish black (in life with greenish tinge), sometimes with some slight yellowish longitudinal markings along the sutures; seminal vesicle usually, but not in all species, with sharp lateral projections, and posterior side broadly rounded (figs. 13-28) 2
– Brown opaque area of hind wing confined to apical one-third, starting approximately halfway between nodus and pterostigma, without conspicuous metallic shine, or hind wing fully hyaline; thorax matt black with extensive blue lateral markings; vesicle rounded laterally and posteriorly with a more or less conspicuous acute tip (figs. 29-33) 5
2. Hind wing fully opaque, brown, vesicle rounded (figs. 25-26). Large species, hind wing 27-28 mm. Mt. Kinabalu only .... *E. basalis*
– Base of hind wing hyaline at least to Ax 10 3
3. 'Auricles' of tergite 2 pale yellowish on dorsal surface, or at least much paler than rest of tergite 2; opaque area of hind wing starting usually at or just basal to nodus, subcostal space hyaline at least in basal part; seminal vesicle rounded (figs. 27-28). Size variable, with hind wing 25-28 mm. West, central and northern Borneo, but not in the Kinabalu region .... *E. tricolor*
– 'Auricles' on dorsal surface brownish black, concolorous with rest of tergite 2; opaque area of hind wing distal to Ax 10-15 rather than distal to nodus or just basal to it; lateral projections of vesicle acute 4
4. Larger species with hind wing more than 26 mm; radial space in hind wing hyaline to nodus; vesicle with lateral projections long and sharp (figs. 23-24); 'auricles' long and slender. Northwestern Borneo .... *E. subnodalis*
– Smaller, but very variable species, hind wing 22-24 mm; radial space of hind wing opaque from same level as rest of opaque distal part; vesicle very variable from broadly rounded and flat ('*laidlawi*') (figs. 13-14) to broadly transverse with long acute lateral sides ('*subcostalis*') (figs. 21-22); 'auricles' more or less triangular and usually shorter than vesicle in lateral view .... *E. subcostalis*
5. Distal one-third to two-fifths of hind wing opaque, brown without metallic blue shine; labrum, mandible and gena with distinct blue and creamish blue markings .... *E. impar*
– Hind wing hyaline; labrum, mandible and gena without, or with very faint, pale markings .... *E. ameeka* sp. n.

The *Euphaea tricolor* group

The *Euphaea tricolor* group, as defined by Ris (1930) consists of *tricolor*, *subcostalis*, *subnodalis*, *amphicyana* and *basalis*. Later, Kimmins (1936) added *Euphaea laidlawi* to this group of species. All species of this group, except *amphicyana* from Mindanao, are endemic to Borneo. The status and distribution of the Bornean species of *Euphaea* has not been discussed since Lieftinck (1940: 343-344, fig. 2) commented upon *E. subnodalis*.

The *Euphaea tricolor* group superficially represents a homogeneous group of species, of which Laidlaw (1924) presumes a close relationship to the *masoni* group of mainland southeast Asia. On closer examination, two species are obviously distinct, viz. *basalis* and *tricolor* (see key, and diagnoses below), but the other three nominal species are closely related indeed. *Subnodalis*, however, seems to be definable on its large size, and the shape of the opaque area in the hind wing. The seminal vesicle of specimens with this combination of characters is also without variation, but this shape, although of smaller size, also occurs in *subcostalis*. We have been unable to find any charac-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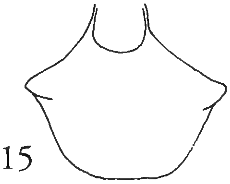
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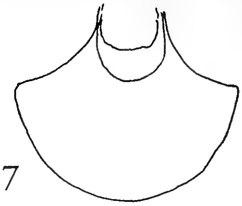
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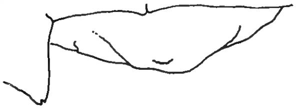
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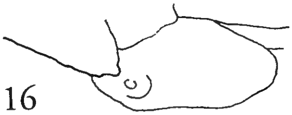
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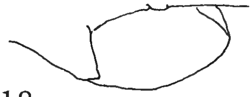
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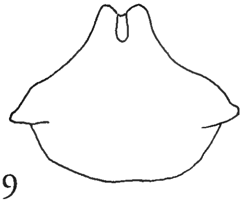
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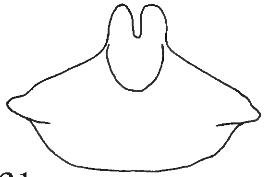
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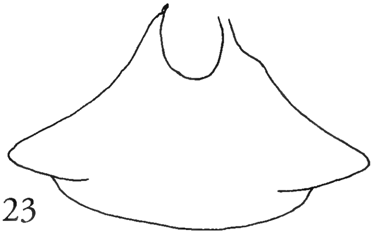
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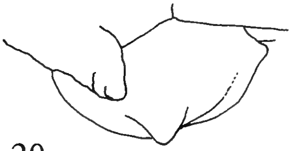
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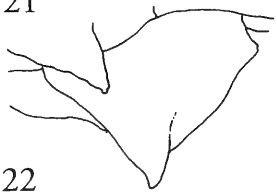
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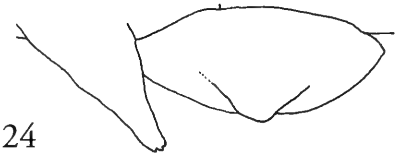
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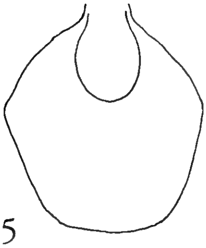
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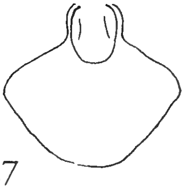
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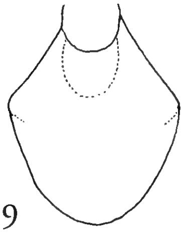
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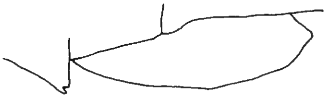
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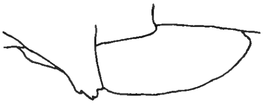
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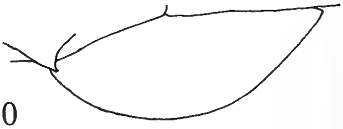
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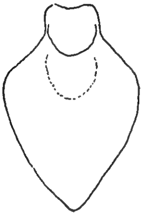
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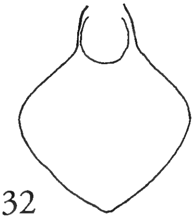
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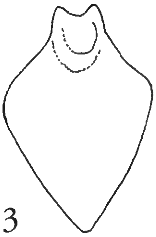
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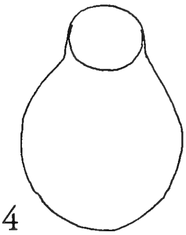
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ters that can unambiguously delimit a subdivision among the rest of the specimens of the *tricolor* group. Both the shape of the opaque area in the hind wing, and the shape of the seminal vesicle, appeared to be most variable. The shape of the vesicle, although frequently considered of taxonomic importance, is also very variable in both species of the *E. impar* group discussed below. Consequently, *subcostalis* and *laidlawi* are here considered to represent only extremes of a very variable species. Since the variation seems have a geographical component, we cannot exclude that microspecies within this complex can be distinguished when more material becomes available with intermediate forms only occurring in narrow zones. Actually, *laidlawi* specimens may represent such hybrids between 'typical' *subcostalis* and *subnodalis*. We suggest a further study of the geographical variation of this group in Borneo, based on an extensive sampling program throughout Borneo, but particularly in the northwestern part of the island.

Euphaea basalis (Laidlaw)
(figs. 9, 25-26, 36)

Pseudophaea basalis Laidlaw, 1915: 32 (type locality Kina Balu).

Pseudophaea basalis. – Laidlaw 1920: 326-327 (Kinabalu); Laidlaw 1924: 298 (key); Kimmins 1969: 306 (holotype ♂).

Euphaea basalis. – Ris 1930: 88-89 (characters); Laidlaw 1931: 241; Laidlaw 1934: 550; Schmidt 1934: plate 17 (1) (pair of wings); Lieftinck 1954: 16 (distribution); Asahina et al. 1983: fig. 39 (pair of wings).

Diagnosis. – Hind wing dark without basal hyaline area, blue metallic in basal ca. 16 mm; costal, subcostal and cubital space, and quadrangle black. Semical vesicle round and rather flat, in lateral view hardly reaching beyond 'auricle' (figs. 25-26); length 1.2 mm. Superior anal appendage (fig. 9) relatively slender with inner ventral scoop-like tubercle visible in distal three-fifths in lateral view.

Hind wing 27-29 mm.

Female unknown.

Distribution. – Only known from Mt. Kinabalu (1000-1500 m) (fig. 36). Apparently occurring at low densities only.

Material examined (RMNH). – 4 ♂, all from Sabah, Kinabalu Mt. (Marai Parai, Tahuban river, Silau Silau river, Liwagu river) (all in RMNH).

Euphaea subcostalis Selys
(figs. 10, 13-22, 37)

Euphaea subcostalis Selys, 1873: 483 (sep. 19) (original description, type locality Labuan).

Pseudophaea subcostalis. – Laidlaw 1915: 32-33 (record Kina Balu); Laidlaw 1920: 326 (records Tampassuh, Sarabas, Mt. Murud, Ulu Akar).

Euphaea subcostalis. – Laidlaw 1931: 241 (Borneo); Schmidt 1934: plate 17 (3) (pair of wings); Lieftinck 1954: 18 (references, distribution); Asahina 1983, fig. 39 (pair of wings).

Euphaea laidlawi Kimmins, 1936: 77-78, figs. (original description, type locality Sarawak, Palawan). – Lieftinck 1954: 17 (references, distribution); Kimmins 1969: 307 (holotype ♂ BMNH [= lectotype]). **Syn. n.**

Diagnosis. – Hind wing rather short and broad, with opaque area distal to ca. Ax 12-15, with metallic blue area extending to Px 6-8, distal margin oblique to Costa; costal space hyaline up to level of Ax 12-15, but subcostal space brown. Seminal vesicle very variable, see below. Anal appendages with superiors (fig. 10) rather robust, with scoop-like ventral inner tubercle virtually extending from base to tip in lateral view.

Variation. – Kimmins (1936: 77-78) described *E. laidlawi* based on two males collected by Everett at Lawas in 1896. A specimen with the same locality and collector is kept in the Leiden Museum, but it is not certain that this represents the para(lecto)type. The specimen fits the description exactly, including the low profile of the vesicle in lateral view (figs. 13-14). Such specimens have not been found on any other locality in Borneo. On the other hand, all kinds of intermediates in the shape of the vesicle between this form and the 'genuine' *subcostalis* can be found (figs. 15-22). The coloration of the wing and the shape of tergite 10, is, as far as we can see, also very variable and of no value for distinguishing taxa.

Distribution. – Widespread in lowland Borneo, but rather scarce in NW part of Sabah, where it is found only at lower altitudes of Mt. Kinabalu and mountain ranges extending southward. At higher altitudes it is replaced by *E. subnodalis*. Forms previously considered as *E. laidlawi* are mainly from the coastal region of NW Borneo (southern Sabah, Sarawak and Brunei). *E. subcostalis* is especially common in streams through lowland rain forest, where it has not been recorded above 600 m. The males can be found perching in high densities in sunny patches along rivulets running through canopy gaps. Kimmins (1936) men-

Figs. 13-34. Seminal vesicles of male *Euphaea* species in ventral and lateral view. – 13-22, *E. subcostalis*. 13-14, Sarawak, Lawas, paratype of *E. laidlawi* (JvT 9043); 15-16, Mt. Marapok (JvT 8775); 17-18, Sabah, Kinabalu area, Kamadaian river (JvT 9153); 19-20, Sarawak, Merirai valley (JvT 8777); 21-22, Sabah, Danum valley, (JvT 8747); 23-24, *E. subnodalis*, Sabah, Long Pasia, Maga river (JvT 8750); 25-26, *E. basalis*, Sabah, Kinabalu Park, Liwagu river (JvT 8735); 27-28, *E. tricolor*, Borneo, Kalimantan, Singkawang (JvT 9052); 29-30, *E. ameeka* sp. n., Brunei (JvT 8375); 31, idem, ventral view only (JvT 8376); 32, *E. impar*, Kalimantan, Bautau Bessi (JvT 8977); 33, same species and locality (JvT 8978); 34, *E. cora*, Samar Is.

tions habitat segregation with *E. tricolor*. This observation is confirmed by Dr. A. G. Orr (pers. comm.) 'At Kuala Belalong Field Studies Centre *E. tricolor* is restricted to the main stream of the Sg. Belalong, and is abundant. *E. subcostalis* is restricted to small side tributaries and is also very abundant. The two may occasionally interact at the mouths of such tributaries'.

Material examined (RMNH). – 101 specimens from Sabah (Gn Marapok, Kamadaian river, Quioin Hill, Kalabakan, Danum Valley), Sarawak (Akar river, Kapit, Matang, Lawas), Brunei (Belalong) and Kalimantan (Midden Oost Borneo Expeditie, Batau Bessi, Kariorang, Nunukan, Bengen river). The type locality (Labuan) is not indicated on the map. This island off the northwest coast of Borneo was an important trading centre during the 19th century, and useless as an indication of the actual sampling station.

Euphaea subnodalis (Laidlaw)

(figs. 11, 23-24, 38)

Pseudophaea subnodalis Laidlaw, 1915: 31-32 (type locality Mt. Kinabalu).

Pseudophaea subnodalis. – Laidlaw 1930: 326 (Kina Balu); Kimmins 1969: 307 (holotype ♂ BMNH).

Euphaea subnodalis. – Ris 1930: 88-89 (key, distribution); Schmidt 1934: plate 17 (4) (pair of wings); Lieftinck 1940: 343-344, fig. 2 (references, material, compared with *subcostalis* and *laidlawi*, anal appendages); Lieftinck 1954: 18 (references, distribution); Asahina et al 1983: fig. 39 (pair of wings).

Diagnosis. – Very similar to *subcostalis*, but larger and with hind wings relatively narrower. Hind wing with opaque dark coloration distal to Ax 10-15, but costal and radial space hyaline between base of wing and nodus; metallic blue (or blue-green) basal area extending to Px 10, running only somewhat oblique to Costa. Length of hind wing 26-28 mm. Seminal vesicle 1.1 mm, and profile usually considerably higher than in *subcostalis*, posteriorly broadly rounded and lateral projections more or less acute and expanded. 'Auricle' considerably longer and narrower than in *subcostalis*, reaching beyond the vesicle in lateral view (figs. 23-24). Last abdominal segment remarkably elevated. Anal superior appendages with ventral tubercle of more complex nature than in *subcostalis*, with a transversal ridge running near base (see also *tricolor*) (fig. 11).

Distribution and biology. – NW Borneo (Sabah) above 1000 m (fig. 38). This species seems to inhabit larger streams at higher altitudes than *E. subcostalis* s.l. It was apparently formerly common around 1000 m on Mt. Kinabalu, but the population density seems to be much lower today, possibly due to the heavy pressure of urban settlements on river systems below 1500 m. In the southernmost part of Sabah, close to the borders of Sarawak and Kalimantan, this species was common at ca. 1000 m altitude in 1987, when this area was still covered with virtually undisturbed submontane rain forest. It occurs sympatrically with *E. tricolor* in that area, with *tricolor* at much lower densities.

Material examined (all RMNH). – 33 specimens from Sabah (Kinabalu, Gn. Marapok, and various rivers around Long Pasia).

Euphaea tricolor Selys

(figs. 12, 27-28, 39)

Euphaea tricolor Selys, 1859: sep. 8 (original description, type locality Saratoga [= lapsus pro Sarawak]).

Pseudophaea tricolor. – Laidlaw 1920: 326 (records Retuh, Saribas, Baram).

Euphaea tricolor. – Laidlaw 1931: 241 (Borneo); Schmidt 1934: plate 17 (2) (pair of wings); Lieftinck 1954: 18; Asahina et al. 1983: fig. 39 (pair of wings).

Diagnosis. – Hind wing with opaque area distal to nodus; blue metallic area from nodus to Ax 12 with distal margin somewhat oblique. 'Auricles' pale coloured on dorsal surface. Seminal vesicle more or less diamond-shaped with rounded lateral sides (figs. 27-28). Anal appendages with superiors relatively short with tip distinctly squarish; in lateral view superior appendage is broader terminally than basally.

Distribution and biology. – Widespread in western and central Borneo, but possibly lacking in the Kinabalu region and certainly absent from Southeast Borneo (fig. 39).

Material examined (RMNH). – 27 specimens from Sabah (Gn. Marapok, Padas river), Sarawak (Dingey river, Tebang), Brunei (Belalong), Kalimantan (Mahakkam, Bloe-oe, Penaring, Bengkajang).

The *Euphaea impar* group

The group of *Euphaea impar* consists of three species, viz. *E. impar*, *E. cora* and *E. ameeka* sp. n. Ris (1930) considered *E. inaequipar* as a distinct species, but Lieftinck (1940) synonymized both taxa. *E. cora* has been recorded from the Philippine islands (Mindanao, Samar) and is not further discussed here (but see figs. 2, 7 and 34). It seems to be a rather rare species (M. Hämäläinen, personal comm.). We were able to study a male and female from Samar from the collection of Dr. Hämäläinen. In the Leiden Museum there are two female specimens from the Philippine Islands (Basilan I., leg. Baker (ex UMMZ, no 2448-1920), and Tobedo, 300 m, 15 May 1951, leg. H. Townes) [locality not found].

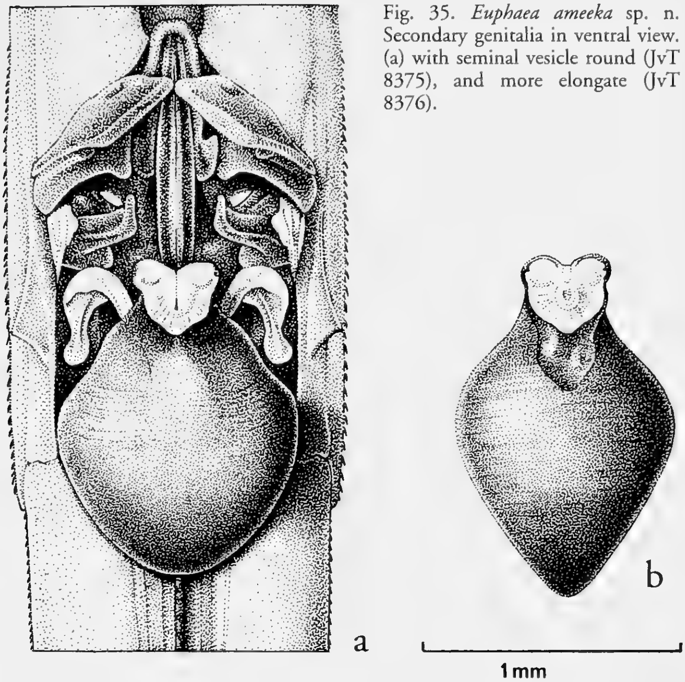


Fig. 35. *Euphaea ameeka* sp. n. Secondary genitalia in ventral view. (a) with seminal vesicle round (JvT 8375), and more elongate (JvT 8376).

Euphaea ameeka sp. n.
(figs. 1, 6, 29-30, 40)

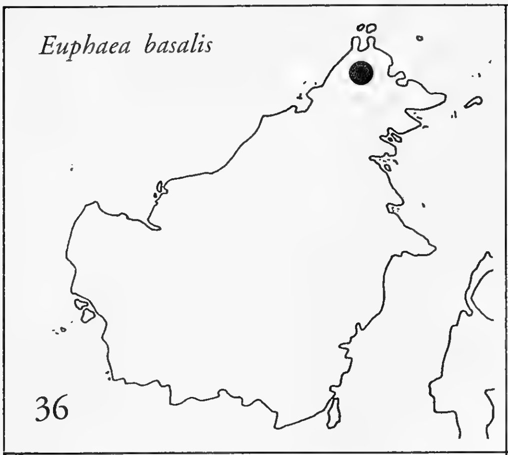
Type material. – Holotype ♂, 'BRUNEI Darussalam. Surroundings Ingai base camp along Ingai river. Stream in freshwater swamp forest running into S. Ingai, 20 min. walk S of base camp. 4°09'21"N 114°42'56"E. 12 Sep 1992. D. Thompson' (in RMNH) [no 12/9/11] [JvT 4888]. – Paratypes 14♂ 1♀ (all Brunei Darussalam): Ulu Belai, between Ingai and Topi rivers, c. 4°08'N 114°43'E, 3 Oct 1992, 1♂ (D. Thompson) [JvT 5016] in RMNH; Bkt Teraja, 9 Sep 1993, 2♂ (A. G. Orr) [JvT 8363/8364] in RMNH; Belait district, Sg. Mendaram, Sep. 1993, 2♂ (A.G. Orr) in RMNH [JvT 8374/8375]; Menteri pools, 28 Oct 1993, 1♂ (A.G. Orr) in RMNH [JvT 8376]; Belait district, near Labi, Sg. Mendaram, 3 Feb. 1995, 8♂ 1♀ (A. G. Orr) in RMNH [JvT 9792/9800].

Description

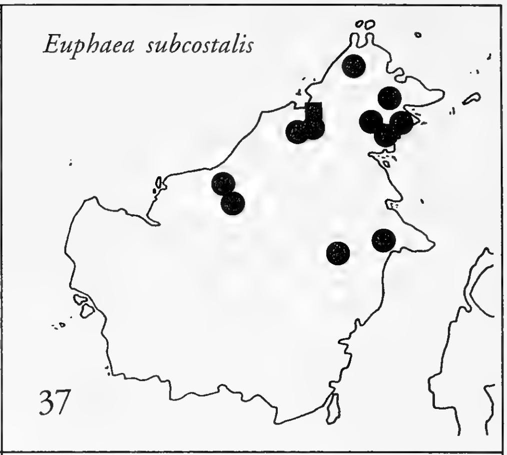
Male holotype. – Head. Labium in ventral view with base pale coloured, the central part suffused with brown; lateral lobe and movable hook brownish black except for the pale base of lobe, median lobe glossy brownish black with central part pruinose, median cleft reaching to two-fifth the height of median lobe; maxilla as far as visible in ventral view pale; labrum, mandibles and clypeus glossy brownish black; remaining part of head matt black without any pale markings.

Thorax. Prothorax matt black with a paired elongate transversal marking on middle lobe. Synthorax (fig. 1) matt black with extensive bright blue (pale blue in preserved material) coloration covering most parts; dorsal carina with anterior triangle and antealar region black, mesepisternum blue except for narrow line against mesopleural (=humeral) suture and pre-alar ridge and posteriormost part of mesopleural suture; mesokatepisternum (= mesinfraepisternum) brownish black with a small blue spot against mesepisternum, and a pale creamish spot near lower side of mesepimeron; metepisternum above interpleural suture blue, anteriorly leaving only one-fifth black, metepisternum below interpleural suture black leaving anterior part up to and inclusive the stigma black, a small black spot against interpleural suture circa halfway the blue area; metepimeron black with an elongate blue marking on upper half from anterior one-fourth to hind margin, the marking widening at posterior end and axtending along hind margin of metepimeron.

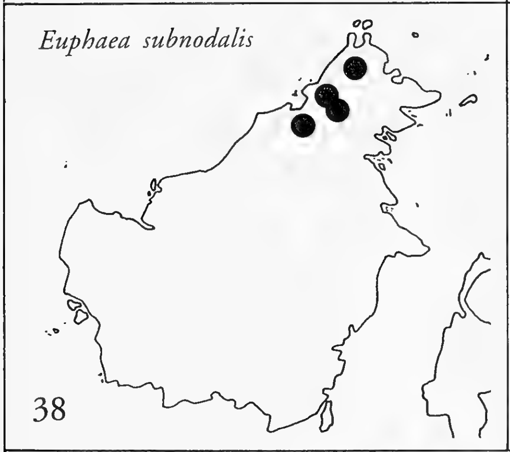
Legs black. Wings with veins black, an indistinct yellowish brown lustre; fore and hind wing transparent without any opaque black marking; fore wings with 18-19 Ax, 24-26 Px; hind wing with 17 Ax, 20-


Euphaea basalis

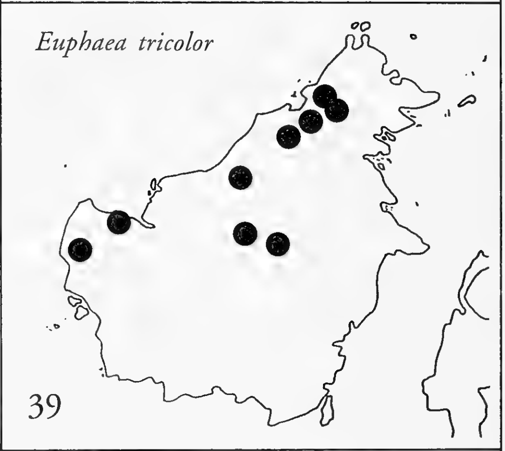
36


Euphaea subcostalis

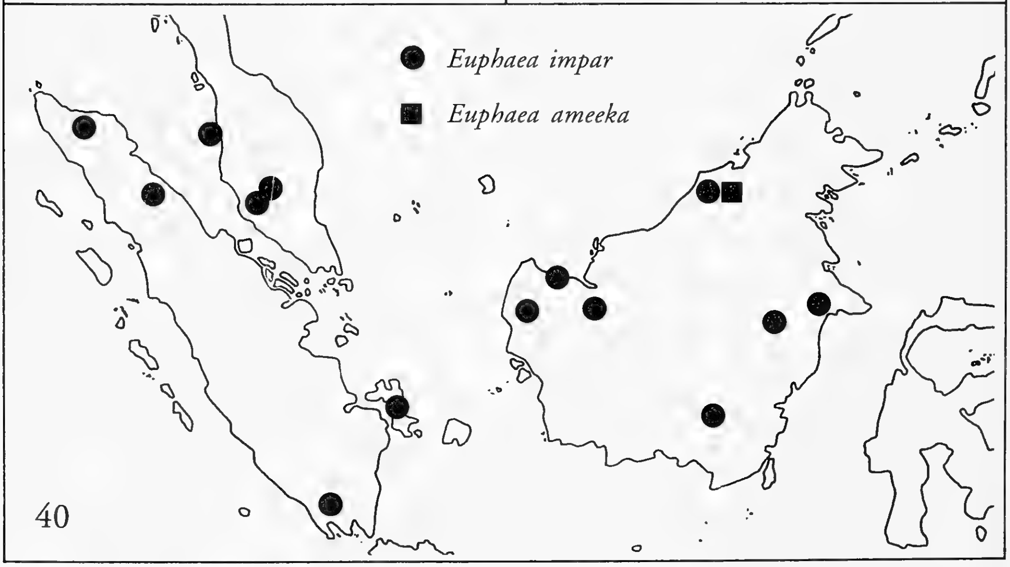
37


Euphaea subnodalis

38


Euphaea tricolor

39



40

21 Px; discoidal cell in all wings with one cross-vein; 2-3 Cux; origin of R3 $2^1/_2$-3 cells distal to subnodus; pterostigma dark brown, covering 7-8 cells.

Abdomen. Fully matt black except for a paired subquadrangular blue spot lateral on tergite 1, covering circa 3/5 of segment length, and a very inconspicuous longitudinal line on both sides of segment 2; segment 10 with distal half triangularly raised into a dorsal projection. Seminal vesicle variable, from broadly rounded (fig. 35a) to more elongate, posteriorly acute. Appendages with superior (fig. 6) in distal half with smoothly rounded ventral tubercle.

Measurements. Hind wing 25 mm, abdomen incl. appendages 32 mm.

Female (paratype JvT 9800). – Pale coloration darker than in male, dirty yellow (in life dark olive green).

Head. Labium including lateral lobes yellowish white, with only tips of middle lobe and movable hooks glossy black; labrum glossy brownish black with a paired subtriangular yellowish white spot, each covering the lateral third, but leaving narrow black anterior and lateral borders; mandibles glossy yellowish white with a brownish black border dorsally and anteriorly; clypeus brownish black; remaining part of head matt black, except yellowish white gena, more or less extending above clypeus, and an elongate pale marking between lateral ocellus and antenna.

Thorax. Prothorax matt black, but middle lobe with triangular dirty yellow markings laterally and lateral tubercle dirty greyish yellow. Synthorax mostly blueish or dirty yellow; mesepisternum blueish, but leaving black borders against dorsal carina, hind margin and dorsal one-fourth over mesopleural suture; also a darker central line over dorsal two-thirds of mesepisternum; rest of synthorax mostly pale coloured, but dark patches over dorsal part of interpleural and metapleural sutures, a subquadrangular marking on mesokatepisternum, and metepimeron brown in central part. Wings hyaline, with 19-21 Ax and 20-22 Ax in fore wing, and 15-16 Ax and 19-20 Px in hind wing.

Abdomen. Brown, darker on dorsal side, but segment 1 on lateral side with pale triangular marking pointed anteriad, widening posteriorly and emarginated on dorsal side; segment 2 with yellow lateral line, segment 3-7 latero-anteriorly with triangular pale marking, relatively large on segment 3 and smaller on each following segment; these segments followed by a longitudinal line on segments 3-5, wider on 3 than on on following segments; lateral lines on all segments posteriorly ending against transversal suture.

Measurements: hind wing 24 mm, abdomen 25 mm.

Remarks

Variation. – Males. There is hardly any variation in the coloration of the paratypes. Wing venation is as follows: fore wing with 18-21 Ax and 23-26 Px; hind wing with 15-18 Ax and 19-24 Px.

The shape of the seminal vesicle is variable as in *E. impar*: in some specimens it has a distinctly elongate shape, while in others in is more or less round (fig. 35). Hind wing 24-25 mm, abdomen incl. appendages 29-31 mm.

Differential diagnosis. – Apparently a close relative of *Euphaea impar*. Both species are structurally similar, but differ in the shape of the wing. The coloration of male head and thorax differs in most characters rather subtlely. However, the shape of the blue markings on the mesepisternum (cf figs. 1 and 3), and the absence of any opaque dark markings in the hind wing of *Euphaea ameeka* are distinctive. The blue and creamish markings on the head of *E. impar* are hardly visible in *ameeka*. The female is very similar to the *E. impar*, including the markings on the head, but the central black line over labrum is very narrow in *E. impar*. Dorsal half of mesepisternum brownish black in *E. impar*, and with extensive dark olive green markings in *E. ameeka*. Pale lateral lines wider and extending to segment 7 (rather than to 5) in *E. impar*. *E. ameeka* is also a close relative of another species of the *Euphaea impar* group as defined by Ris (1930), viz. *E. cora* Ris. Since this species also has fully hyaline wings, the general appearance is very similar. The structure of the male superior anal appendages of *E. cora* (fig. 5), however, differs distinctly from both *E. impar* and *E. ameeka* (fig. 4).

Although we have not found any structural genitalic characters, *E. impar* and *E. ameeka* are considered distinct species, since they occur sympatrically in Brunei. In that region these species show habitat segragation in the upper courses of streams in Brunei forests (A. G. Orr, pers. comm.). Despite their sympatrical occurrence, no intermediates have been noticed. Specific isolation of calopterygoids is, as far as known, especially enforced during the pre-mating phase of reproductive behaviour. Isolation during copulation, e.g. by differences in the shape of the secondary genitalia, is less common. It is generally only observable between distantly related species. This phenomenon

Figs. 36-40. Distribution patterns of *Euphaea* species occurring on Borneo. All species except *E. impar* are endemic to Borneo. Based on collection of RMNH Leiden and published records. – 36, *E. basalis*; 37, *E. subcostalis*, the square is the type locality of *E. laidlawi*; 38, *E. subnodalis*; 39, *E. tricolor*; 40, *E. impar* (circle) and *E. ameeka* sp. n. (square).

is also known in the Calopterygidae and Chlorocyphidae. For instance, morphological differences between the two European species of *Calopteryx*, *C. virgo* (L.) and *C. splendens* (Harris), are nearly absent, while hybrids have never been documented.

A comparative study of the reproductive behaviour of *E. impar* and *E. ameeka* would provide an excellent opportunity to contribute to our understanding of the speciation processes of the euphaeids.

Etymology. – Named after daughter Ameeka of the first collector of this species, Dr. D. J. Thompson. A noun in apposition.

Distribution. – Brunei (fig. 40).

Euphaea impar Selys
(figs. 3, 8, 32-33, 40)

Selected references

Euphaea impar Selys, 1859: sep. 7 [type locality Mt. Ophir, Malacca].

Euphaea impar. – Laidlaw 1902: 87 (record Aring river, Peninsular Malysia); Ris 1930: 85-86 (key); Lieftinck 1940: 341-343 (synonymy, references, material); Lieftinck 1954: 16-17 (references, synonymy, habitat, distribution Malaya, Anambas, Sumatra, Bangka, Borneo); Asahina et al. 1983, fig. 39 (pair of wings); Asahina 1993: 5 (record Thailand); Thompson & van Tol 1995 (records Brunei).

Euphaea inaequipar Selys, 1859: sep. 7 [type locality Saratoga [= lapsus pro Sarawak]).

Euphaea inaequipar. – Ris 1930: 86 (key); Lieftinck 1940: 342 (status discussed).

Diagnosis. – Head with significantly more blue coloration than in *E. ameeka*. Labrum dark brown with a large central blue marking, leaving only narrow dark margins on all sides, blue marking medially transversed by a dark stripe, which is widest in the middle; mandibles pale blue with anterior and basal side dark, clypeus glossy brownish black; remaining part of head matt black, except for blue coloured genae below antennae.

Thorax. Prothorax mainly matt black, middle lobe without blue markings. Synthorax mainly blue coloured, although blue markings are less extensive than in *E. ameeka*. Mesepisternum only blue in anterior lower third (fig. 3), remaining part matt black. Wings with fore wing hyaline, base of hind wing hyaline, opaque brown marking in hind wing from Px 12 to tip of wing.

Abdomen. Brownish black to black. Shape of seminal vesicle as variable as in *E. ameeka* (fig. 32). Anal appendages with distal half of superior smoothly rounded ventral tubercle (fig. 10).

Measurements. Hind wing c. 25 mm, abdomen incl. appendages c. 31 mm.

Geographical variation. – Specimens from Sumatra are similar in structure and markings to those from Borneo.

Distribution. – Thailand, Peninsular Malaysia, Sumatra, Borneo.

Material examined (all RMNH). – 214 specimens from Sabah (Gn Marapok), Brunei (Ingai river), Kalimantan (Katoergau Mts, Raja Mts, Bengkajang, Bagak river, Penaring, Poteng Mts, Batau Bessi, Kariorang, Maloewi, Ampah, Santubang, Gunungsari, Bengen river), Sumatra (Tanggamoes Mts, Deli Laut Tador), Bangka Island and West Malaysia (Penang Island, Kledang Mts, Templer Park, Mupor river).

ACKNOWLEDGEMENTS

We would like to thank D. J. Thompson and A. G. Orr most cordially for the opportunity to study and describe *Euphaea ameeka*. DaveThompson and Bert Orr also put their field notes of the ecology and behaviour of *Euphaea* species of Borneo at our disposal, and extensively commented on a draft of this paper. We also wish to thank Dr. M. Hämäläinen (Espoo, Finland) for the loan of a pair of *Euphaea cora*, and Dr. D.A.L. Davies for comments. Figure 35 was prepared by E. J. Bosch (National Museum of Natural History, Leiden).

REFERENCES

Anonymus, 1905. Stielers Hand-Atlas. Ed. 9. – Justus Perthes, Gotha: map 1-100.

Anonymus, 1925/1926. Namenverzeichnis zu Stielers Hand-Atlas. Ed. 10. [Hundertjahr-Ausgabe]. – Justus Perthes, Gotha: 1-315.

Asahina, S., 1993. Further contributions to the odonate fauna of Thailand based on the recent collection made by Bro. A. Pinratana and Mr. Yunosuke Kimura. – Tombo 36: 2-11, figs. 1-25.

Asahina, S., Y. Wada & T. Yamasaki, 1983. A revisiting to North Borneo. Part 3. – Gekkan Mushi no 149: 23-29, figs. 31-42. [In Japanese].

Coomans de Ruiter, L., 1936. Biologische waarnemingen over beekjuffers van Borneo (Een groep van mooi gekleurde libellen). – Tropische Natuur 25 (5): 69-78, figs. 1-5, plate 1.

Hämäläinen, M., 1985. *Euphaea pahyapi* spec. nov. from peninsular Thailand (Zygoptera: Euphaeidae). – Odonatologica 14: 341-344.

Kimmins, D. E., 1936. The Odonata of the Oxford University Sarawak Expedition. – Journal Federated Malay States Museums 18: 65-108, figs. 1-17.

Laidlaw, F. F., 1915. Contributions to a study of the dragonfly fauna of Borneo. – Part III. A collection made on Mount Kina Balu by Mr. J. C. Moulton in September and October 1913. – Proceedings Zoological Society of London: 25-39, figs. 1-5.

Laidlaw, F. F., 1920. Contributions to a study of the dragonfly fauna of Borneo. Part IV. A list of species known to occur in the island. – Proceedings of the Zoological

Society of London 1920: 311-342, figs. 1-4.

Laidlaw, F. F., 1924. A survey of the dragonfly fauna of the Malay Peninsula, with notes on that of neighbouring countries. Part II. Journal of the Malaysian Branch of the Royal Asiatic Society 2 (3): 296-308, plates 3-5.

Laidlaw, F. F., 1931. A revised list of the dragonflies (Odonata) of Borneo. – Journal of the Federated Malay Museums 16 (3/4): 234-250.

Laidlaw, F. F., 1934. A note of the dragonfly fauna (Odonata) of Mount Kinabalu and of some other mountain areas of Malaysia, with a description of some new or little known species. – Journal of the Federated Malay States Museums 17(3): 549-561.

Lieftinck, M. A., 1940. Descriptions and records of Southeast Asiatic Odonata (II). – Treubia 17 (4): 337-390, figs. 1-18.

Lieftinck, M. A., 1954. Handlist of Malaysian Odonata. A catalogue of the dragonflies of the Malay peninsula, Sumatra, Java and Borneo, including the adjacent small islands. – Treubia 22 (Suppl.): i-xiii + 1-202 + 1 map.

Ris, F., 1930. Vier neue Calopterygiden (Odonata) von den Philippinen und Palawan. – Mitteilungen der Münchner Entomologischen Gesellschaft 20: 71-92, plate 4-7.

Schmidt, E., 1934. Odonata der Deutschen Limnologischen Sunda-Expedition. I. Imagines. Mit Beschreibungen zweier neuer *Ictinus* aus Celebes und Neu-Guinea. – Archiv für Hydrobiologie (Suppl.) 13: 316-397, figs. 1-93 + plates 14-17.

Selys Longchamps, E. de, 1859. Additions au synopsis des Caloptérygines. – Bulletin de l'Académie royale de Belgique (série 2) 7 (7): sep. 1-16.

Selys Longchamps, E. de, 1873. Troisièmes additions au synopsis des Caloptérygines. – Bulletin de l'Académie royale de Belgique (série 2) 35 (5): sep. 1-66.

Thompson, D.J. & J. van Tol, 1995. Dragonflies from four forest types in Brunei. – Brunei Museum Journal (in press).

Watson, D. A. L. & A. F. O'Farrell, 1992. Odonata (Dragonflies and damselflies), p. 294-310, figs. 17.1-17.23. In: CSIRO, The insects of Australia. A textbook for students and research workers. Melbourne University Press.

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BOOK REVIEW

Wiebes, J. T., 1994. The Indo-Australian Agaoninae (pollinators of figs). – Verhandelingen, Koninklijke Nederlandse Akademie van Wetenschappen, Afdeling Natuurkunde (Series 2) 92: 1-208. [ISBN 0-444-85779-6]. Price NLG 85.00.

As a counterpart to the treatment of the African Agaoninae, as published by Wiebes in 1992 (same series, volume 89: 1-298), this publication summarizes the present knowledge of the systematics of the Indo-Australian Agaoninae. In a short introductory chapter the challenges for the future are enumerated, partly consisting of previously described taxa incertae sedis, and partly of still incompletely understood phylogenetic relationships. Wiebes also provides a short history of the study of the Indo-Australian fig wasps, starting only in 1883. A special word is devoted to the work of Girault whose taxa 'took a long time before a few of these were recognized, and most had better been forgotten'. Not a hymenopterist myself, and looking through the bibliography, I noticed that these species were described in privately published brochures with titles as 'Some gem-like or marvellous inhabitants of the woodlands heretofore unknown and by most never seen nor dreamt of' and 'Some beauties inhabitant not of commercial boudoirs but of nature's bossom, notably new insects'. I sincerely hope that publications with such melodious titles will be referred to for many years to come, since I consider it very unlikely that articles with such titles will pass an editor of any 'serious' journal now.

The present book, however, qualifies for any high standard of the 1990's. The keys are clear and extensive, but not too verbose. The descriptions all follow the same format, and provide careful enumerations of relevant characters, as well as data on host fig and distribution. There is a surprisingly small amount of illustrations.

The quality of printing of the illustrations is also inferior to that of the text. I presume that only xerox copies of the original art work have been used for reproduction in the present publication.

All students of Chalcidoidea will very much appreciate the efforts of Wiebes and the publishers. The information, otherwise only available in many short papers, can now easily be retrieved from this book. I also expect that other systematists with interest in co-evolution will start a re-evaluation of the phylogeny of this group in future (and, of course, of the figs as well). Previously published authoritive papers by Wiebes on this topic (e.g. in Ann. Rev. Ecol. Syst. 10: 1-12), and the summaries of basic data as in the present volume, provide a sound basis for every student of this difficult field of research.
[J. van Tol].

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TANZANIAN MICRO-CADDISFLIES (TRICHOPTERA: HYDROPTILIDAE)

Wells, A. & T. Andersen, 1995. Tanzanian micro-caddisflies (Trichoptera: Hydroptilidae). – Tijdschrift voor Entomologie 138: 143-167, figs. 1-63. [ISSN 0040-7496]. Published 15 June 1995.

The genus *Tangatrichia* is erected for a new species from the West Usambara Mountains in north-eastern Tanzania, *T. gracilenta.* In addition, 24 other new species of micro-caddisflies are described from north-eastern and central Tanzania: *Catoxyethira apicospinosa, C. bombolensis, C. ciliata, C. crenulata, C. crinita, C. elongata, C. incompta, C. lanceolata, C. ruvuensis, Scelotrichia glandulosa, Stactobia kaputensis, Dhatrichia cinyra, D. divergenta, Hydroptila bumbulensis, H. mazumbaiensis, H. morogorensis, H. tannerorum, H. usambarensis, Ugandatrichia dentata, U. tanzaniensis, Orthotrichia bisetula, O. hydroptiloides, O. nigrovillosa, O. scutellata.* Two other established species, *Catoxyethira ocellata* Statzner, 1977 and *Orthotrichia barnardi* Scott, 1963, are recorded from Tanzania for the first time and a new record is given for *Hydroptila cruciata* Ulmer, 1912, one of the two species known previously to occur in Tanzania.

The East African Hydroptilidae fauna now totals 36 species; the Tanzanian fauna comprises 29 species in eight genera including three genera in the tribe Stactobiini: *Stactobia* and *Scelotrichia* each with one species and *Catoxyethira* with ten species. In Hydroptilini, a new monotypic genus *Tangatrichia* as well as two species in *Dhatrichia,* two species in *Ugandatrichia,* and six species in *Hydroptila* are recorded. For the Orthotrichiini six species are listed in *Orthotrichia.* Notes are given on distributions and apparent affinities of new taxa and a key to males of Tanzanian genera and species is provided.

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Key words. – Trichoptera, Hydroptilidae, new genus, new species, Tanzania.

Information on caddisflies of the Afrotropical Region was summarised by Scott (1986) who listed eleven hydroptilid genera (one endemic), and 49 species. Gibon (1985, 1987a, 1987b, 1991) has described 21 species from the Ghana, Guinea, Mali, the Ivory Coast and Togo and Mey (1992) recently described a new species from Kenya. For East Africa alone, six micro-caddisfly genera and nine species were listed by Johanson (1992), not including the species described by Mey (1992). In a preliminary account of part of the Tanzanian fauna studied here, from the Kaputu stream only, Andersen & Johanson (1993) recorded eight genera and 12 species. In this present study, which covers a broader area of north-eastern and central Tanzania, 28 species are listed in eight genera, 25 species and one genus being newly described. New distribution records are given for three established species, one of which is a widespread African/Asian species, another a Central African species and the third South African.

Of the two hydroptilid subfamilies only Hydroptilinae has been recorded from the Afrotropical Region; the more primitive Ptilocolepinae is restricted to the Holarctic Region. Three tribes are represented: Stactobiini Botosaneanu, 1956, Orthotrichiini Nielsen, 1948 and Hydroptilini Stephens, 1836. Two stactobiine genera, *Catoxyethira* Ulmer, 1912 and *Stactobia* McLachlan, 1880 were listed for the East African fauna by Johanson (1992), but none for Tanzania. New Tanzanian species are here described in each of these genera, and in a third stactobiine genus, *Scelotrichia* Ulmer, 1951. One species is referred to each of *Scelotrichia* and *Stactobia* and nine to *Catoxyethira,* and a new record is given for *Catoxyethira ocellata* Statzner, 1977. The relatively high diversity of *Catoxyethira* in tropical Africa, the features of the genus and its possible relationships with other members of the Stactobiini are discussed briefly.

Five genera in the Hydroptilini are recorded here for East Africa. Two of these, *Ugandatrichia* Mosely, 1939 and *Hydroptila* Dalman, 1819, were included by Johanson (1992) in his list for East Africa. Johanson also listed *Argyrobothrus* Barnard, 1934 which was synonymised with *Oxyethira* Eaton, 1873 by Ross (1948); since Johanson gave no support for reinstating the name, his action is not accepted here. The record is based on an unidentified species from Uganda in a paper by Kimmins (1958). As Gibon (1987b) notes, *Oxyethira* is poorly represented in Africa in comparison, for example, with North America or Eurasia. De Moor (1993) lists only three species for South Africa and no *Oxyethira* males were found in collections on which the present study is based. Perhaps when more is known of the biology of some of the other African genera, it will be found that other species are filling the filamentous green algal-feeding niche that *Oxyethira* species generally occupy elsewhere.

Two new *Ugandatrichia* species are described here, representing the first Tanzanian records of the genus; other East African records are from Uganda and Kenya. In *Hydroptila*, only *H. cruciata* Ulmer, 1912, described from Tanzania (Ulmer 1912), was previously known from East Africa. Five new Tanzanian species are described here, and a new record is given for *H. cruciata*. The fourth Hydroptilini genus recorded for Tanzania, *Dhatrichia* Mosely, 1948, is also recorded for the first time for East Africa. Two new species are described, bringing the total for this Afrotropical genus to five. The fifth genus, *Tangatrichia* gen. n., is newly described and monotypic; its affinities within the tribe are discussed.

Of the two genera in the tribe Orthotrichiini, only *Orthotrichia* Eaton, 1873 is known to occur in East Africa. The other genus, *Ithytrichia* Eaton, 1873 is recorded from South Africa, from immatures only (Scott 1986). Four new species in *Orthotrichia* are described here, raising the total for Tanzania to six species, and a new record is given for *Orthotrichia barnardi* Scott, 1963, known previously from South Africa only.

MATERIAL AND METHODS

All material studied here was collected in connection with an expedition by the Museum of Zoology, University of Bergen, to central and north-eastern Tanzania during October to December 1990. One Malaise trap at the Kaputu Stream in the West Usambara Mountains was run by the staff at the Mazumbai Forest Reserve Station for shorter periods during January to August 1991. The main collecting sites along the Kaputu Stream are described in detail by Andersen & Johanson (1993). They also outline the main methods used to collect and preserve the specimens. Additional material was taken by sweep-netting and light-trapping at other localities in the West and East Usambara Mountains in the Tanga region and at two lowland sites in the Morogoro region. These localities are listed below; where maps were available, Universal Transverse Mercator Grid (UTM) reference and accurate altitude are given.

Amani East Forest Reserve, Zigi River (UTM: 37MDE609365), 470 m a.s.l., East Usambara Mts, Tanga region, 2.xii.1990, sweep net. Fast flowing river, 10 m wide, with large stones; in lowland rain forest area.

Bombole (UTM: 37MDE596388), 830 m a.s.l., East Usambara Mts, Tanga region, 1.xii.1990, sweep net. Small rapid river with large stones; in forested area.

Dule, Bumbuli River (UTM: 37MDE403633), 1220 m a.s.l., West Usambara Mts, Tanga region, 26.xi.1990, sweep net. Rapid river, 5 m wide, with large stones; in a cultivated area.

Gogoi, (UTM: 37MDE378509) 1100 m a.s.l., West Usambara Mts, Tanga region, 30.xi.1990, sweep net. Two small streams with waterfalls; in area with rain forest and cultivated land.

Gologolo, Lushoto (UTM: 37MDE182770), 1860 m a.s.l., West Usambara Mts, Tanga region, 25.xi.1990, sweep net. Rapid stream, 1.5 m wide, with stony and sandy bottom and waterfalls; in rain forest area.

Kimboza, Ruvu River, about 150 m a.s.l., Morogoro region, 20.x.1990, sweep net. Large slow flowing river, 20-30 m wide, with sandy base, in parts with faster flow over stones; banks forested.

Mlesa (UTM: 37MDE6003745), 800 m a.s.l., East Usambara Mts, Tanga region, 1.xii.1990, sweep net. Rapid river with large stones and waterfalls; in forested area.

Shakoi River (UTM: 37MDE404730), 1420 m a.s.l., West Usambara Mts, Tanga region, 24.xi.1990, sweep net. Rapid stream with large stones and heavily vegetated banks; in cultivated area.

Campus, Sokoine University of Agriculture, about 550 m a.s.l., Morogoro, Morogoro region, 26.x.-11.xi.1990, light trap. Garden at the foothills of the Uluguru Mts.

Specimens were prepared for study following the methods of Wells (1990a). Attempts to associate females proved difficult and thus only males of new species are described. All types are lodged in the collection of the Museum of Zoology, University of Bergen, Norway (ZMBN).

SYSTEMATIC PART

Check list of East African Hydroptilidae

Tribe Stactobiini
Catoxyethira Ulmer, 1912
    syn. *Sperotrichia* Marlier, 1978
1. *apicospinosa* sp. n., Tanzania.
2. *bombolensis* sp. n., Tanzania.

3. *ciliata* sp. n., Tanzania.
4. *crenulata* sp. n., Tanzania.
5. *crinita* sp. n., Tanzania.
6. *elongata* sp. n., Tanzania.
7. *incompta* sp. n., Tanzania.
8. *lanceolata* sp. n., Tanzania.
9. *ocellata* Statzner, 1977, Zaire; Tanzania.
10. *pinheyi* Kimmins, 1958, Zimbabwe; Uganda.
11. *ruvuensis* sp. n., Tanzania.

Scelotrichia Ulmer, 1951
syn. *Madioxyethira* Schmid, 1960
12. *glandulosa* sp. n., Tanzania.
13. *kenyella* (Mey, 1992), Kenya.

Stactobia McLachlan, 1880
syn. *Afritrichia* Mosely, 1939
14. *aurea* (Mosely, 1939), Uganda.
15. *kaputensis* sp. n., Tanzania.

Tribe Hydroptilini
Dhatrichia Mosely, 1948
16. *cinyra* sp. n., Tanzania.
17. *divergenta* sp. n., Tanzania.

Hydroptila Dalman, 1819
18. *bumbulensis* sp. n., Tanzania.
19. *cruciata* Ulmer, 1912, Tanzania.
syn. *H. hirra* Mosely, 1948
20. *mazumbaiensis* sp. n., Tanzania.
21. *morogorensis* sp. n., Tanzania.
22. *tannerorum* sp. n., Tanzania.
23. *usambarensis* sp. n., Tanzania.

Tangatrichia gen. n.
24. *gracilenta* sp. n., Tanzania.

Ugandatrichia Mosely, 1939
25. *acuta* Mosely, 1939, Kenya; Uganda.
26. *dentata* sp. n., Tanzania.
27. *minor* Mosely, 1939, Kenya.
28. *nigra* Mosely, 1939, Uganda.
29. *tanzaniensis* sp. n., Tanzania.

Tribe Orthotrichiini
Orthotrichia Eaton, 1873
30. *aequatoriana* Kimmins, 1957, Uganda.
31. *barnardi* Scott, 1963, South Africa; Tanzania.
32. *bisetula* sp. n., Tanzania.
33. *hydroptiloides* sp. n., Tanzania.
34. *nigrovillosa* sp. n., Tanzania.
35. *scutellata* sp. n., Tanzania.
36. *straeleni* Jaquemart, 1956, Zaire; Tanzania, Uganda.

East Africa, as defined here, comprises the countries Tanzania, Kenya, Uganda, Burundi and Rwanda. From Burundi and Rwanda, however, no hydroptilids are recorded. In the list only synonyms applied to the East African species are included.

Key to males of hydroptilid genera and species in Tanzania

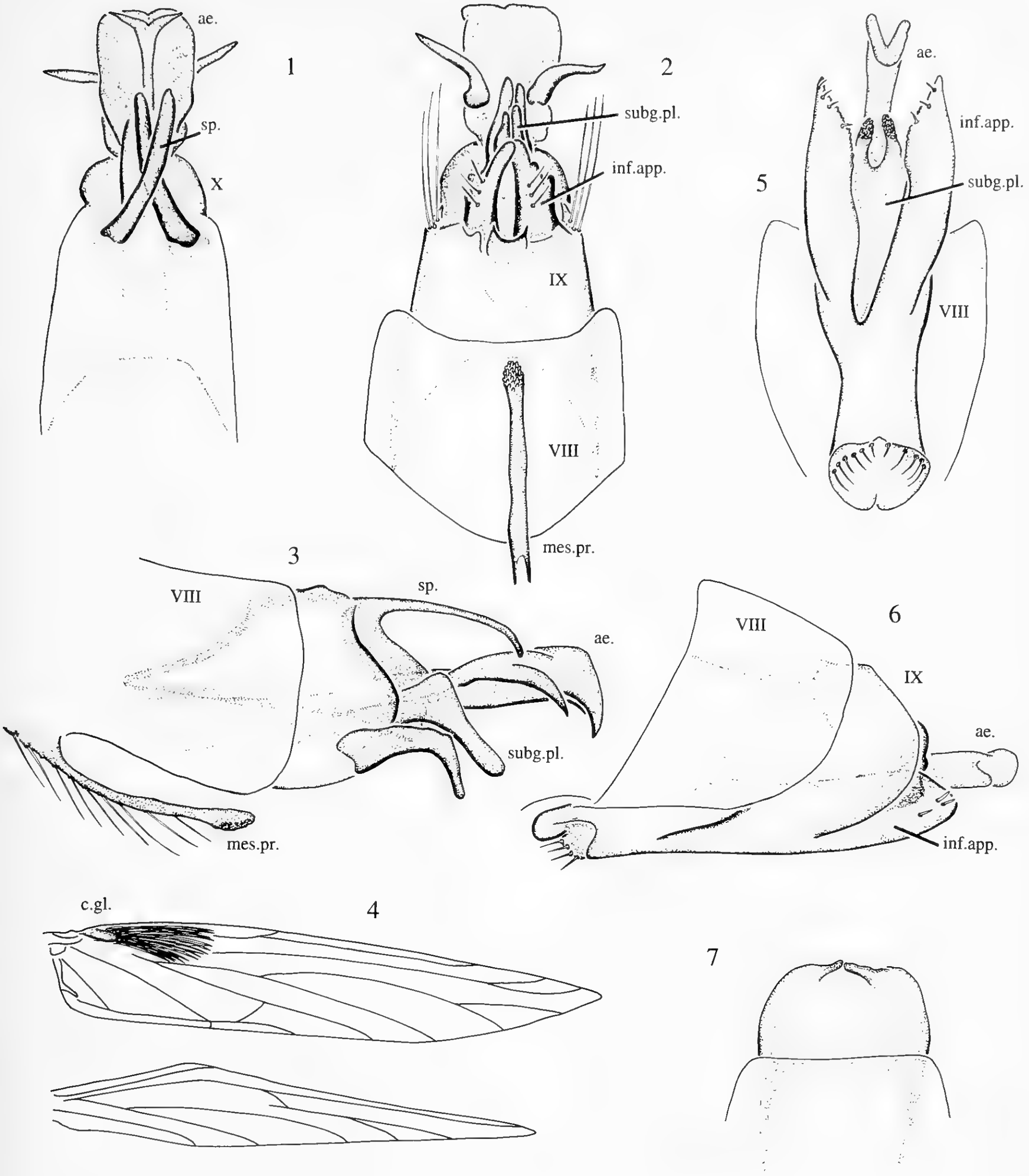
1. Mesoscutellum with transverse suture 2
– Mesoscutellum without suture 4
2. Tibial spur formula 0, 2, 4 .... *Scelotrichia glandulosa* sp. n.
– Tibial spur formula 1, 3, 4 or 1, 2, 4 3
3. Tibial spur formula 1, 2, 4 ....*Stactobia kaputensis* sp. n.
– Tibial spur formula 1, 3, 4 (*Catoxyethira* Ulmer) 8
4. Ocelli absent 5
– Three ocelli present 6
5. Forewing with jugal lobe, metascutellum pentagonal to triangular (*Hydroptila* Dalman) 17
– Forewing without jugal lobe, metascutellum rectangular (*Orthotrichia* Eaton) 22
6. Wings slender, attenuate apically, venation reduced (see figs. 4, 32, 54) 7
– Wings broad, forewing rounded apically, venation complete (fig. 26) (*Ugandatrichia* Mosely)....... 27
7. Antennal flagellar segments with scattered clothing hair; metascutellum triangular, truncate anteriorly (fig. 50) .... *Tangatrichia gracilenta* sp. n.
– Antennal flagellar segments with clothing hair in basal whorl; metascutellum rounded anteriorly (*Dhatrichia* Mosely) 28
8. ..Abdominal sternite VIII with one pair of stout, apico-lateral or mesal spines (figs. 12-25) 9
– .....Abdominal sternite VIII without stout spines (figs. 8-10) 16
9. Abdominal sternite VIII with apico-lateral spines (figs. 22-25) 10
– .Abdominal sternite VIII with mesal spines (figs. 12-21) 12
10. ......Abdominal sternite VIII with cluster of lon stout setae mid-ventrally (fig. 22) .... *Catoxyethira crinita* sp. n.
– Abdominal sternite VIII without cluster of long, stout setae mid-ventrally 11
11. ..Inferior appendages positioned mid-ventrally in a deep excision in abdominal sternite VIII (see Statzner, 1977, fig. 24) .. *Catoxyethira ocellata* Statzner
– Abdominal sternite VIII without deep excision midventrally (fig. 25) .... *Catoxyethira ciliata* sp. n.
12. ......Abdominal sternite VIII with a shorter, thi spine between the paired spines (fig. 21) .... *Catoxyethira crenulata* sp. n.
– ..Abdominal sternite VIII with one pair of spines only 13
13. ...Paired spines on abdominal sternite VIII about equal in length to inferior appendage (fig. 13) ...

.... *Catoxyethira ruvuensis* sp. n.
– Paired spines on abdominal sternite VIII almost 2 × length of inferior appendage, or longer ...14
14. Length of paired spines on abdominal sternite VIII 2.5 to 3 × length of inferior appendage (fig. 18) .... *Catoxyethira elongata* sp. n.
– ....Length of paired spines on abdominal sternit VIII no more than 2 × length of inferior appendage (figs. 14, 16) 15
15. Paired spines on abdominal sternite VIII straight in lateral view (fig. 16), curved inwards in ventral view (fig. 17) .... *Catoxyethira lanceolata* sp. n.
– .Paired spines on abdominal sternite VIII curved upwards in lateral view (fig. 14), more or less straight in ventral view (fig. 15) .... *Catoxyethira apicospinosa* sp. n.
16. Subgenital plate and inferior appendages elongate, subequal in length; inferior appendages cylindrical (figs. 9, 10) .... *Catoxyethira bombolensis* sp. n.
– Subgenital plate about 2 × length of inferior appendages; inferior appendages broader basally than distally (fig. 8) .... *Catoxyethira incompta* sp. n.
17. With pair of sclerotised strap-like structures above inferior appendages (fig. 48) 18
– Without pair of sclerotised strap-like structures above inferior appendages (figs. 39, 42, 43, 46) 19
18. Inferior appendages in ventral view slender, curved, narrowed slightly towards apex without black spine apically (see Mosely, 1948, fig. 48) ....*Hydroptila cruciata* Ulmer
– Inferior appendages in ventral view stout basally, apically bifid, with strong, black spine ventrally, pale, slender spine dorsally (fig. 48) ....*Hydroptila bumbulensis* sp. n.
19. Inferior appendage short, sub-glubose in ventral view, irregular in shape (fig. 46) .... *Hydroptila tannerorum* sp. n.
– Inferior appendage elongate, cylindrical or somewhat sinuous, with length at least 3 × width 20
20. Aedeagus greatly dilated distally, with single small spine subapically (fig. 39) .... *Hydroptila usambarensis* sp. n.
– Aedeagus slender or weakly dilated distally, with one or two spines apically 21
21. Inferior appendages in ventral view dilated in basal half, tapered and out-turned apically; aedeagus with small spine apically (figs. 41, 42) .... *Hydroptila morogorensis* sp. n.
– Inferior appendages in ventral view sub-cylindrical; aedeagus divided distally to form a pair of spines in series (figs. 43, 44) .... *Hydroptila mazumbaiensis* sp. n.
22. ....Abdominal segment IX laterally with pai membranous, digitate processes with 1 or 2 apical setae (e.g. figs. 55-57) 23
– Abdominal segment IX without paired processes laterally (e.g. figs. 58-63) 24
23. Inferior appendages symmetrical (fig. 7) .... *Orthotrichia barnardi* Scott
– Inferior appendages asymmetrical (fig. 55) ....*Orthotrichia bisetula* sp. n.
24. Tibial spur formula 0, 2, 4................................ .... *Orthotrichia hydroptiloides* sp. n.
– Tibial spur formula 0, 3, 4 25
25. Inferior appendages fused, in ventral view rectangular (fig. 59) .... *Orthotrichia scutellata* sp. n.
– Inferior appendages discrete or partially fused, in form of two unequal lobes 26
26. Inferior appendages rounded, asymmetrical, the left apically with small sclerotised knob; an elongate process extending distally into a spine at right apico-lateral angle of segment IX (fig. 61) .... *Orthotrichia nigrovillosa* sp. n.
– Inferior appendages tapered distally, the right one twisted; a simple, apically rounded process at right apico-lateral angle of segment IX (see Jacquemart, 1956, fig. 2) .... *Orthotrichia straeleni* Jacquemart
27. Inferior appendages set into deep excision in abdominal sternite IX, irregular in shape, with small inner spur subapically (fig. 28) ....*Ugandatrichia tanzaniensis* sp. n.
– Abdominal sternite IX with shallow, ventral excision; inferior appendages stout, with inner spur at base (figs. 27, 30) .... *Ugandatrichia dentata* sp. n.
28. Length of inferior appendages in ventral view about 2 × width (fig. 35) .... *Dhatrichia divergenta* sp. n.
– Length of inferior appendages in ventral view 3 to 4 × width (fig. 37)......... *Dhatrichia cinyra* sp. n.

Stactobia McLachlan

Stactobia McLachlan, 1880: 515. Type species *Hydroptila fuscicornis* Schneider, 1845 by subsequent designation (Mosely 1933). For full generic synonymy see Marshall (1979).

The genus *Stactobia* was reviewed by Marshall (1979). It is well represented in the Palaearctic and Afrotropical regions and some parts of the Oriental region. The larvae are scrapers, feeding on organic material in madicolous and hydropetric habitats. One species, placed by Marshall (1979) in the *vaillanti* species group, was known previously from East Africa, from Uganda. The new species resembles the West African *S. vaillanti* Schmid, 1959 described from Guinea by Schmid (1959), more closely than the East African *S. aurea* (Mosely, 1939).



Figs. 1-3. *Stactobia kaputensis* sp. n., male genitalia. 1, dorsal view; 2, ventral view; 3, lateral view. – Figs. 4-7. *Scelotrichia glandulosa* sp. n., male. 4, wings; 5, genitalia, ventral view; 6, genitalia, lateral view; 7, genitalia, dorsal view. – Abbreviations. – ae: aedeagus; c.gl.: costal gland; inf.app.: inferior appendage; mes.pr.: mesal process; sp.: spine; subg.pl.: subgenital plate; VIII, IX, X: abdominal segments VIII, IX, X.

Stactobia kaputensis sp. n.
(figs. 1-3)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 9, 1450 m a.s.l., 19.-23.xi.1990, Malaise trap, ZMB´s Tanzania Expedition (slide, ZMBN No. 194). – Paratypes: 36♂ (3 slides) data as for holotype except loc. 2-11, 30.x.-26.xi.1990; 2♂ data as for holotype except loc. 7, 1.-8.viii.1991; 2♂ data as for holotype except loc. 5, 6. xi. 1990, sweep net; 2♂ data as for holotype except Gogoi, 30.xi.1990, sweep net; 3♂ data as for holotype except East Usambara Mts, Amani East Forest Reserve, Zigi River, 2.xii.1990, sweep net; 9♂ data as for holotype except East Usambara Mts, Bombole, 1.xii.1990, sweep net; 1♂ data as for holotype except East Usambara Mts, Mlesa, 1.xii.1990, sweep net.

Description

Small, and (in alcohol) uniformly brown; antennae with 18 segments; ocelli 3; tibial spurs 1, 2, 4. Anterior wing length 1.4-2.1 mm. Genitalia as in figs. 1-3. Abdominal sternite VII with a long straight mesal process, reaching posteriorly almost to the apical margin of segment VIII. Segment IX well developed. Segment X extending distally in a pair of stout, elongate, sclerotised spines. Inferior appendages broad-based, forming irregular lobes distally. A distinct lobe above the inferior appendages and apparent in lateral view probably represents the subgenital plate. Aedeagus elaborate and swollen apically, with several sets of spines.

Etymology. – Named for the Kaputu Stream in the West Usambara Mountains, Tanzania.

Biology and distribution. – Taken at several sites in both East and West Usambara Mountains, both along smaller streams and larger rivers at altitudes between 470 m and 1650 m a.s.l. In the Malaise traps along the Kaputu Stream this species was trapped frequently both at sites with slow flow over gravel, stones and mud, and at sites with fast flow over bedrock and stones (see Andersen & Johanson 1993). Swarming specimens were netted by day mostly in areas of fast flow over bedrock and stones or near waterfalls.

Remarks. – *Stactobia kaputensis* sp. n. closely resembles *S. vaillanti* from which it is distinguished by the shape of the inferior appendages in lateral view and the bigger spines on the aedeagus.

Scelotrichia Ulmer

Scelotrichia Ulmer, 1951: 73. Type species: *Scelotrichia saranganica* Ulmer, by original designation and monotypy. See Wells (1990a) for full generic synonymy.

Worldwide, the genus *Scelotrichia* is represented by some 29 species, the majority described from SE Asia. Only two African species were known previously, *S. marshalli* (Statzner, 1977) from Zaire and *S. kenyella* (Mey, 1992) from Kenya. Both of these species and a new species described here are relatively conservative in genitalic form compared to some of the Bornean and New Guinean species. All lack areas of scent scales (androconia) on the forewings, but the new species has a small sac-like costal gland at the base of a tuft of hair in the forewing. At least in the Tanzanian species, the body vestiture is hairy, not scaly as in many of the species of the Malay Archipelago. Conceivably, the African species represent a relict fauna.

Like *Stactobia*, some *Scelotrichia* species are madicolous. Others are found living on aquatic mosses on rocks in fast flowing waters (see Schmid 1960, Wells 1990a, 1990b). No details are known of the biology of these African species.

Scelotrichia glandulosa sp. n.
(figs. 4-7)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 5, 1650 m a.s.l., 2.-6.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 195). – Paratypes: 33♂ (5 slides) data as for holotype except loc. 2-11, 30.x.-26.xi.1990; 14♂ (4 slides) data as for holotype except 31.x. & 6.xi.1990, sweep net; 5♂ data as for holotype except loc. 8, 5.xi.1990, sweep net; 25♂ data as for holotype except Gologolo, Lushoto, 25.xi.1990, sweep net.

Description

Males relatively large, in alcohol uniformly dark coloured; antennae 19-segmented, segments elongate; ocelli 3; tibial spurs 0, 2, 4, with a small rounded knob in the place of the spur on foreleg. Forewing (fig. 4) with a small sac-like gland adjacent to a tuft of hair in the proximal costal region; length 2.8-3.5 mm. Genitalia as in figs. 5-7. Segment VIII reduced ventrally, rounded dorsally. Segment IX (dorsal plate) appears to be reduced, possibly represented by the paired sclerotised lobes shown in fig. 7. Inferior appendages stout, tapered apically and with small serrations on inner margin subapically, fused basally and extended anteriorly to a pronounced round mesal structure at the margin of sternites VII and VIII. Subgenital plate bifid and rugose apically, lobes separated by a deep, rounded concavity. Aedeagus simple, straight, apically bilobed in ventral view.

Etymology. – From the Latin *glandulosus*, glandulous, referring to the gland in the forewing.

Biology and distribution. – Known only from the West Usambara Mountains, where it was taken along streams at altitudes between 1400 m and 1860 m a.s.l. In the Malaise traps along the Kaputu Stream this species was trapped in highest numbers at a site with fast flow over gravel and stones above a waterfall (see Andersen & Johanson 1993). Swarming specimens were netted by day mostly near waterfalls.

Remarks. – This species appears to resemble quite closely the other African congeners, but differs in the form of the ventral plate and tergite X and in having fine serrations on inner distal margin of inferior appendages. Neither Statzner (1977) nor Mey (1992) mention any glands on the wings or make any mention of anything unusual about the wings of their species. Females of *Scelotrichia glandulosa* sp. n. were collected with the male and have the usual conservative form.

Catoxyethira Ulmer

Catoxyethira Ulmer, 1912: 82. Type species: *Catoxyethira fasciata* Ulmer, by monotypy.
Sperotrichia Marlier, 1978: 294. Type species: *Sperotrichia mali* Marlier, by original designation and monotypy. Synonymised by Marshall (1979).

Catoxyethira is proving to be particularly diverse in tropical Africa (see Gibon 1985, 1987a, 1991). This work adds nine new species to the previous 17 (one with two subspecies) known from Africa. The only other members of the genus are a dubious Taiwanese species known only from immatures and originally described in *Hydroptila* (see discussion in Marshall 1979), and a Vietnamese species (Oláh 1989) which may well be referable to *Chrysotrichia* Schmid, 1958. One species has been described from each of South Africa (Kimmins 1958), Zimbabwe (Morse 1974), and Mali (Marlier 1978), three from Zaire (Ulmer 1912, Statzner 1977), six from the Ivory Coast (Gibon 1985) and five from Guinea (Gibon 1987a, 1991).

Catoxyethira shares many features of general body form with the Holarctic genus *Stactobiella* Martynov, 1924, the neotropical *Bredinia* Flint, 1968 and the SE Asian/New Guinean/northern Australian genus *Chrysotrichia*, particularly the very short metascutellum on the adult thorax. Only the spur number differs, *Catoxyethira* having a tibial spur formula of 1, 3, 4. The African species fall into two main groups on the basis of genitalic form: those with and those without a pair of dark spines on abdominal sternite VIII. Species lacking the spines are scarcely distinguishable from some of the SE Asian *Chrysotrichia*. Although from available information it appears that the larval forms of *Catoxyethira* and *Chrysotrichia* are also similar, these similarities are probably plesiomorphous. Members of the two genera probably also occupy comparable niches, but again the hydropetric niche may well be plesiomorphic in the tribe.

One African species, *Catoxyethira pinheyi* Kimmins, 1958, is quite widespread, being recorded from Victoria Falls, Mali and the Ivory Coast. It closely resembles (and may be the senior synonym of) *Catoxyethira ocellata* Statzner, 1977 from Zaire, which is here recorded from Tanzania. Most other species appear to be quite restricted in their distributions.

Catoxyethira incompta sp. n.
(fig. 8)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 4, 1680 m a.s.l., 20.-26.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 196).

Description

Antennae damaged. Anterior wing length 1.7 mm. Genitalia as in fig. 8. Abdominal segment VIII long, produced distally into lateral lobes, spines absent. Segment IX short, retracted within segment VIII. Segment X membranous, broadly rounded and slightly concave apico-mesally. Subgenital plate broad-based, tapered distally to narrow apex; apex bifid, lobes acute. Inferior appendages short, slender and in close proximity distally, with paired long setae dorsally. Aedeagus simple, straight.

Etymology. – From the Latin *incomptus*, unadorned, referring to the relatively simple appearance of the male genitalia.

Biology and distribution. – Known only from the type locality, where the specimen was collected from a site of moderate flow over fine sand, gravel and stones (see Andersen & Johanson 1993).

Remarks. – *Catoxyethira incompta* sp. n. most closely resembles *C. improcera* Statzner, 1977 and *C. mali* (Marlier, 1978). It differs in lacking the lateral processes above the inferior appendages seen in *C. improcera* and the paired dorsal structures of *C. mali* which are referred to by Marlier (1978) as anal appendages.

Catoxyethira bombolensis sp. n.
(figs. 9, 10)

Type material. – Holotype ♂, TANZANIA, Tanga region, East Usambara Mts, Bombole, 830 m a.s.l., 1.xii.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 197). – Paratypes: 7♂ (4 slides) data as for holotype; 1♂ data as for holotype except Amani East Forest Reserve, Zigi River, 2.xii.1990, sweep net.

Description

Antennae 18-segmented. Anterior wing length 1.3-1.5 mm. Genitalia as in figs. 9, 10. Abdominal sternite VIII elongate, without paired spines, with a U-shaped apico-mesal cleft. Tergite X about half length of inferior appendages, membranous. Inferior appendages elongate, cylindrical. Subgenital plate forming a

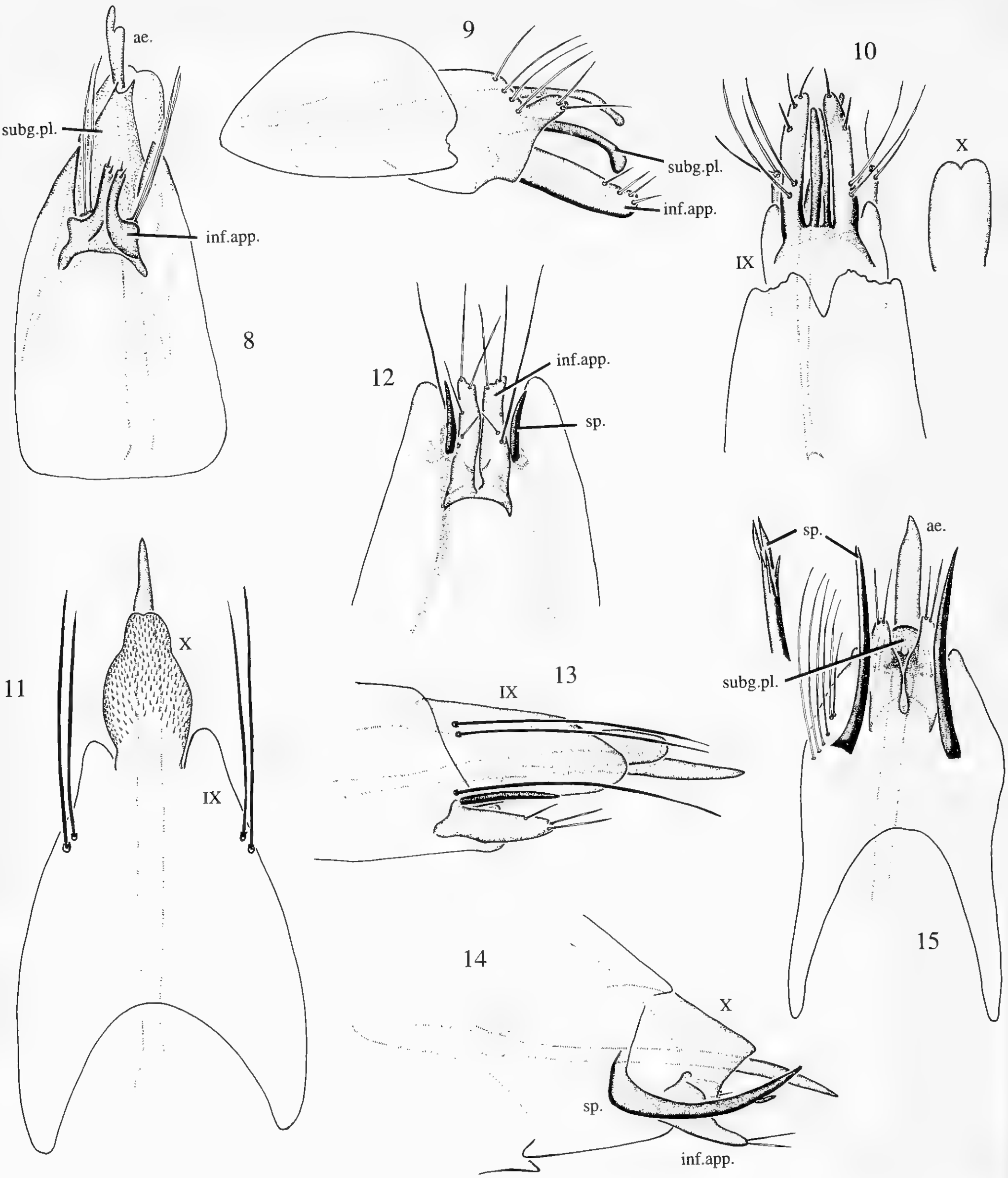


Fig. 8. *Catoxyethira incompta* sp. n., male genitalia, ventral view. – Figs. 9, 10. *Catoxyethira bombolensis* sp. n., male genitalia. 9, lateral view; 10, ventral view. – Figs. 11-13. *Catoxyethira ruvuensis* sp. n., male genitalia. 11, dorsal view; 12, ventral view; 13, lateral view. – Figs. 14, 15. *Catoxyethira apicospinosa* sp. n., male genitalia. 14, lateral view; 15, ventral view. Abbreviations. – As for figs. 1-7.

pair of straight narrow processes in ventral view; in lateral view slightly swollen apically, and curved ventrally.

Etymology. – Named after the village of Bombole in the East Usambara Mountains, Tanzania.

Biology and distribution. – Known only from East Usambara Mountains, from beside rivers with fast flow over large rocks at altitudes between 470 m and 830 m a.s.l.

Remarks. – This species groups with *Catoxyethira improcera* and *C. mali* in lacking paired, dark, socketed spines. However, the form of sternite VIII with the small apico-mesal excision is distinctive.

Catoxyethira ocellata Statzner

Catoxyethira ocellata Statzner, 1977: 396.

Biology and distribution. – *Catoxyethira ocellata* is known from Zaire and Tanzania. The Ruvu River at the site at which the five specimens were collected is large and slow flowing with a sandy and stony substrate.

Remarks. – This species closely resembles *Catoxyethira pinheyi* Kimmins, 1958 from Zimbabwe, Ivory Coast and Uganda. It shares with *C. pinheyi* features such as inferior appendages set into a deep mid-ventral excision in the apical margin of abdominal sternite VIII and dorsal spines on sclerite VIII at apicolateral angles. *Catoxyethira ocellata* has three pairs of fine setae on each side of the inferior appendages whereas, according to Kimmins (1958) and verified in the type by Wells, there is a single slender, acute spine on each side of the inferior appendages in *C. pinheyi*; the shape of the inferior appendages also differs slightly. These differences are probably minor and the two may be synonyms.

Material examined. – 5♂ (4 slides) TANZANIA, Morogoro region, Kimboza, Ruvu River, 20.x.1990, sweep net, ZMB's Tanzania Expedition.

Catoxyethira ruvuensis sp. n.
(figs. 11-13)

Type material. – Holotype ♂, TANZANIA, Morogoro Region, Kimboza, Ruvu River, 150 m a.s.l., 20.x.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 198). – Paratypes: 4♂ (2 slides) data as for holotype.

Description

Antennae 18-segmented. Anterior wing length 1.1-1.3 mm. Genitalia as in figs. 11-13. Abdominal segment VIII stout, laterally extended into broadly rounded lobes about as long as inferior appendages, spines ventrally at base of lobes; posterolaterally a pair of elongate moderately thick setae. Tergite X broadest in basal half, rounded apically, covered with spinules. Inferior appendages subrectangular in ventral view, a pair of thick setae mesolaterally. Subgenital plate appears to be reduced. Aedeagus simple, straight.

Etymology. – Named after the Ruvu River, originating in the Uluguru Mountains, Tanzania.

Biology and distribution. – Known only from the type locality at Ruvu River, a large slow-flowing river with sandy and stony substrate.

Remarks. – This species groups with *Catoxyethira pinheyi* and *C. ocellata* in the form of tergite X and general arrangement of the genitalia. However, the inferior appendages are only shallowly set into the posterior margin of segment VIII, and the paired spines are positioned ventrally beside the inferior appendages, not apico-laterally.

Catoxyethira apicospinosa sp. n.
(figs. 14, 15)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Dule, Bumbuli River, 1220 m a.s.l., 26.xi.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 199).

Description

Antennae damaged. Anterior wing length 2 mm. Genitalia as in figs. 14, 15. Abdominal segment VIII stout, short mid-dorsally and ventrally, paired spines of moderate length, positioned ventro-laterally, curving upwards in lateral view, slightly curved in ventral view, and with a number of spinules in apical region. Tergite X membranous, rounded. Inferior appendages tapered slightly in distal half. Subgenital plate in form of a small sclerotised median crescentic structure. Aedeagus straight, simple.

Etymology. – From the Latin, *apex*, top, and *spine*, thorn, referring to the few stout spinules at the apex of the ventral spines.

Biology and distribution. – Known only from the type locality in West Usambara Mountains, from a river with fast flow and a base of large rocks.

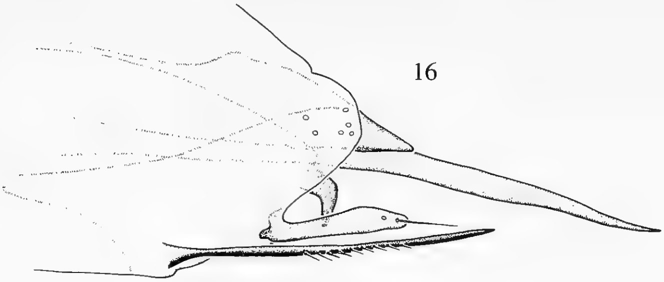
Remarks. – This species closely resembles *Catoxyethira lanceolata* sp. n., but abdominal segment VIII is far wider, the ventral spines curve upwards in lateral view and have few and stouter spinules near the apex; the inferior appendages are narrower.

Catoxyethira lanceolata sp. n.
(figs. 16, 17)

Type material. – Holotype ♂, TANZANIA, Tanga region, East Usambara Mts, Mlesa, 800 m a.s.l., 1.xii.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 200). – Paratype: 1♂ data as for holotype.

Description

Antennae damaged. Anterior wing length 1.6 mm. Genitalia as in figs. 16, 17. Abdominal sternite VIII very short, paired spines stout, curved, covered in fine spinules and arising slightly off centre midway along



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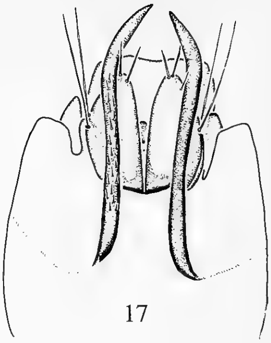

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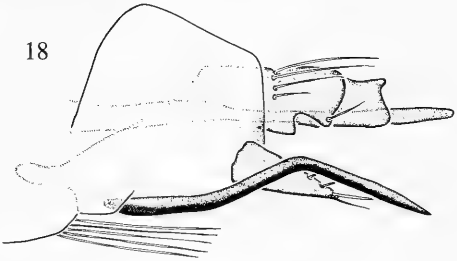

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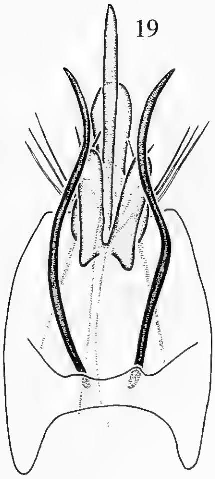

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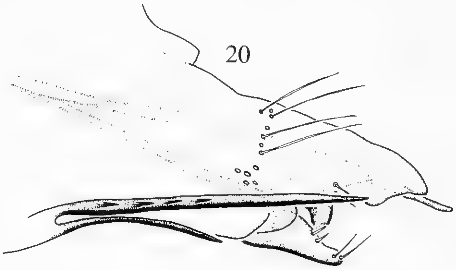

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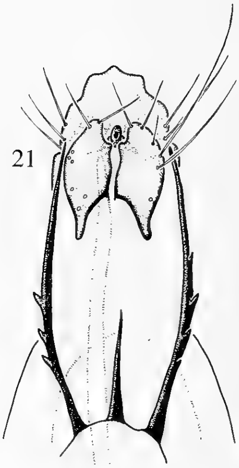

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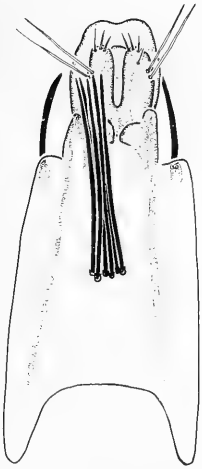

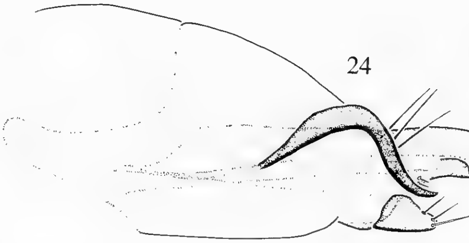

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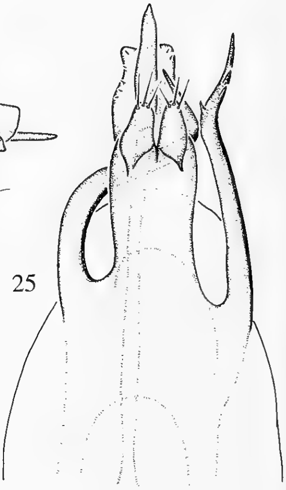

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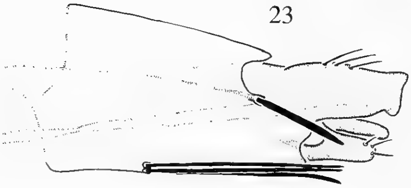


23

the length of the sternite, extending distally beyond the inferior appendages, inturned apically, in lateral view slender, straight. Tergite X membranous, broad in ventral view, triangular in lateral view. Inferior appendages stoutly ovate in ventral view, in lateral view about three times as long as wide. Subgenital plate in ventral view broad with an apico-mesial downwardly directed sclerotised process, in lateral view appearing as a small down-turned lobe. Aedeagus simple, straight.

Etymology. – From the Latin *lancea*, light spear, referring to the lance-like ventral spines on abdominal sternite VIII.

Biology and distribution. – Known only from the type locality in the East Usambara Mountains, from a small, fast-flowing river with waterfalls and a base of large rocks.

Remarks. – This species and *C. apicospinosa* sp. n. from the same locality show close resemblance, yet each is quite distinctive. Particularly, in this species the paired spines are longer and in ventral view are curved, in lateral view straight and lance-like.

Catoxyethira elongata sp. n.
(figs. 18, 19)

Type material. – Holotype ♂, TANZANIA, Morogoro region, Kimboza, Ruvu River, 150 m a.s.l., 20.x.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 201). – Paratypes: 2♂ (slides) data as for holotype.

Description

Antennae 18-segmented, flagellar segments elongate. Anterior wing length 1.5-1.9 mm. Genitalia as in figs. 18, 19. Abdominal sternite VIII sub-quadrate in ventral view; paired spines symmetrical, slender, somewhat sinuous, covered in minute spinules, arising in close proximity slightly behind antero-ventral margin and extending beyond tergite X. Tergite X short, membranous, rounded apically. Inferior appendages elongate. Subgenital plate slightly longer and narrower than tergite X. Aedeagus straight, simple.

Etymology. – From the Latin *elongatus*, prolonged, referring to the general shape of the male genitalia.

Biology and distribution. – Known only from the type locality at Ruvu River, a large slow-flowing river with sandy and stony substrate.

Remarks. – In general form, male genitalia of this species resemble those of *Catoxyethira lanceolata* sp. n. and *C. apicospinosa* sp. n., but differ mainly in that the ventral spines are narrower and more elongate and arise closer to the anterior margin of sternite VIII.

Catoxyethira crenulata sp. n.
(figs. 20, 21)

Type material. – Holotype ♂, TANZANIA, Morogoro region, Morogoro, Sokoine University of Agriculture, 550 m a.s.l., 26.x.-11.xi.1990, light trap, ZMB's Tanzania Expedition (slide, ZMBN No. 202). – Paratypes: 11♂ (3 slides) data as for holotype.

Description

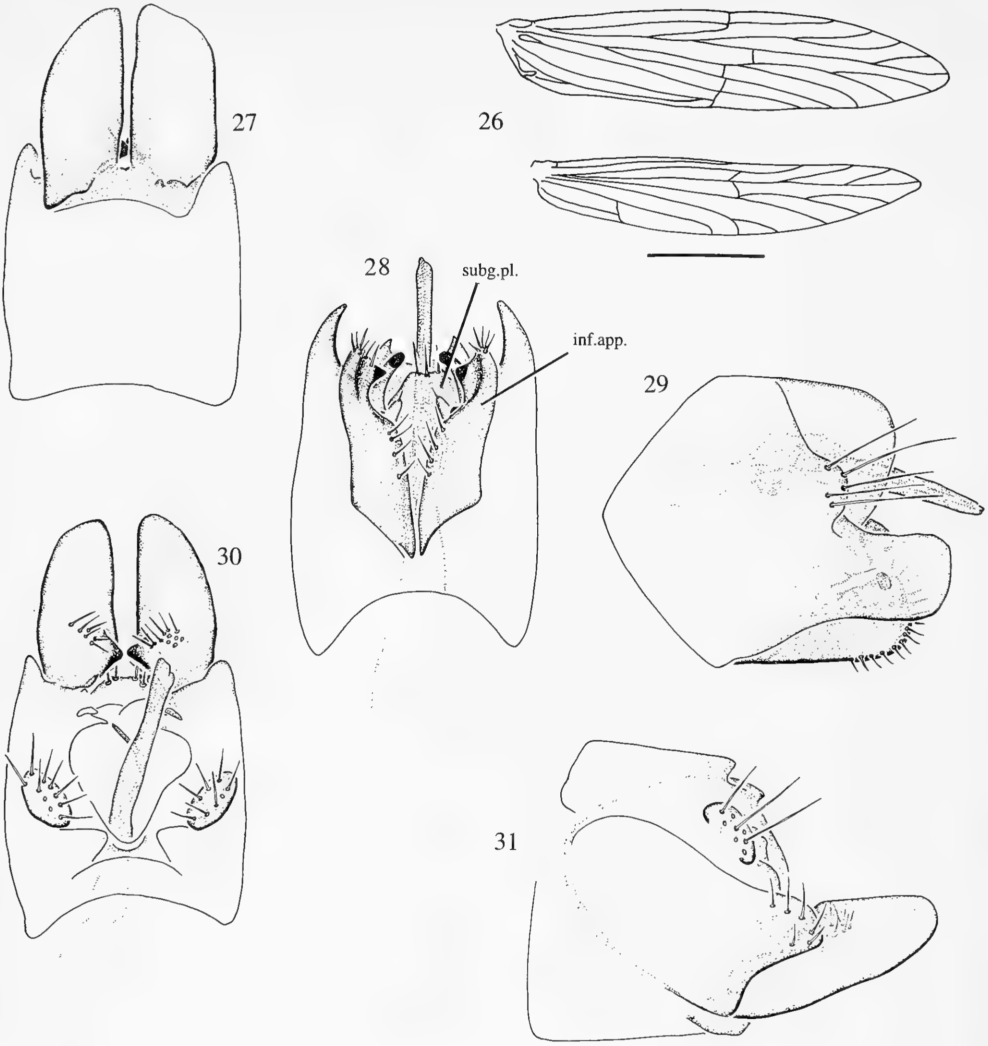
Antennae 17-segmented. Anterior wing length 1.5-1.8 mm. Genitalia as in figs. 20, 21. Sternite VIII with paired spines slender, sclerotised, barbed in basal half, extending posteriorly to just slightly below the tips of the inferior appendages, basally between the spines another short spine. Tergite X broad, membranous. Inferior appendages stout, short, with a subapical notch on the inner margin. Subgenital plate produced and downturned apically. Aedeagus slender, simple.

Etymology. – From the diminutive form of the Latin *crena*, notch, and the suffix *-atus*, provided with, referring to the small, subapical notch on the inner margin of the inferior appendage.

Biology and distribution. – Known only from the type locality on the campus of Sokoine University of Agriculture in Morogoro. The university is situated in the foothills of the Uluguru Mountains and several small, slow-flowing streams and ditches are found on the area.

Remarks. – This species closely resembles *Catoxyethira veruta* Morse, 1974 from Kariba, Zimbabwe (as Southern Rhodesia) from which it is distinguished in ventral view by the more closely placed ventro-lateral spines, the small subapical notch on the inner margin of the inferior appendages, and the shape of the subgenital plate, and in lateral view by the irregular shape of the inferior appendages and of tergite X (dorsal plate). Morse (1974) likened *C. veruta* to *C. pinheyi*. However, resemblances between *C. pinheyi* and *C. crenulata* sp. n. are slighter than those of the new species and *C. veruta*.

Figs. 16, 17. *Catoxyethira lanceolata* sp. n., male genitalia. 16, lateral view; 17, ventral view. – Figs. 18, 19. *Catoxyethira elongata* sp. n., male genitalia. 18, lateral view; 19, ventral view. – Figs. 20, 21. *Catoxyethira crenulata* sp. n., male genitalia. 20, lateral view; 21, ventral view. – Figs. 22, 23. *Catoxyethira crinita* sp. n., male genitalia. 22, ventral view; 23, lateral view. – Figs. 24, 25. *Catoxyethira ciliata* sp. n., male genitalia. 24, lateral view; 25, ventral view.



Figs. 26, 28, 29. *Ugandatrichia tanzaniensis* sp. n., male. 26, wings (scale bar = 1.0 mm); 28, genitalia, ventral view; 29, genitalia, lateral view. – Figs. 27, 30, 31. *Ugandatrichia dentata* sp. n., male genitalia. 27, ventral view; 30, dorsal view; 31, lateral view. – Abbreviations. – inf.app.: inferior appendage; subg.pl.: subgenital plate.

Catoxyethira crinita sp. n.
(figs. 22, 23)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 5, 1650 m a.s.l., 6.-12.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 203). – Paratypes: 4♂ (slides) data as for holotype except loc. 2-10, 30.x.-3.xii.1990; 1♂ (slides) data as for holotype except East Usambara Mts, Bombole, 1.xii.1990, sweep net.

Description

Antennae 18-segmented. Anterior wing length 1.5-2.0 mm. Genitalia as in figs. 22, 23. Sternite VIII elongate, length about twice width, spines short, at apico-lateral angles; a cluster of long, stout, dark setae mesally on sternite. Tergite X broad, a little longer than inferior appendages, in lateral view stout, apically truncate. Inferior appendages simple lobes, about twice as long as wide, rounded apically. Subgenital plate a narrow, apically rounded lobe. Aedeagus simple, slender, straight.

Etymology. – From the Latin *crinis* hair, and the suffix *-atus*, provided with, referring to the meso-ventral tuft of long hair on sternite VIII.

Biology and distribution. – Taken both in the West and East Usambara Mountains, beside slow to fast flowing streams and rivers flowing over stones, sand, gravel and mud, at altitudes between 830 m and 1650 m a.s.l.

Remarks. – In the position and form of the lateral spines on segment IX, *C. crinita* sp. n. is similar to *C. disymetrica* Gibon, 1991 from Guinea. It is distinguished, however, from all other African species by having a cluster of elongate dark coloured setae medially on sternite VIII.

Catoxyethira ciliata sp. n.
(figs. 24, 25)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 3, 1720 m a.s.l., 20.-29.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 204). – Paratypes: 503♂ (8 slides) data as for holotype except loc. 2-10, 30.x.-13.xii.1990; 29♂ data as for holotype except loc. 7, 4.i.-8.vii.1991; 3♂ data as for holotype except Mazumbai Forest Reserve, small stream at 1480 m a.s.l., 24.xi.-4.xii.1990; 1♂ data as for holotype except Gogoi, 30.xi.1990, sweep net.

Description
Anterior wing length 1.8-2.1 mm. Genitalia as in figs. 24, 25. Abdominal sternite VIII with paired spines unequal, stout, elongate and curved and positioned apico-laterally. Tergite X expanded in basal part, narrowed sub-apically, slightly expanded distally, apex almost truncate, covered in fine spinules. Inferior appendages short, about half length of tergite X, rounded distally. Subgenital plate membranous.

Etymology. – From the Latin *cilium*, eyelash, and the suffix *-atus*, provided with, referring to the fine spinules on the tergite X.

Biology and distribution. – Known only from the West Usambara Mountains, from streams and rivers at altitudes between 1100 m and 1650 m a.s.l. In the Malaise traps at Kaputu Stream this species was trapped in highest numbers at sites with moderate to fast flow over gravel, stones and bedrock near waterfalls (see Andersen & Johanson 1993).

Remarks. – This species is clearly identified by the stout, unequally curved paired sclerotised spines which arise mid-laterally.

Ugandatrichia Mosely

Ugandatrichia Mosely, 1939: 36. Type species: *Ugandatrichia minor* Mosely, by original designation.

Ugandatrichia occurs in Africa, South and Southeast Asia and New Guinea. Scott (1967) described the hydropetric larva of a species from Zimbabwe and since similar larvae have been collected from the type locality of the New Guinean species, life in fast flowing waters is probably the usual niche for the genus.

The two new species described here appear to occur sympatrically in the Kaputu Stream. Only males are described here as although a number of females were collected, they could not be assigned with certainty to species. They closely resemble the holotype female of *U. acuta* Mosely, 1939 in having patches of black androconia on sternite VIII, but differ in general genitalic shape.

Ugandatrichia tanzaniensis sp. n.
(figs. 26, 28, 29)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 7, 1535 m a.s.l., 2.-6.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 205). – Paratypes: 16♂ (3 slides) data as for holotype except loc. 3-11, 30.x.-29.xi.1990; 1♂ data as for holotype except loc. 5, 6.xi.1990, sweep net; 1♂ data as for holotype except loc. 8, 5.xi.1990, sweep net; 2♂ data as for holotype except Gologolo, Lushoto, 25.ix.1990, sweep net; 2♂ data as for holotype except East Usambara Mts, Bombole, 1.xii.1990, sweep net.

Description
Large, and in alcohol uniformly dark coloured; antennae all damaged; wings (fig. 26) broad, venation complete; anterior wing length 3.4-3.7 mm. Male genitalia as in figs. 28, 29. Segment IX short mid dorsally and ventrally, produced laterally to form a lobe that is stout and apically somewhat truncate in lateral view, apically acute in ventral view. Segment X broadly rounded in lateral view, in dorsal view broadly bi-concave apically. Inferior appendages divergent, irregularly divided in distal half, with inner sclerotised spur on ventral lobe, small digitiform lobe mid-dorsally and apically sclerotised process more distally. Subgenital plate in lateral view forming a pair of sclerotised lobes. Aedeagus simple, with titillator.

Etymology. – Named for the country Tanzania.

Biology and distribution. – Known both from the West and East Usambara Mountains, beside rapidly flowing streams and smaller rivers at altitudes between 830 m and 1860 m a.s.l. In the Malaise traps along the Kaputu Stream this species was trapped most frequently at sites with fast flow over bedrock and stones, but also at sites with slow flow over gravel, stones and mud (see Andersen & Johanson 1993). Swarming specimens were netted by day mostly near waterfalls or in areas of fast flow over bedrock and stones.

Remarks. – Both this species and the following, *U. dentata* sp. n. group with the other East African *Ugandatrichia* species in having tergite IX deeply excavated dorsally. *Ugandatrichia tanzaniensis* sp. n. differs from *U. dentata* in having sternite IX very short medially. In this respect it resembles the southern African *U. rhodesiensis* Scott, 1976, from which it is distinguished clearly by narrower, longer lateral lobes on segment IX which appear subquadrate in lateral view.

Ugandatrichia dentata sp. n.

(figs. 27, 30, 31)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 8, 1510 m a.s.l., 5.xi.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 206). – Paratypes: 44♂ (3 slides) data as for holotype except 5.xi. & 6.xi. 1990; 5♂ data as for holotype except loc. 8, 29.x. & 5.xi. 1990; 15♂ (1 slides) data as for holotype except loc. 5-7, 29.x.-13.xii.1990, Malaise trap; 2♂ data as for holotype except loc. 7, 4.ii.-8.viii.1991, Malaise trap; 84♂ (5 slides) data as for holotype except Dule, Bumbuli River, 26.xi.1990; 70♂ data as for holotype except East Usambara Mts, Mlesa, 1.xii.1990

Description

Large; body uniformly very dark coloured; antennae dark in proximal third, pale in median section and dark in distal third; wings broad, anterior wing length 2.4-4.6 mm. Male genitalia as in figs. 27, 30, 31. Segment IX with deep cleft mid-dorsally and a pair of small ovoid lobes laterally. Segment X difficult to discern. Inferior appendages stout, in lateral view with inner margins almost parallel, closely aligned, outer margins rounded, with large black spur dorsally at base on inner margin. Subgenital plate short, rounded apically. Aedeagus simple, titillator present.

Etymology. – From the Latin *dentatus*, toothed, referring to the large, black spur on the inner margin of the inferior appendage.

Biology and distribution. – Taken both in the West and East Usambara Mountains, beside rapidly flowing rivers at altitudes between 800 m and 1650 m a.s.l. In the Malaise traps along the Kaputu Stream this species was trapped most frequently at a site with fast flow over gravel and stones above a waterfall (see Andersen & Johanson 1993). Swarming specimens were abundant by day mostly near waterfalls or beside stretches of fast flow over bedrock and stones.

Remarks. – This species groups with *Ugandatrichia tanzaniensis* sp. n., *U. minor* Mosely, 1939, *U. nigra* Mosely, 1939 and on the basis of similarities between females of *U. acuta* and unassociated females of *U. tanzaniensis* and/or *U. dentata* sp., n. probably also with that species. The form of the inferior appendages of *U. dentata* is almost identical with that of *U. sourya* (Schmid, 1960) from Pakistan. *Ugandatrichia dentata* is readily distinguished from *U. tanzaniensis* by the short lateral lobes and stouter inferior appendages.

Dhatrichia Mosely

Dhatrichia Mosely, 1948: 78. Type species: *Dhatrichia inasa* Mosely, by original designation and monotypy.

The genus *Dhatrichia* was first recorded from the Yemen and subsequently a second species was described from Zaire (Statzner 1977) and a third from the Ivory Coast (Gibon 1987b). Two new species are described here and are the first to be recorded from East Africa. Male genitalia of each are distinctive although conforming in general features with congeners. The two new species were collected together beside slower reaches of the Kaputu Stream where the substrata are sand, gravel, some mud and stones.

Dhatrichia divergenta sp. n.

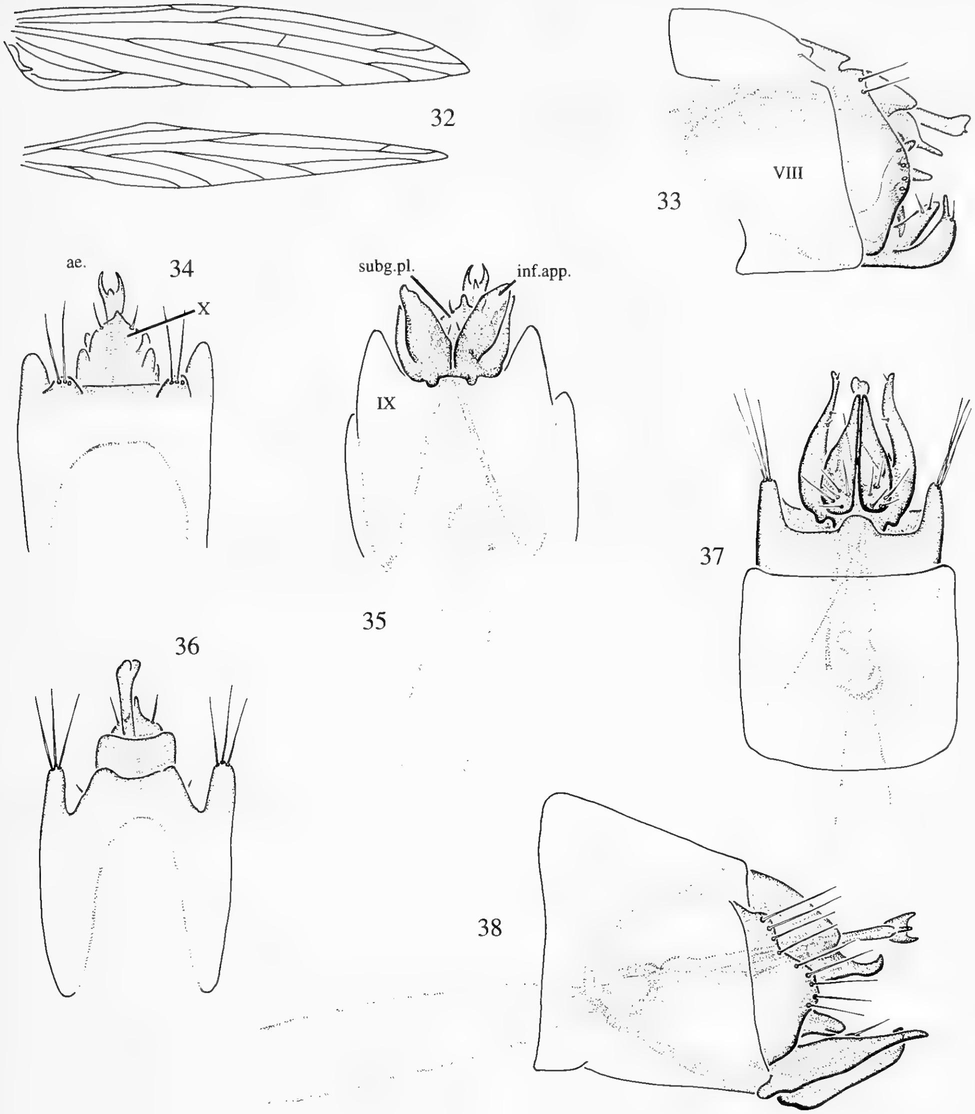
(figs. 33-35)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 7, 1535 m a.s.l., 4.-12.ii.1991, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 208). – Paratypes: 11♂ (9 slides) data as for holotype; 73♂ (3 slides) data as for holotype except loc. 2-10, 29.x.-29.xi.1990; 1♂ data as for holotype except Mazumbai Forest Reserve, small stream at 1480 m a.s.l., 26.xi.-4.xii.1990.

Description

Small, pale, antennae short, 19-segmented, segments quadrate; wings as for *Dhatrichia cinyra* sp. n., anterior wing length 1.4-1.8 mm. Genitalia as in figs. 33-35. Abdominal segment IX short mid-dorsally and ventrally, forming pronounced lobes laterally in ventral and dorsal views. Abdominal segment X a short membranous band only. Inferior appendages short and stout, bilobed and strongly upturned in lateral view, the ventral lobe with a slender apical process. Subgenital plate membranous, also with a slender projection; the origins of two other lobes seen in lateral view are unclear.

Etymology. – From the Latin *divergens*, widespreading, referring to the diverging lobes of the inferior appendages in ventral view.



Figs. 32, 36-38. *Dhatrichia cinyra* sp. n., male. 32, wings; 36, genitalia, dorsal view; 37, genitalia, ventral view; 38, genitalia, lateral view. – Figs. 33-35. *Dhatrichia divergenta* sp. n., male genitalia. 33, lateral view; 34, dorsal view; 35, ventral view. – Abbreviations. – ae: aedeagus; inf.app.: inferior appendage; subg.pl.: subgenital plate; VIII, IX, X: abdominal segments VIII, IX, X.

Biology and distribution. – Known only from streams in the Mazumbai area in the West Usambara Mountains, at altitudes between 1420 m and 1650 m a.s.l. In the Malaise traps along the Kaputu Stream this species was most abundant at a site with moderate flow over mud, fine sand and larger stones (see Andersen & Johanson 1993).

Remarks. – As with the next species, *Dhatrichia divergenta* sp. n. shows similarities in general form to other congeners. It can be recognised by the stouter, more robust appearance of the inferior appendages.

Dhatrichia cinyra sp. n.
(figs. 32, 36-38)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu

Stream, loc. 4, 1680 m a.s.l., 1.-6.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 207). – Paratypes: 251♂ (8 slides) data as for holotype except loc. 2-11, 27.x.-3.xii.1990; 1♂ data as for holotype except loc. 7, 4.-12.ii.1990; 1♂ data as for holotype except Gogoi, 30.xi.1990, sweep net.

Description

Small, uniformly pale fuscous in colour; antennae short, 19-segmented, segments stout; wings (fig. 32) slender, tapered to acuminate apices; forewing with jugal lobe, length 1.7-1.9 mm. Genitalia as in figs. 36-38. Abdominal segment IX well retracted into VIII, with lateral lobes prominent. Segment X forming a short, stout plate, almost truncate apically. Inferior appendages slender, comprising three lobes, the ventral-most pair in ventral view in the form of a harp, being slender and bowed, with slightly outturned apices. In lateral view, the subgenital plate appears to be divided into two lobes, a rounded ventral lobe and a narrower, upturned dorsal lobe. Aedeagus straight, tightly constricted medially and tapered distally to a flared apex, titillator present.

Etymology. – From the Latin *cinyra*, a kind of harp, referring to the shape of the ventral-most pair of lobes of the inferior appendages in ventral view.

Biology and distribution. – Collected along streams in the West Usambara Mountains, at altitudes between 1100 m and 1650 m a.s.l. In the Malaise traps along the Kaputu Stream this species was most abundant at sites with fast flow over gravel, stones and bedrock (see Andersen & Johanson 1993).

Remarks. – In general form, males of this species resemble those of *Dhatrichia inasa* Mosely, 1948, the type species from Yemen and *D. bipunctata* Statzner, 1977 from Zaire, but *D. cinyra* is sp. n. is clearly distinguished by the shape of the inferior appendages.

Hydroptila Dalman

Hydroptila Dalman, 1819: 125. Type species: *Hydroptila tineoides* Dalman, by monotypy. See Marshall (1979) for full generic synonymy.

Several of the *Hydroptila* species groups recognised by Marshall (1979) are represented in Africa, particularly in northern Africa. These include the *sparsa, capensis, occulta* and *pulchricornis* groups. Prior to this work, however, only the widespread *Hydroptila cruciata* Ulmer, 1912 (with *H. hirra* Mosely, 1948 in synonymy), in Marshall's *occulta*-group, was recorded from East Africa (see Johanson 1992). A new record is given here for this species, and five new species are described. Two of the new species *H. usambarensis* sp. n. and *H. morogorensis* sp. n., clearly align with *sparsa*-group species and *H. bumbulensis* sp. n. shares features of the *occulta*-group. The affinities of *Hydroptila mazumbaiensis* sp. n. and *H. tannerorum* sp. n. are unclear.

Sites at which *Hydroptila* species were collected varied from slow reaches of streams to fast riffles.

Hydroptila usambarensis sp. n.
(figs. 39, 40)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Dule, Bumbuli River, 1220 m a.s.l., 26.xi.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 209). – Paratypes: 5♂ (slides) data as for holotype; 1♂ (slides) data as for holotype except East Usambara Mts, Mlesa, 1.xii.1990; 3♂ data as for holotype except East Usambara Mts, Bombole, 1.xii.1990.

Description

Post-occipital scent organs on head each comprising a cluster of pale androconia beneath inner side of post-occipital lobes; antennae 24-segmented; flagellar segments rectangular, with scattered sensilla placodea. Anterior wing length 1.3-1.8 mm. Genitalia as in figs. 39, 40. Without lateral lobes of the usual form on abdominal segment IX, but with apico-lateral angles of abdominal segment IX rounded, setose. Tergite X membranous, quadrate in dorsal view. Inferior appendages elongate, in ventral view parallel-sided, apically produced slightly on inner side, in lateral view, irregular in shape. Subgenital plate subtriangular, paired setae basal. Aedeagus dilated in distal half, a small spine subapically.

Etymology. – Named after the Usambara Mountains, Tanzania.

Biology and distribution. – Taken from rivers both in the East and West Usambara Mountains, at sites with fast flow over large stones at altitudes between 800 m and 1220 m a.s.l.

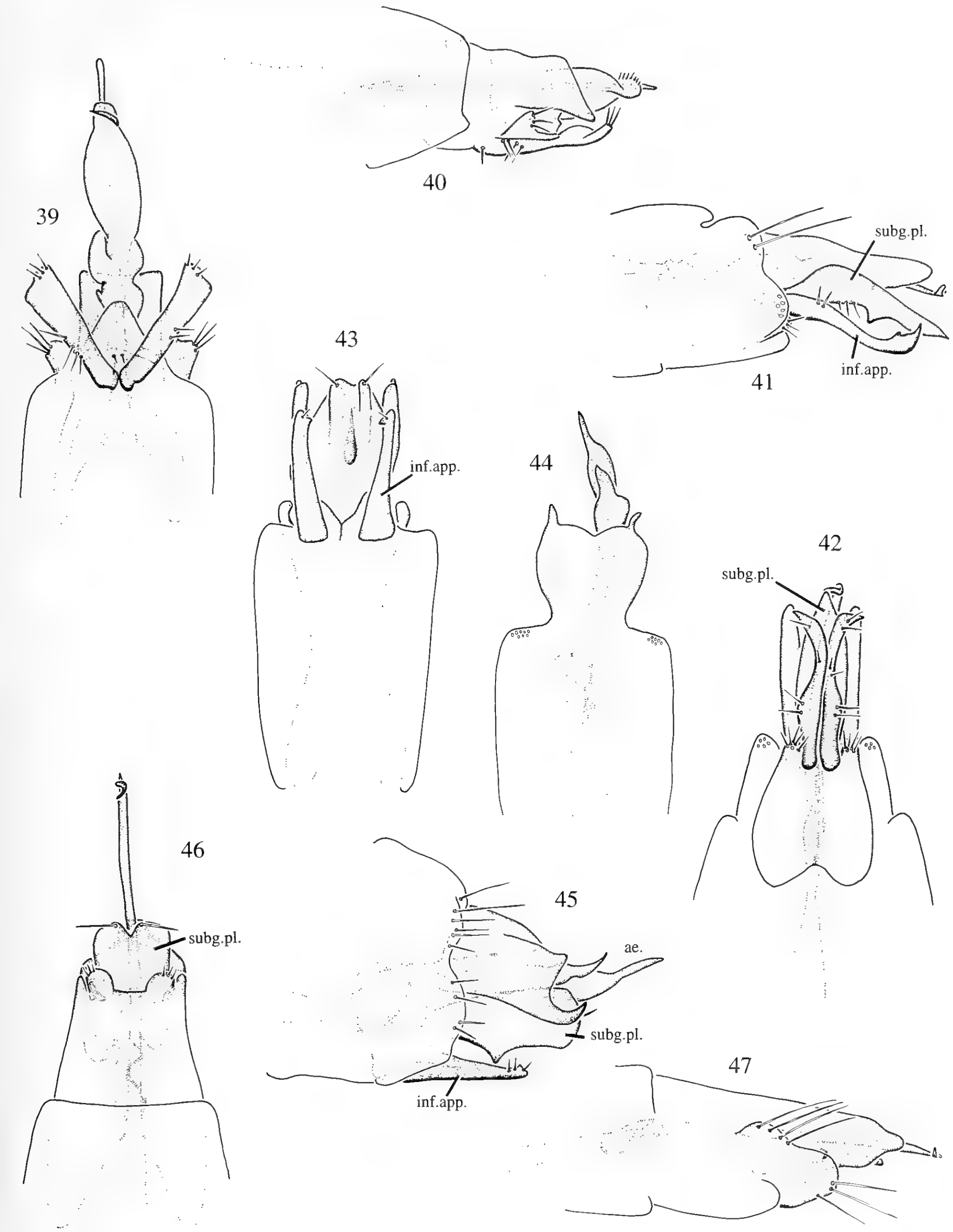
Remarks. – This is probably a *sparsa*-group species, although the form of the lateral lobes differs from others. *Hydroptila usambarensis* is distinguished by the unusual shape of the aedeagus which is dilated distally anterior to a small, subapical spine.

Hydroptila morogorensis sp. n.
(figs. 41, 42)

Type material. – Holotype ♂, TANZANIA, Morogoro region, Morogoro, Sokoine University of Agriculture, 550 m a.s.l., 26.x-11.xi.1990, light trap, ZMB's Tanzania Expedition (slide, ZMBN No. 210).

Description

Post-occipital scent organs on head small; antennae



Figs. 39, 40. *Hydroptila usambarensis* sp. n., male genitalia. 39, ventral view; 40, lateral view. – Figs. 41, 42. *Hydroptila morogorensis* sp. n., male genitalia. 41, lateral view; 42, ventral view. – Figs. 43-45. *Hydroptila mazumbaiensis* sp. n., male genitalia. 43, ventral view; 44, dorsal view; 45, lateral view. – Figs. 46, 47. *Hydroptila tannerorum* sp. n., male genitalia. 46, ventral view; 47, lateral view. – Abbreviations. – ae: aedeagus; inf.app.: inferior appendage; subg.pl.: subgenital plate.

25-segmented; flagellar segments with sparse scattered sensilla placodea. Anterior wing length 1.4 mm. Genitalia as in figs. 41, 42. Lateral lobes on abdominal segment IX rounded, setose. Tergite X membranous, in lateral view stout, rounded apically. Inferior appendages elongate, irregular in shape, swollen near base, tapered and turned outwards towards apex in ventral view; in lateral view swollen subapically, upturned distally. Subgenital plate broad, membranous, apically acute in ventral view, a triangular medial projection in lateral view. Aedeagus slender with a small apical spine.

Etymology. – Named after the city of Morogoro, Tanzania.

Biology and distribution. – Known only from the type locality on the campus of Sokoine University of Agriculture in Morogoro, in an area with several small, slow-flowing streams and ditches.

Remarks. – This is a *sparsa*-group species showing general resemblance to *H. usambarensis* sp. n., but differing in detailed shape of genitalic structures, particularly in having the aedeagus simple and slender, and inferior appendages in ventral view slightly expanded proximally, slender and out-turned distally.

Hydroptila mazumbaiensis sp. n.
(figs. 43-45)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 7, 1535 m a.s.l., 4.-12.ii.1991, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 211). – Paratypes: 1♂ (slide) data as for holotype; 2♂ data as for holotype except loc. 5-10, 30.x.-26.xii.1990.

Description

Post-occipital scent organs on head small, densely covered with setae and in the form of a balloon-like structure with a central duct which appears to open ventrally, without discernible androconia; antennae damaged; flagellar segments with sparse sensilla placodea on apical rim, elsewhere scattered sensilla auricillica. Mesoscutellum diamond-shaped. Anterior wing length 2.2 mm. Genitalia as in figs. 43-45. Lateral lobes on abdominal segment IX rounded apically, membranous. Tergite X broad, rounded laterally and in lateral view produced and upturned apico-laterally. Inferior appendages slender, tapered, apically with a pale spur on inner margin. Subgenital plate broad in ventral view, paired setae on apical margin, in lateral view with a median spur ventrally. Aedeagus with slender apical and subapical spines, swollen below each spine.

Etymology. – Named after the village of Mazumbai, West Usambara Mountains, Tanzania.

Biology and distribution. – Known only from the Kaputu Stream in the West Usambara Mountains, where it was taken between 1420 m and 1650 m a.s.l., at sites with slow to fast flow over mud, sand, gravel and larger stones (see Andersen & Johanson 1993).

Remarks. – The affinities of this species are unclear. The ventral spur on the subgenital plate suggests that it may be an *occulta*-group species. The form of the aedeagus is distinctive in having distally a pair of flange-like structures in series.

Hydroptila tannerorum sp. n.
(figs. 46, 47)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 7, 1535 m a.s.l., 4.-12.ii.1991, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 212). – Paratypes: 4♂ (slides) data as for holotype; 7♂ data as for holotype except loc. 4-8, 30.x.-13.xii.1990.

Description

Post-occipital scent organs on head small, in the form of a cluster of black androconia; antennae damaged. Anterior wing length 1.9-2.0 mm. Genitalia as in figs. 46, 47. Abdominal sternite VII with a small acute mesal process. Abdominal segment IX produced apico-laterally into broadly rounded lobes. Tergite X membranous, broad-based, tapered distally to truncate apex. Inferior appendages short, fused mesally, forming rounded lobes laterally in ventral view, in lateral view with a hooked process dorsally. Subgenital plate wide in ventral view, with paired setae at sides of a slender apico-mesal cleft. Aedeagus slender, a short curved spine subapically.

Etymology. – Named after Mrs and Mr Tanner, who initiated the establishment of the Mazumbai Forest Reserve.

Biology and distribution. – Collected from the Kaputu Stream, West Usambara Mountains only, from stream sites with slow to moderate flow over sand, gravel and stones and some mud at altitudes between 1510 m to 1680 m a.s.l. (see Andersen & Johanson 1993).

Remarks. – Males of this species have the genitalic structures, particularly the inferior appendages, reduced and the antero-lateral angles of segment IX strongly produced posteriorly. The affinities of this species are unknown.

Hydroptila cruciata Ulmer

Hydroptila cruciata Ulmer, 1912: 83.
Hydroptila hirra Mosely, 1948: 81; Malicky, 1986: 234.

Biology and distribution. – In Africa this species is found in Cape Verde, Benin, Guinea, the Ivory Coast, Niger, Tanzania, Togo, Transvaal and it also occurs in Yemen and Palestine (see Malicky 1986, Gibon 1987b). Aspects of the life history were described by Botosaneanu & Guidicelli (1981). The present specimens were taken in a light trap in an area with several small slow-flowing streams and ditches.

Remarks. – *Hydroptila cruciata* is widely distributed and can be recognised amongst congeners by the long strap-like spines that intersect mid-ventrally in the male genitalia. Another prominent feature of the male is the shape of the post-occipital scent organs which are large, subrectangular and occupy about one third of the dorsal head.

Material examined. – 8♂ (4 slides), 9♀, TANZANIA, Morogoro region, Morogoro, Sokoine University of Agriculture, 18.x.-11.xi.1990, light trap, ZMB's Tanzania Expedition.

Hydroptila bumbulensis sp. n.
(figs. 48, 49)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Dule, Bumbuli River, 1220 m a.s.l., 26.xi.1990, sweep net, ZMB's Tanzania Expedition (slide, ZMBN No. 213).

Description

Post-occipital caps on head, angular and covering small tufts of scent hairs; antennae 31-segmented; flagellar segments sub-quadrate with dense scattered sensilla placodea. Wings slender, elongate; anterior wing length 2.1 mm. Genitalia as in figs. 48, 49. Lateral lobes on abdominal segment IX short, membranous. Tergite X broad, membranous. Inferior appendages in ventral view stout, about twice as long as greatest width, apico-ventrally with a darkly sclerotised process; in lateral view, inferior appendages greatly expanded dorsally in distal half. Below the subgenital plate, and dorsal to the inferior appendages is a pair of sclerotised processes which lie across each other. Subgenital plate narrow medially, with the usual paired apical seta situated on each side of a small median cleft. At the base of and between the inferior appendages is a short, slender, sclerotised median process. Aedeagus simple.

Etymology. – Named after the River Bumbuli in the West Usambara Mountains, Tanzania.

Biology and distribution. – Known only from the type locality, the Bumbuli River at Dule in the West Usambara Mountains. At the collecting site the river was fast flowing over large stones.

Remarks. – This is an *occulta*-group species closely resembling *Hydroptila cruciata* and the Malaysian species, *H. berkait* Wells & Huisman, 1992, both in the *occulta*-group. It differs from *H. cruciata* in the form of the inferior appendages, and the parameres.

Tangatrichia gen. n.

Type species. – *Tangatrichia gracilenta* sp. n., male, by present designation.

Diagnostic characters. – Showing strong resemblance to the Stactobiini taxa in the form of wings, and male genitalia, especially the elongate internal apodemes and form of the aedeagus, but groups with the Hydroptilini genera on basis of presence of post-occipital lobes on head and absence of suture on mesoscutellum. In general form of male genitalia resembling *Hydroptila*, but distinguished by presence of ocelli, and slender, elongate apodemes on abdominal segment IX; and by scattered arrangement of vestiture and absence of sensilla placodea on antennal segments.

Etymology. – From Tanga region of Tanzania referring to the type locality, and the Greek *trichos*, hair.

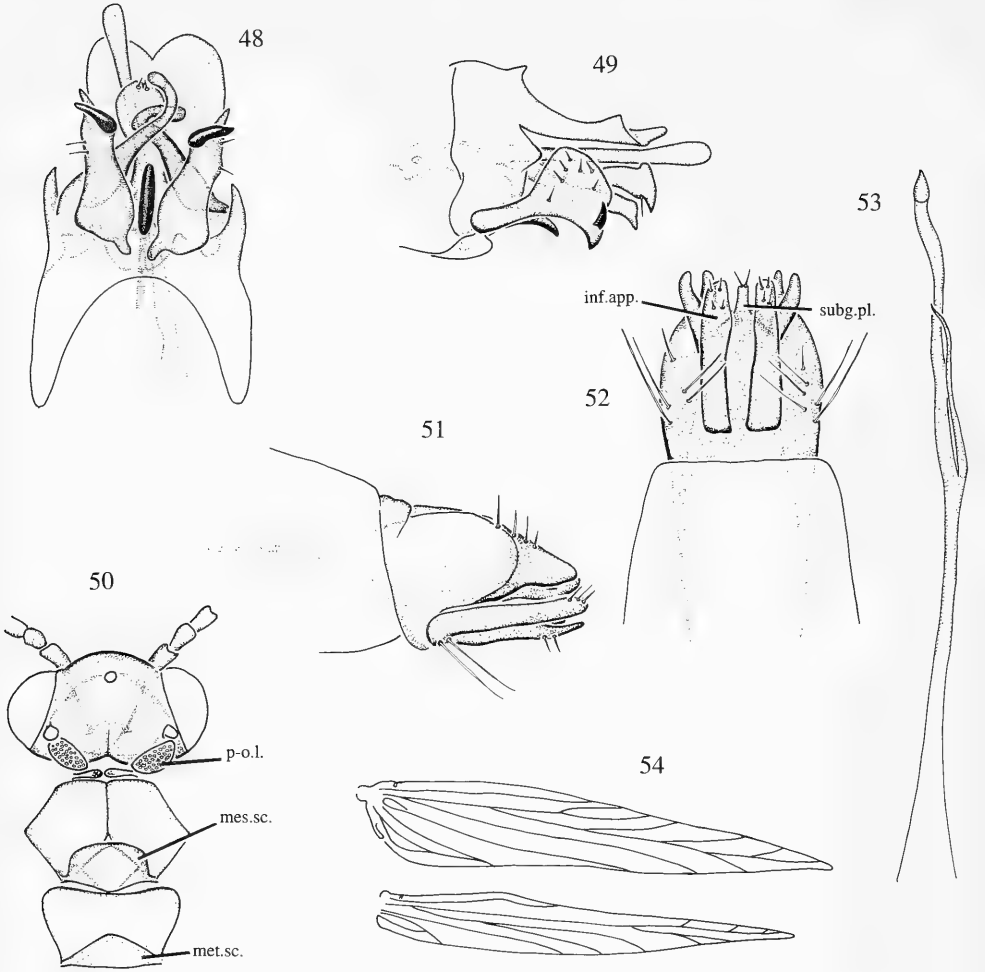
Description

Adult. Wings (fig. 54) attenuate, with strongly reduced venation; forewing with jugal lobe. Head with 3 ocelli; tentoria, including posterior bridge, complete; post-occipital lobes on head, but no associated scent glands; antennae with segments elongate, clothing hair scattered and sensory structures sensilla auricillica only. Thorax (fig. 50) with mesoscutellum sub-rectangular, without suture; metascutellum triangular. Tibial spur formula 0, 2, 4.

Genitalia resembling some Stactobiini taxa in general form, in having long internal apodemes on abdominal segment IX, but with basic arrangement of genitalic structures as in *Hydroptila.* The aedeagus is slender and straight, with a short straight titillator.

Remarks. – This genus is erected for a single species that groups with *Hydroptila* on the basis of presence of jugal lobe on forewing, form of tentorium, antennal segments, shape of thoracic scutellae, and of male genitalic structures in general, but not presence of ocelli and shape of abdominal segment IX. In these latter respects, and in having only sensilla auricillica on the antennal segments this genus shows similarity to the Australian/Malaysian genus *Jabitrichia* Wells, 1990 (Wells 1990c, O'Connor & Ashe 1992), from which it is distinguished by differences in male genitalic structures and arrangement of hair on antennal segments.

The one species referred to this genus was collected only in the West Usambara Mountains, from streams



Figs. 48, 49. *Hydroptila bumbulensis* sp. n., male genitalia. 48, ventral view; 49, lateral view. – Figs. 50-54. *Tangatrichia gracilenta* gen. n., sp. n., male. 50, head and thorax, dorsal view; 51, genitalia, lateral view; 52, genitalia, ventral view; 53, aedeagus; 54, wings. – Abbreviations. – inf.app.: inferior appendage; mes.sc.: mesoscutellum; met.sc.: metascutellum; p-o.l.: postoccipital lobes; subg.pl.: subgenital plate.

with slow to fast flow over stones, gravel, sand and mud.

Tangatrichia gracilenta sp. n.
(figs. 50-54)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 5, 1650 m a.s.l., 2.-6.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 214). – Paratypes: 51♂ (8 slides), data as for holotype except loc. 1-10, 30.x.-13.xii.1990; 135♂ (some damaged) data as for holotype except loc. 7, 4.i.-8.vi.1991; 3♂ (2 slides) data as for holotype except Mazumbai Forest Reserve, small stream at 1480 m a.s.l., 26.xi.-4.xii.1990; 3♂ (2 slides) data as for holotype except loc. 8, 5.xi.1990, sweep net.

Description

In general features as for genus. Small, pale, wings as in fig. 54, anterior wing length 1.5-1.6 mm. Genitalia as in figs. 51-53. Abdominal segment IX short mid-ventrally, antero-lateral apodemes long and slender. Segment X membranous, bifid distally.

Inferior appendages simple, elongate rectangular in ventral view, well separated medially. Subgenital plate narrowed abruptly in distal half, paired setae apically. Aedeagus long, slender, slightly twisted distally, with a short titillator arising at one-third length, but not twisted as is more usual in hydroptilids.

Female unknown.

Etymology. – From the Latin *gracilis*, slender, gracile, referring to the general shape of the species.

Biology and distribution. – Collected in the Mazumbai area in the West Usambara Mountains only, from streams with slow to fast flow between 1420 m to 1770 m a.s.l. In the Malaise traps at the Kaputu Stream this species was most abundant at a site with slow flow over mud, sand, gravel and stones (see Andersen & Johanson 1993).

Remarks. – See generic description.

Orthotrichia Eaton

Orthotrichia Eaton, 1873: 141. Type species: *Hydroptila angustella* McLachlan, 1865 by original designation. For full generic synonymy see Marshall (1979).

Orthotrichia is a diverse genus in tropical Africa. This work adds four new species to the previous 16 described from Africa. Most species are recorded from Central Africa, while two are listed in the South African fauna (de Moor 1993), two others are known from East Africa (Johanson 1992), including *O. straeleni* Jacquemart, 1956 which is recorded from Tanzania, as well as Uganda and Zaire, and one from Mali in West Africa (Marlier 1978). Marshall (1979) included the African species in the *angustella-* and *costalis-* species groups.

The South African species, *Orthotrichia barnardi* Scott, 1963, is here recorded from Tanzania for the first time. One of the four new species, *O. bisetula* sp. n., differs only slightly from *O. barnardi* and the Central African *O. kalengiensis* Statzner, 1977 and another, *O. nigrovillosa* sp. n., groups with *O. straeleni*, *O. spinicauda* Kimmins, 1958, from Zimbabwe and *O. nova* Marlier, 1978, from Mali. A third, *O. scutellata* sp. n., is distinctive and not aligned closely with any of the other species, although conforming with congeners. The fourth new species is enigmatic and is referred tentatively to *Orthotrichia* as *O. hydroptiloides* sp. n.

Orthotrichia bisetula sp. n.
(figs. 55, 56)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 10, 1420 m a.s.l., 20.-26.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 215). – Paratypes: 19♂ (3 slides) data as for holotype except loc. 10-11, 14.xi.-3.xii.1990; 2♂ (slides) data as for holotype except Shakoi River, 24.xi.1990, sweep net.

Description

Antennae 29-segmented; flagellar segments elongate, with dense sensilla placodea and at least one sensory pit per segment. Anterior wing length 2.4-2.8 mm. Genitalia as in figs. 55, 56. Abdominal segment IX with a pair of unequal, membranous, lateral digitate processes, each with a pair of setae apically. Tergite X broadly rounded apically, not sclerotised, covered with tiny spinules. Aedeagus of typical elongate slender form. Inferior appendages asymmetrical, left shorter than right, its inner apical angle produced; dorsal process V-shaped, anterior apodeme slender, elongate. A pair of unequal sclerotised spines dorso-laterally.

Etymology. – From the Latin *bis,* two and *setula,* diminutive for bristle, to describe the paired setae on the digitiform process in the male genitalia.

Biology and distribution. – Collected from streams and rivers with slow to rapid flow in the West Usambara Mountains, between 1400 m and 1420 m a.s.l. In the Malaise traps at the Kaputu Stream this species was only taken at the lowermost sites where the stream is moderate to slow flowing over mud, sand, gravel and stones (see Andersen & Johanson 1993).

Remarks. – This species, *Orthotrichia barnardi* and *O. kalengiensis,* all have lateral digitate processes on segment IX. They are distinguished by differences in the shape of the inferior appendages and lateral spines.

Orthotrichia barnardi Scott
(fig. 57)

Orthotrichia barnardi Scott, 1963: 470.

Biology and distribution. – Known from South Africa and northern Tanzania. The present specimens were taken at slow to fast flowing streams and rivers, at altitudes between 1220 m and 1400 m a.s.l.

Remarks. – This species closely resembles *Orthotrichia bisetula* sp. n. and *O. kalengiensis.* It is distinguished by the nearly symmetrical inferior appendages, see fig. 57.

Material examined. – 1♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 11, 13.-14.xi.1990, Malaise trap, ZMB's Tanzania Expedition; 1♂ (slide) as previous except Dule, Bumbuli River, 26.xi.1990, sweep net.

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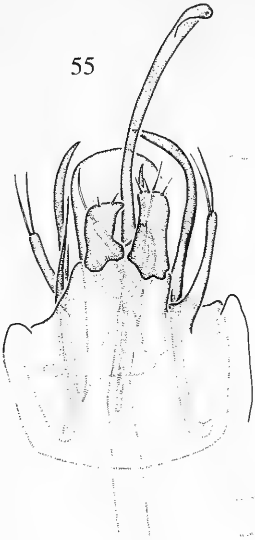

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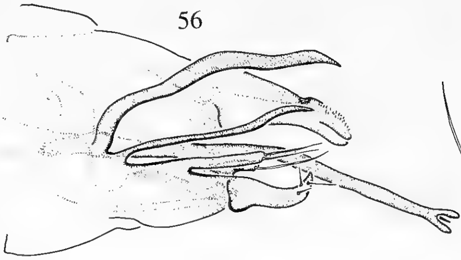

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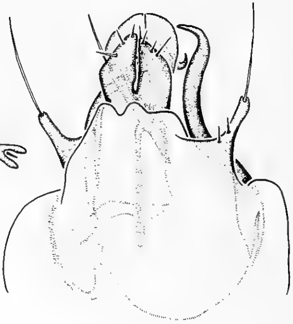

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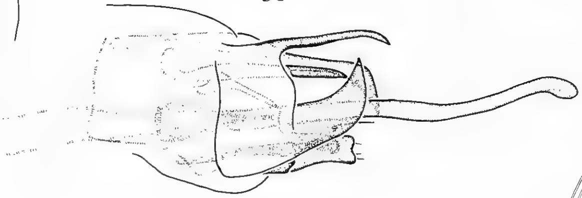

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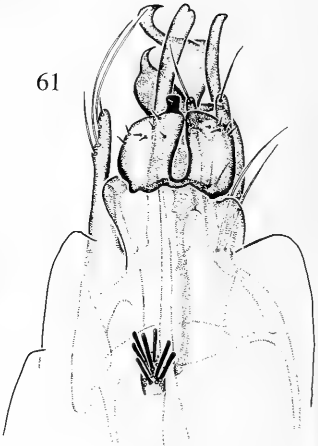

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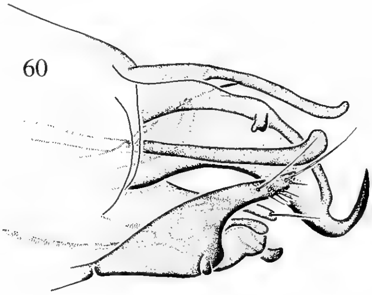

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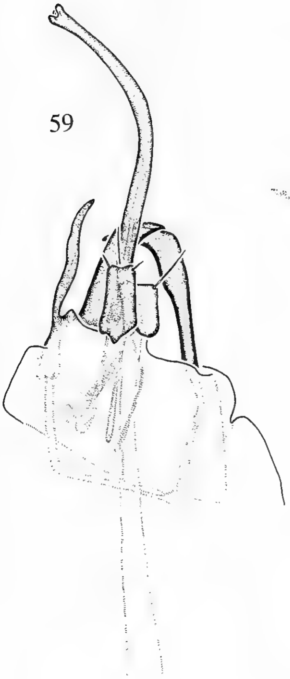

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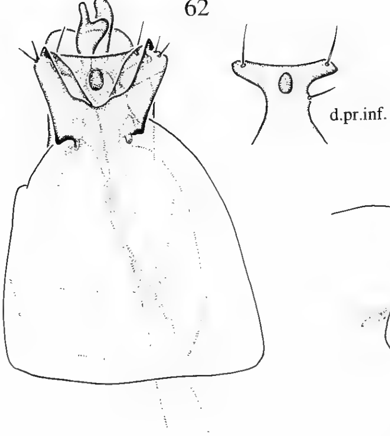

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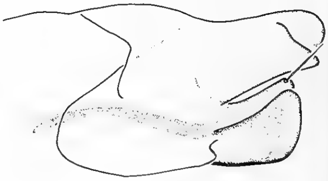

Orthotrichia scutellata sp. n.
(figs. 58, 59)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 5, 1650 m a.s.l., 6.-12.xi.1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 216).

Description

Antennae damaged. Anterior wing length 2.4 mm. Genitalia as in figs. 58, 59. Abdominal segment IX without membranous lateral digitate processes, but with a pair of unequal sclerotised spines. Tergite X reduced to a stout spine. Aedeagus of typical elongate slender form. Inferior appendages fused, rectangular, with a seta at each apical angle and with a pair of thin sclerotised lobes dorsally; dorsal process also fused, quadrate, setae at apical angles; anterior apodeme slender, elongate. A pair of unequal, sclerotised spines laterally, the left slender and curved, the right broader and hooked distally. Internally a pair of short, slender parameres.

Etymology. – From the Latin *scutella,* little flat dish, plate, and the suffix *-atus,* provided with, referring to the fused dorsal process of the inferior appendages, forming a single plate.

Biology and distribution. – Known only from the type locality, Kaputu Stream in the West Usambara Mountains, where it was taken at a site where the stream is fast flowing over gravel and stones (see Andersen & Johanson 1993).

Remarks. – This is a distinctive species, characterised by the fused inferior appendages and their dorsal process in the form of a simple plate.

Orthotrichia nigrovillosa sp. n.
(figs. 60, 61)

Type material. – Holotype ♂, TANZANIA, Tanga region, West Usambara Mts, Mazumbai, Kaputu Stream, loc. 10, 1420 m a.s.l., 29.xi.-3.xii. 1990, Malaise trap, ZMB's Tanzania Expedition (slide, ZMBN No. 217). – Paratypes: 4♂ (1 slide) data as for holotype except loc. 4-11, 12.-29.xi.1990.

Description

Antennae damaged; flagellar segments elongate, with dense scattered sensilla placodea and one sensory pit per segment. Anterior wing length 2.3-2.4 mm. Genitalia as in figs. 60, 61. Abdominal sternite VIII with a mesal process bearing blunt, dark setae. Abdominal segment IX without lateral digitate processes. Tergite X sclerotised, distally in the form of stout hooks and spines. Aedeagus of typical elongate slender form. Inferior appendages superficially symmetrical save for a small, square sclerotised process apically on the left inferior appendage; dorsal process U-shaped, well displaced to right side; anterior apodeme slender, elongate. A pair of unequal, sclerotised processes laterally, the left slender, with long setae distally, the right with curved setate process basally and sclerotised spine distally.

Etymology. – From the Latin *niger,* black, dark, and *villus,* tuft of hair, referring to the dark, blunt setae on the mesal process of abdominal segment VIII.

Biology and distribution. – Known only from the Kaputu Stream in the West Usambara Mountains, at sites between 1400 m and 1680 m a.s.l. with slow to moderate flow over mud, sand, gravel and stones (see Andersen & Johanson 1993).

Remarks. – *Orthotrichia nigrovillosa* sp. n., *O. spiralina* Statzner, 1977, *O. straeleni, O. spinicauda* and *O. nova* all have a more complex development of lateral processes on segment IX than the above mentioned group of species. In *O. nigrovillosa* this takes the form of an elongate lobe with setae distally on the outer side on the left and on the right a similar structure basally, extended dorsally in a sclerotised spine. The shape of the inferior appendages differs between species.

Orthotrichia hydroptiloides sp. n.
(figs. 62, 63)

Type material. – Holotype ♂, TANZANIA, Morogoro region, Morogoro, Sokoine University of Agriculture, 550 m a.s.l., 11.xi.1990, light trap, ZMB's Tanzania Expedition (slide, ZMBN No. 218).

Description

Ocelli absent. Tibial spurs 0, 2, 4. Meso- and metascutellum subrectangular, metascutellum about half length of mesoscutellum. Antennae damaged, remaining flagellar segments with scattered clothing hair, basal whorl of hair and sensilla placodea lacking. Anterior wing length 1.4 mm. Genitalia as in figs. 62, 63. Abdominal segment IX broad anteriorly, without

Figs. 55, 56. *Orthotrichia bisetula* sp. n., male genitalia. 55, ventral view; 56, lateral view. – Fig. 57. *Orthotrichia barnardi* Scott, 1963, male genitalia, ventral view. – Figs. 58, 59. *Orthotrichia scutellata* sp. n., male genitalia. 58, lateral view; 59, ventral view. – Figs. 60, 61. *Orthotrichia nigrovillosa* sp. n., male genitalia. 60, lateral view; 61, ventral view. – Figs. 62, 63. *Orthotrichia hydroptiloides* sp. n., male genitalia. 62, ventral view; 63, lateral view. Abbreviations. – d.po.inf.: dorsal process of inferior appendage.

spines or digitate processes. Tergite X membranous, broad. Aedeagus without spiral titillator, swollen and twisted distally, with divided apex. Inferior appendages symmetrical, stout, fused basally, in lateral view expanded distally and broadly rounded apically; dorsal process fused, more or less T-shaped, with a setae laterally on the right side of base; anterior apodeme slender, elongate and curved.

Etymology. – Named after the genus *Hydroptila,* using the suffix *-oides,* resembling, referring to the general shape of the male genitalia.

Biology and distribution. – Known only from the type locality on the campus of Sokoine University of Agriculture in Morogoro in an area with several small, slow-flowing streams and ditches.

Remarks. – This species is placed in *Orthotrichia* on the basis of general head, thoracic and wing features and the form of the male genitalic structures. The tibial spur formula is aberrant, however, and in the male genitalia the aedeagus is quite unlike the typical and generally invariant form, and the anterior, internal shape of abdominal segment IX is unusual. The spur formula conforms with that of *Hydroptila* and in general appearance the male genitalia resemble those of *H. cortensis* Mosely, 1937. However, the wing lacks a jugal lobe, the thoracic scutellae conform with those of *Orthotrichia* and upon close inspection the genitalia certainly show features typical of *Orthotrichia,* with the characteristic form of the inferior appendages, their dorsal process and basal apodeme.

Close examination of species of *Tricholeiochiton* Kloet & Hincks, 1944 reveals a basal apodeme similar to, but less distinctive than that of males of most species in *Orthotrichia.* The aedeagus of *O. hydroptiloides* sp. n. is dissimilar to that of other *Orthotrichia,* but shows some resemblance to the form typical of *Tricholeiochiton.* However, the arrangement of hair on the antennal segments appears to be of the form found in *Orthotrichia.*

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References

Andersen, T. & K. A. Johanson, 1993. Caddis flies (Trichoptera) from a mountain rain forest in NE Tanzania. – In Otto, C. (ed.) Proceedings of the 7th International Symposium on Trichoptera, pp. 59-64. – Backhuys, The Netherlands.

Botosaneanu, L. & J. Guidicelli, 1981. Observations morphologiques, éthologiques et écologiques sur *Hydroptila hirra* Mosely (Trichoptera : Hydroptilidae). – In Moretti, G. (ed.) Proceedings of the 3rd International Symposium on Trichoptera, pp. 21-29. – W. Junk, The Hague.

Dalman, J. W., 1819. Några nya insekt-genera beskrifna. – Kungliga Svenska Vetenskapsakademiens Handlingar 40: 117-127.

Eaton, A. E., 1873. On the Hydroptilidae, a family of the Trichoptera. – Transactions of the Entomological Society of London 1873: 125-149.

Gibon, F.-M., 1985. Recherches sur les Trichoptères d'Afrique occidentale, II. Stactobiini (Hydroptilidae) de Côte-d'Ivoire. – Revue Française d'Entomologie (N.S.) 7: 149-155.

Gibon, F.-M., 1987a. Studies on West African Trichoptera. 7. Two new *Catoxyethira* from Guinea (Hydroptilidae). – Aquatic Insects 9: 115-118.

Gibon, F.-M., 1987b. Recherches sur les Trichoptères d'Afrique occidentale, 8 - Hydroptilini (Hydroptilidae). – Revue d'Hydrobiologie Tropicale 20: 121-130.

Gibon, F.-M., 1991. Trichoptères d'Afrique occidentale (XIII). Trois nouvelles *Catoxyethira* de Guinée (Hydroptilidae). – Revue Française d'Entomologie (N.S.) 13: 125-130.

Jacquemart, S., 1956. Trois *Orthotrichia* nouveaux du Lac Kivu (Trichoptera, Hydroptilidae). – Bulletin de l'Institut Royal des Science Naturelles de Belgique 32 (9): 1-6.

Johanson, K. A., 1992. A catalogue of the caddis flies of East Africa (Insecta, Trichoptera). – Steenstrupia 18: 113-141.

Kimmins, D. E., 1958. On some Trichoptera from S. Rhodesia and Portuguese East Africa. – Bulletin of the British Museum (Natural History). Entomology Series 7: 359-368.

Malicky, H., 1986. The caddisflies of Saudi Arabia and adjacent regions (Insecta, Trichoptera). – Fauna of Saudi Arabia 8: 233-245.

Marlier, G., 1978. Sur une collection de Trichoptères de l'Afrique occidentale. – Revue de Zoologie Africaine 92: 283-302.

McLachlan, R., 1880. A monographic revision and synopsis of the Trichoptera of the European Fauna. Part IX, pp. 501-523, with supplement, pp. xiii-lxxxiv. – London.

Marshall, J. E., 1979. A review of the genera of the Hydroptilidae (Trichoptera). – Bulletin of the British Museum (Natural History). Entomology Series 39: 135-239.

Mey, W., 1992. Beschreibung von vier neuen Köcherfliegen aus Ostafrika (Insecta, Trichoptera). – Mitteilungen aus dem Zoologischen Museum in Berlin 68: 259-265.

Moor, F. C. de, 1993. Factors influencing the distribution of Trichoptera in South Africa. – In Otto, C. (ed.)

Proceedings of the 7th International Symposium on Trichoptera, pp. 51-58. – Backhuys, The Netherlands.

Morse, J. C., 1974. New caddisflies (Trichoptera) from southern Africa. – Journal of the Kansas entomological Society 47: 328-344.

Mosely, M. E., 1933. The genus *Stactobia* McL. (Trichoptera). – Stylops 2: 162-165.

Mosely, M. E., 1939. Trichoptera. – Ruwenzori Expedition (1934-35) 3: 1-40.

Mosely, M. E., 1948. Trichoptera. – Expedition to Southwest Arabia (1937-8) 1: 67-85.

Oláh, J., 1989. Thirty-five new hydroptilid species from Vietnam (Trichoptera, Hydroptilidae). – Acta Zoologica Hungarica 35: 255-293.

O'Connor, J. P. & P. Ashe, 1992. *Jabitrichia wellsae* sp. n. (Trichoptera, Hydroptilidae) from Tasek Bera, Malaysia. – Aquatic Insects 14: 255-257.

Ross, H. H., 1948. Notes and descriptions of Nearctic Hydroptilidae (Trichoptera). – Journal of the Washington Academy of Sciences 38: 201-206.

Schmid, F., 1959. Le genre *Stactobia* McL. – Miscelánea zoològica 1: 1-56.

Schmid, F. 1960. Trichoptères du Pakistan III. – Tijdschrift voor Entomologie 103: 83-109.

Scott, K. M. F., 1963. Some new caddis flies (Trichoptera) from the Western Cape province. IV: Some Hydroptilidae. – Annals of the South African Museum 46: 469-478.

Scott, K. M. F., 1967. The larval and pupal stages of *Ugandatrichia* Mosely (Trichoptera : Hydroptilidae) from Rhodesia, with the description of a new species. – Annals of the Cape Provincial Museums. Natural History 11: 117-127.

Scott, K. M. F., 1986. A brief conspectus of the Trichoptera (caddisflies) of the Afrotropical Region. – Journal of the Entomological Society of Southern Africa 49: 231-238.

Statzner, B., 1977. Taxonomische Studien an den Hydroptilidae-Imagines aus dem zentralafrikanischen Bergbach Kalengo. – Deutsche entomologische Zeitschrift (Neue Folge) 25: 393-405.

Ulmer, G., 1912. Trichoptera aus Äquatorial-Afrika. – Wissenschaftliche Ergebnisse der Deutschen Zentral-Afrika-Expedition (1907-08) 4: 81-125.

Ulmer, G., 1951. Köcherfliegen (Trichopteren) von den Sunda-Inseln (Teil I). – Archiv für Hydrobiologie, Supplement 19: 1-528.

Wells, A., 1990a. The micro-caddisflies (Trichoptera : Hydroptilidae) of North Sulawesi. – Invertebrate Taxonomy 3: 363-406.

Wells, A., 1990b. The hydroptilid tribe Stactobiini (Trichoptera: Hydroptilidae) in New Guinea. – Invertebrate Taxonomy 3: 817-849.

Wells, A., 1990c. New species and a new genus of micro-caddisfly from northern Australia, including the first Australian record of the tribe Stactobiini (Trichoptera: Hydroptilidae). – Transactions of the Royal Society of South Australia 114: 107-128.

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ISLANDS AND CICADAS ADRIFT IN THE WEST-PACIFIC. BIOGEOGRAPHIC PATTERNS RELATED TO PLATE TECTONICS

Boer, A. J. de, 1995. Islands and cicadas adrift in the west-Pacific. Biogeographic patterns related to plate tectonics. – Tijdschrift voor Entomologie 138: 169-244, figs. 1-56. [ISSN 0040-7496]. Published 15 November 1995.

The cicadas of the Indo-Pacific region (Sulawesi, Maluku, New Guinea, and the East-Melanesian archipelagos) show an extreme rate of endemism and speciation. Congruent patterns of distribution lead to the recognition of several areas of endemism in the region. Provided that the cicadas evolved by vicariant speciation in response to geotectonic changes, cicada phylogeny and distribution should indicate palaeogeological relationships between the areas of endemism. An *a priori* knowledge of the tectonic history is therefore essential to realize the importance of many of the biogeographic data and to interpret them correctly. High endemism found in cicadas makes them a promising group for area cladistic study. A combination of biogeographic and phylogenetic data of cicadas might lead to a better insight in the enormously complex geotectonic history of the archipelagos, which separate the Asian and Australian continents.

These archipelagos evolved at the interaction zone of three converging geotectonic plates, the Eurasian, Pacific, and Australian plates. Conversion between the Pacific and Australian plates forced the subduction of the intermediate Tethys Sea plate under the Pacific. This subduction gave rise to a system of volcanic island arcs along the Pacific plate margin. One of these island arcs collided at its western end with southeast Asia and fragmented as a result of that collision. Many of the now existing land masses in the area are of composite geological origin. They result from various collisions involving fragments of the Pacific island arc, rifted microcontinents of Australian origin, and the continental margins of southeast Asia and, especially, Australia. A review of the most recent geological literature is provided in the first chapter and gives a more or less coherent tectonic history of the area in question.

Biogeographical data of two unrelated monophyletic groups of cicadas are analysed: the subtribe Cosmopsaltriaria of the family Cicadidae and the sister tribes Chlorocystini and Prasiini of the family Tibicinidae. Distributional patterns in the various genera of these two groups show that, even if the distributional ranges of the genera largely overlap, these genera are generally concentrated with most, and often endemic, species in different areas. The areas thus recognized largely coincide with the recognized geological entities as microcontinents or island arc fragments. This suggests that the various genera evolved in isolation on such geological entities, which can thus be regarded as the 'source areas' of the genera. If this is true, the phylogenetic relationships of the cicada genera should indicate relationships between the presumed source areas of these genera, which reflect the historic relationships between the corresponding geological entities. To test this hypothesis the most likely source area for each of the genera is derived from their present-day distribution patterns. These source areas are substituted for the genera in the generic cladograms of the two cicada groups and thus two area cladograms are obtained. The taxon-area cladograms are compared to an area cladogram derived from the geological literature, which shows the alleged fragmentation sequences of the main historic island arc. Congruencies between the two taxon-area cladograms and the geological cladogram suggest that vicariance as a result of fragmentation indeed played a major role in the evolution of the Indo-Pacific cicadas. The presumed sequences of fragmentation of the island arc do coincide with the main branching sequences in the taxon-area cladograms. Moreover, the cicada area cladograms indicate area relationships that suggest some more detailed palaeogeographical reconstructions of the various island arcs in relation to some of the rifted microcontinents than the one obtained from the geological data alone. It is clear that geological and biogeographical data supplement each other and that their combination will lead to a better understanding of the evolution of both the earth's surface and its biota.

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Key words. – Cicadas, Biogeography, Chlorocystini, Cosmopsaltriaria, Prasiini, palaeogeography, west-Pacific, Indo-Pacific.

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Introduction

Biogeography of the cicadas of Sulawesi, New Guinea and the west Pacific

The New Guinea orientated genera

Area cladistics

INTRODUCTION

This study contains a comparison of the biogeographic patterns found in two unrelated groups of cicadas from Sulawesi, Maluku, New Guinea, and East-Melanesia. The observed similarities between these biogeographic patterns suggest a common underlying geotectonic cause, which indicates that vicariant speciation played a major role in the evolution of the two groups compared.

General remarks on biogeography

Biogeography is the discipline which concerns itself with the study of the distribution of species and higher taxa over the world, and with the search for explanations of these distributions. The occurrences of completely different communities of animals and plants in the various parts of the world have intrigued generations of biologists and have, in the second half of the 19th century, led to the recognition of so called floral and faunal regions, in zoogeography beginning with Sclater's (1858) avifaunal regions (see for a historical resumé Nelson & Platnick 1981). Most intriguing, of course, are those areas in the world where two such regions meet, and study has long focussed on the exact determination of border lines between the regions. Well known in this respect are the lines of Wallace (1863, 1876, 1910) separating the Asian and Australian biotas. Later biogeographers have proposed alternative lines, of which those named after T.H. Huxley, R. Lydekker, and M. Weber are best known (for a historical resumé see Simpson 1977).

The concept of plate tectonics, which evolved from earlier theories of Alfred Wegener (1912), became widely accepted only since the early 1970's. These theories enable us to explain the apparent differences between the various biogeographic regions in terms of independent evolutions of their isolated biotas. The border lines separating the regions represent the historic geographical barriers that caused the isolation between the biotas of the regions. The steady change of the surface of the earth constantly causes the development and disappearance of barriers of all kinds, causing isolation between populations of species where they develop, and enabling biotas to mix where they disappear. Of course, it depends on the nature of the barrier and the dispersal abilities of a particular species whether the barrier indeed acts as a mechanism of isolation for the species in question.

Vicariant biogeography is based on the notion that a geographical barrier arising and separating any two parts of an area will not only affect one single species, but might divide the entire biota. The barrier in question is therefore presumed to form an effective mechanism of isolation for a wide range of species of both animals and plants. As a result, general patterns of distribution can be expected to have been formed, in which taxa of various species groups occurring on both sides of the barrier show a sister group relationship. It depends on the age of the geological barrier and the rate of evolution in a particular group whether these vicarying taxa be species or monophyletic groups of a higher taxonomic level.

The above line of reasoning is reversed in area cladistics as developed by Platnick & Nelson (1978). Here the phylogenetic relationships between endemic taxa are regarded as evidence for the palaeogeographical relationships between the distribution areas of these taxa, always provided the distributions of these taxa are not the result of dispersals. In other words, the phylogeny of a monophyletic group reveals the order in which geological barriers fragmented a once undivided ancestral area, which theoretically formed the distribution area of the ancestral species of that monophyletic group. Of course, this is only true when the evolution of the species group in question was caused by vicariance in the first place. This becomes the more likely when several groups of species comply with one and the same generalized area cladogram; when several monophyletic groups are found of which the phylogeny and distribution indicate similar patterns of area relationships. In that case, we can safely assume that these groups did not acquire their distribution patterns independently by chance dispersals, but that they responded similarly to the same geological events. Area cladistic analyses should therefore always be based on two or more, preferably unrelated, groups.

The methods of area cladistics are summarised by Rosen (1978), Humphries & Parenti (1986), and Wiley (1988). In short, an area cladistic analysis requires two or more taxa occurring in the same area. These taxa should have many endemic species with more or less congruent distributions and the phylogenetic relationships should be known. A phylogenetic hypothesis is regarded a prerequisite for analysing historical biogeographic patterns (Cracraft 1988). The methods for reconstructing the relationships between species were developed by Hennig (1950; 1966). A phylogenetic reconstruction, expressed in a cladogram, is based on shared derived characters, the synapomorphies, that indicate a common ancestor. It will be clear that widespread taxa, taxa that occur in all areas of which one wants to study the relationships, are uninformative. In area cladistics, the names of taxa in a taxon cladogram are simply substituted for the names of the areas in which these taxa occur, and a taxon-area cladogram results. A taxon-area cladogram visualizes the relationships between areas as suggested by the phylogenetic and biogeographic data of a single species group; these relationships need not be of a geological nature, they could also indicate routes of dispersal. Congruencies between the taxon-area cladograms of different taxa lead to the recognition of a general area cladogram. Such a general area cladogram shows the area relationships which are supported by the phylogenies and distributions of more than one species group. A general area cladogram is supposed to visualize the palaeogeographical relationships between the areas; each splitting in a branch represents the formation of a geological barrier, which, translated to the taxon cladogram, led to a vicariant speciation event.

West Pacific cicadas as object of study

When a study is undertaken with the aim of revealing a general area cladogram based on the phylogeny and distributions of monophyletic taxa that can be related to the tectonic history of the area, the chances of success increase when a group is selected as a subject of study that has many endemic species in an area with an active geotectonic past. The more species are involved, the more likely it becomes that we will be able to recognize patterns in their distributions, and a high rate of endemism facilitates the recognition of areas of endemism. It stands to reason that the more a particular area has been subjected to geological changes, the greater the chance is that some of these changes gave rise to effective barriers that were followed by vicariant speciations. It might therefore be expected that the cicadas of New Guinea and adjacent areas cannot fail to form an excellent group for study. Not only is the geological history of New Guinea regarded as one of the most complex in the world, the cicadas of the New Guinea region satisfy all our demands of extensive speciation and endemism. Since several genera of New Guinean cicadas also either occur or have their sister groups in adjacent areas such as Maluku (the Moluccas), Sulawesi (Celebes), Australia, and the East-Melanesian islands, these areas are also taken into account in the present study.

New Guinea is a composite area, composed of parts of different geological origin, at the junction of three converging tectonic plates: the Australian, Pacific and Eurasian plates. The evolution of the island involved a series of collisions of various parts of an oceanic island arc and several microcontinents with the northern craton of the Australian continent. A review of the geological literature on the formation of New Guinea and adjacent areas is given in the next chapter.

Cicadas form a group of insects conspicuous by the amount of noise the male produces in attracting the female. The tendency to small distributional ranges must presumably be explained by the peculiar life cycle of these insects. The following data on cicada biology are abstracted from Chandler (1972; 1973), Dubois (1966), Itô & Nagamine (1974a, b), Kuniata & Nagaraja (1992), Monsarrat (1966), Moulds (1990), Nagamine & Teruya (1976), Wilson (1969), and Wilson et al. (1963). Cicadas usually deposit their eggs along the mid-ribs of the underside of green leaves, after some tissue has been curved up by the female. After an incubation period of 4-8 weeks the larvae hatch from the egg, fall to the ground and dig themselves in within a few minutes. The insect now passes through 5 larval stages. These larvae remain under ground at a depth of generally 20-30 cm, where they suck on plant roots. After about 2-8 years, in exceptional cases, (species of the north American genus *Magicicada* Davis, 1925) 13 or 17 years, the last larval stage or nymph emerges, usually after rain fall, and climbs up a stem where metamorphosis takes place. The winged adults live for only 1-2 weeks, which leaves the cicada precious little time to move about and disperse.

Cicadas are currently subdivided into six families, but the soundness of this classification is being disputed (Duffels 1993). Each of the largest two of these families has a large monophyletic group endemic to the area under study. The subtribe Cosmopsaltriaria of the Cicadidae (± 125 species), and a group consisting of the sister tribes Prasiini (± 50 species) and Chlorocystini (± 150 species) of the Tibicinidae are both distributed over Sulawesi, Maluku, New Guinea, and East-Melanesia to Samoa and Tonga.

Results of previous study

The value of cicadas for recognizing areas of endemism has been demonstrated before by Duffels (1977 and later publications). An area of endemism is delimited by the more or less coincident distributions of taxa that occur nowhere else (Nelson & Platnick 1981). Duffels' revisionary work on the subtribe Cosmopsaltriaria (Cicadidae) showed the extreme rate of endemism of the Indo-Pacific cicadas. Duffels (1986) recognized several areas of endemism in the Indo-Pacific region. These areas of endemism are to a large extent congruent with areas of endemism recognized by other workers, studying several different groups (Schuh & Stonedahl 1986, plant bugs of the family Miridae; Kitching et al. 1987, butterflies of the genus *Idea*; Holloway 1987, butterflies; Van Welzen 1990, the plant genus *Guioa* of the Sapindaceae). The area cladogram of the Cosmopsaltriaria indicates that such areas of endemism are sometimes closer related to farther removed areas, than to the immediately adjacent ones.

In these earlier studies the unexpected area relationships were explained with the then available theories on the composite geological origin of the New Guinean region. The island of New Guinea was supposed to have formed after the collision of two, formerly widely separated, island arcs: the Inner- and Outer Melanesian Arcs. The central mountain ranges of New Guinea were allotted to the continental Inner Melanesian Arc, which was supposed to continue to New Caledonia and New Zealand. The northern mountain ranges of New Guinea were supposed to have formed a part of an oceanic and volcanic Outer Melanesian Arc, that, in theory, continued eastward along the Bismarck Archipelago and Solomon Islands to Fiji and Tonga, and westward into northern Maluku. The sister group relationship of the genus *Cosmopsaltria* Stål, 1866, to the genera *Aceropyga* Duffels, 1977, *Diceropyga* Stål, 1870, and *Rhadinopyga* Duffels, 1985, was explained in terms of a vicariant pattern between the Inner and Outer Melanesian Arcs, and was supposed to reflect the invasion of these two island arcs by 'vicariant dispersal' of a common ancestor from southeast Asia (Duffels, 1983 fig. 21). The sister group of the four genera mentioned above, at that time being only the genus *Dilobopyga* Duffels, 1977, is endemic to Sulawesi. This indicates a sister area relationship between Sulawesi and New Guinea + East-Melanesia, which was explained by a similar dispersal event of the ancestor of *Dilobopyga*, but then from southeast Asia to Sulawesi.

Follow-up study

As explained above, an area cladistic study should involve two or more unrelated species groups. Vicariant evolution caused by geotectonic changes implies that various groups of species should show congruent patterns of distribution. To test the general applicability of the hypotheses on the historical biogeography of the subtribe Cosmopsaltriaria, I started a phylogenetic and biogeographic study on a group of tibicinid cicadas centred around the genus *Baeturia* Stål, 1866.

The distribution area of *Baeturia* largely coincides with that of the Cosmopsaltriaria, although the

Cosmopsaltriaria occur on Sulawesi while *Baeturia* does not. Furthermore, preliminary investigations showed that monophyletic species groups within *Baeturia* were indicative for the same areas of endemism as were previously recognized based on the Cosmopsaltriaria data. Similarities were observed between the distributions of the *Cosmopsaltria mimica* complex and the *Baeturia nasuta* group (both mainly occurring in the central mountain ranges of New Guinea); between the *Cosmopsaltria doryca* group and the *Baeturia conviva* group (both in Maluku and western New Guinea); and between the distributions of *Aceropyga – Diceropyga* and the *Baeturia bloetei* group, both occurring in Maluku, northern New Guinea, the Bismarck Archipelago and several East-Melanesian island groups, and absent in Cendrawasih; the Birds Head peninsula of New Guinea (Duffels & De Boer 1990).

However, the relationships between these areas as indicated by the phylogeny of *Baeturia* are in strong contrast with those indicated by the phylogeny of the Cosmopsaltriaria (cf. figs 51-52): the phylogeny of *Baeturia* does not indicate a vicariant pattern between an Inner and an Outer Melanesian Arc, since the *Baeturia nasuta* group from central New Guinea is certainly not the sister group of all other *Baeturia* species, which mainly occupy the Outer Melanesian Arc terranes. A closer comparison of the similarities between the distributions of *Aceropyga – Diceropyga* and the *Baeturia bloetei* group suggests that these groups, notwithstanding some obvious similarities, do not show the same pattern. The relatively small morphological differences between the East-Melanesian species of *Baeturia* suggest a more recent evolution of the *bloetei* group compared to the Cosmopsaltriaria from the same area. Furthermore, the absence of *Baeturia* from the Fiji islands, in contrast with high endemicity of the Cosmopsaltriaria on Fiji, could be explained by a more recent invasion of the west Pacific by *Baeturia*, which would also imply a younger age of the *Baeturia bloetei* group (Duffels 1988a; De Boer 1989; Duffels & De Boer 1990).

If *Baeturia* in fact is a much younger group than the Cosmopsaltriaria, the main biogeographic patterns of these two groups should not be compared at all, since they could not result from the same geological events. Apparent similarities in their distributions then need different explanations. Moreover, it became clear that *Baeturia*, as then defined, did not form a monophyletic group. To be able to recognize the general patterns of vicariance in the Cosmopsaltriaria we should find and study congruencies in distribution patterns between that group and a monophyletic group of approximately the same age and with the same distributional range.

These difficulties could be coped with by extending the group of study. It appeared that all but one species described in *Baeturia*, together with several other New Guinean and several Australian genera, do indeed form a monophyletic group. This group was defined as the '*Baeturia* and related genera complex' (De Boer 1990) and later identified as the tribe Chlorocystini (sensu stricto). In sensu stricto, because several other genera at present included in the Chlorocystini do not belong to this monophyletic group and should be reallocated to other tribes (De Boer 1995d). The Chlorocystini (sensu stricto) cover approximately the same area as did *Baeturia* alone; they range from Maluku to Samoa and Tonga, but, in contrast to *Baeturia*, they reach into Australia as well. Moreover, the oriental Prasiini, [Prasiini (sensu stricto)], which form the presumed sister group of the Chlorocystini (sensu stricto), are mainly distributed in Sulawesi. This means that the distribution of the Chlorocystini – Prasiini together is very similar to that of the Cosmopsaltriaria.

A revision of the '*Baeturia* and related genera complex' was carried out by successively revising the genera and monophyletic groups of species that comprise this complex. In the process of re-shaping this complex into a group of presumed monophyletic genera, several species have been transferred from one genus to another, while for other species new genera had to be erected. The Chlorocystini (sensu stricto) presently comprise 14 genera. Phylogenetic and biogeographic revisions of most of these genera have been published separately (De Boer 1990; 1991; 1992a; 1993a; 1993b; 1995a; 1995b; 1995c). The large genus *Baeturia* was subdivided into seven monophyletic species groups that were revised in separate publications (De Boer 1982; 1986; 1989; 1992b; 1994a; 1994b; 1994c; 1994d), while the six genera that are endemic to Australia will be treated in a combined revision (De Boer in prep).

The distributional patterns of the Chlorocystini (sensu stricto) in combination with their sister group, the Prasiini (sensu stricto) show a striking resemblance to the patterns found in the Cosmopsaltriaria, especially at generic level. Several taxa of these two groups indicate the same areas as areas of endemism and in several cases the area cladograms of these groups agree upon the same relationships between these areas of endemism. We can conclude that the early evolutionary branchings, leading to the present generic diversity in these two groups of cicadas are, in both groups, reactions to the same geotectonic events. Some of the more recent dispersal events gave rise to patterns of distribution in species groups that are strikingly similar to the older vicariant patterns between the genera.

The recent geological literature provides new data, which give reason to abandon the aforementioned 'two Melanesian arcs theory' as the means of explaining the observed vicariant patterns. The central part of New Guinea, formerly supposed to represent a part of the Inner Melanesian Arc, appears to originate partly from one and the same island arc as northern and eastern New Guinea, but is largely construed out of the Australian continental margin. Furthermore, some serious doubts arise as to whether the East-Melanesian island chains (e.g., Solomon Islands, Vanuatu, Fiji, and Tonga), that always have been regarded as of the same geological origin as northern New Guinea and the Bismarck Archipelago, really belong to that same island arc; it appears that the western terranes evolved on the margin of the Pacific plate, while the more eastern island groups developed in connection with the Australian plate. The next chapter contains a review of the most recent geological literature. An attempt is made there to give a more or less coherent tectonic history of the distribution area of the cicadas under study.

A new hypothesis on the historical biogeography of the New Guinean cicadas is developed in the second chapter. Congruence between the areas of endemism and the known geological entities like island arc fragments or microcontinents suggests that fragmentation of the island arc system (or systems) and the subsequent movements of its fragments caused vicariant evolution on the isolated remnants of that arc system and on some of the adjacent microcontinents. Most of the various genera of the Cosmopsaltriaria, the Prasiini (sensu stricto) and the Chlorocystini (sensu stricto), are presumed to have evolved on different fragments of the island arc that had successively broken away from the arc, others are supposed to be of microcontinental origin. The fact that many of the arc fragments reassembled and now form parts of New Guinea might explain why the New Guinean genera all concentrate in different parts of the island. Dispersals after the amalgamation of a particular island arc fragment with New Guinea are responsible for the fact that the areas of origin or source areas of the various genera are no longer recognized as strict areas of endemism for these genera. To test this hypothesis, the present-day distribution pattern of each of the genera is analysed in an attempt to establish the most probable source area of each of these genera; the microcontinent or island arc fragment on which the genus in question evolved. The concentration of species, and especially of endemics, in any of the geologically determined areas indicates such an area as the most probable source area for a particular genus. When various monophyletic subgroups of a genus concentrate in different areas, a historical proximity among these areas is supposed and these areas together are regarded as the source area. The hypothesis of vicariance by island arc fragmentation can be tested by area cladistic analysis. The phylogenetic relationships between the genera of cicadas should indicate area relationships between the presumed source areas that reflect the historic relationships of these source areas within, or relative to, the island arcs.

The final chapter contains an area cladistic analysis of the Cosmopsaltriaria and its presumed sister group (the genus *Meimuna* Distant, 1905) and of the Chlorocystini (sensu stricto) and its presumed sister group (the Prasiini) and an outgroup (the genus *Muda* Distant, 1897). In an attempt to rule out recent dispersal events, the previously established areas of origin of the genera are substituted for the genus names in the cladograms of the two groups, and treated as areas of endemism for these genera. The area cladograms thus obtained are compared with the palaeogeographical data discussed in the first chapter. Area relationships as indicated by the phylogeny and biogeography of the two groups of cicadas suggest several possible palaeogeographical reconstructions. These reconstructions are more detailed than the one based on the geological data alone. Moreover, the biological data sometimes conflict with the geological data.

Although knowledge of the geotectonic history is essential for understanding and explaining the biogeographic patterns, biogeographic data in their turn can supply additional information for reconstructing the geotectonic history.

Palaeogeographic history of Sulawesi, Maluku, New Guinea, and the western Pacific

The geological province of New Guinea is in terms of palaeogeography considered as one of the most complex areas of the world. Its present geography is the result of the interaction of no less than four major tectonic plates, numerous microcontinents and several island arc systems. New Guinea lies at the junction of three converging plates: the Eurasian plate, the Australian plate, and the Pacific plate. The collision of the Indian subcontinent (initially a part of the Indian–Australian plate, but at present presumably a separate plate) with Eurasia, however, had such effects on southeast Asia that it also indirectly affected the shaping of the New Guinean area. It is no wonder then that geologists have not yet reached a consensus on a detailed palaeogeographic reconstruction of the area, although the modern literature tends to agree more and more on the main trends. The present chapter is an attempt to compile the points of view proposed by various geological study groups. As a biologist, the author does not feel competent to discuss and evaluate the geological evidence in corroboration of the various views. The aim of this chapter is to present a more or less coherent geotectonic history

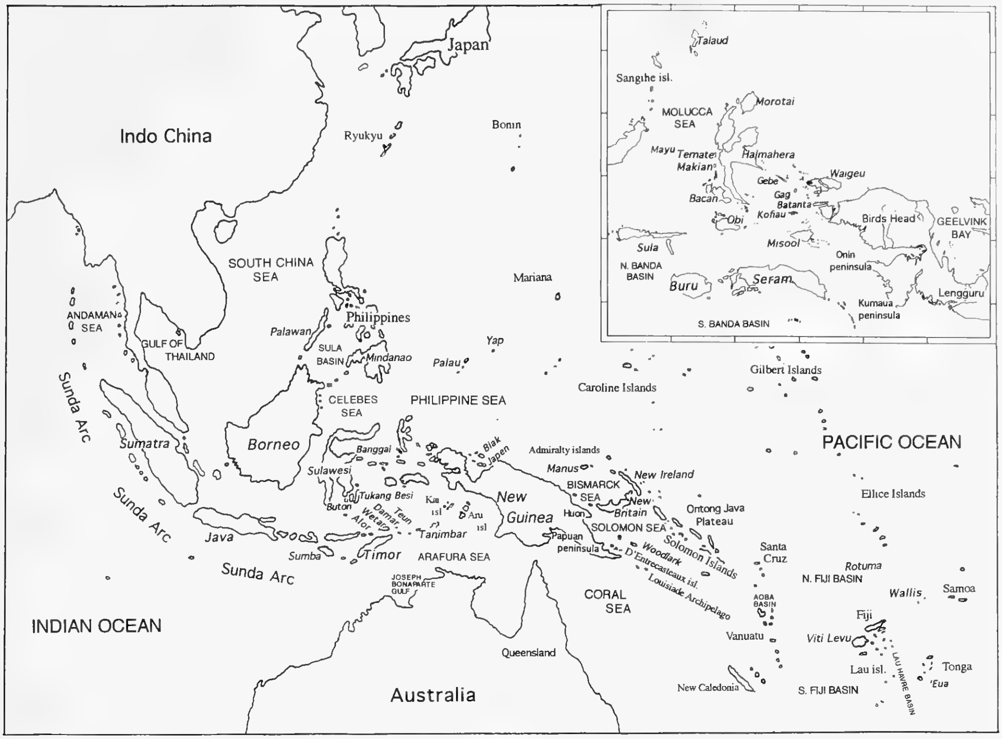


Fig. 1. Present-day map of southeast Asia and the west Pacific with some of the geographical names used in the text.

of the distribution area of the cicadas under discussion, which is to be compared to the biogeographic patterns found.

In order to understand the mechanisms leading to the formation of New Guinea and the west Pacific island chains, we have to consider the break-up of the southern supercontinent Gondwana. Many of the geographical names used in the text are compiled in a present-day map of the area discussed (fig. 1), names of palaeogeological entities are given in the various palaeogeographic reconstructions provided.

Rifting of Gondwana

Until about 160 million years ago (Mya) the southern continents (South America, Africa, India, Australia, and Antarctica) were joined, forming the supercontinent Gondwana. This continent was largely separated from the likewise joined northern continents, or Laurasia, by the Tethys Sea (fig. 2). By that time (160 Mya), or according to Dietz & Holden (1970) as early as 180 Mya, Gondwana started rifting apart. First Africa and South America were separated from the eastward moving India – Australia – Antarctica (fig. 3). Soon afterwards, if not simultaneously (Dietz & Holden 1970), India rifted from Antarctica and from about 70 to 50 Mya India moved northward with an average velocity of 150-200 mm a year (fig. 4) (Nishimura & Suparka 1990; Daly et al. 1991; Veevers 1991). Presumably about 95 Mya Australia and Antarctica became separated (Audley-Charles 1987; Daly et al. 1991), while Australia continued to move mainly eastward.

This major rifting of Gondwana seems to have been preceded and accompanied by sequences of rifting of smaller parts, or microcontinents, all along its northern margins. Parts of Turkey, Iran, Tibet, Malaya, Borneo, and Indo-China all rifted from the northern margins of India and Australia. These microcontinents preceded the continents in their northward course, sweeping in waves of 'island arcs' across the Tethys Sea (Audley-Charles 1987; Hutchison 1989; Burrett et al. 1991). The island of Sumatra is supposed to have rifted from Gondwana in the Middle Jurassic and might originate from the continental part of New Guinea, that is the northern part of the Australian plate (Audley-Charles 1987), while 'Java is constructed by post Jurassic subduction-related processes' (Hamilton 1979; 1986). The exact ori-

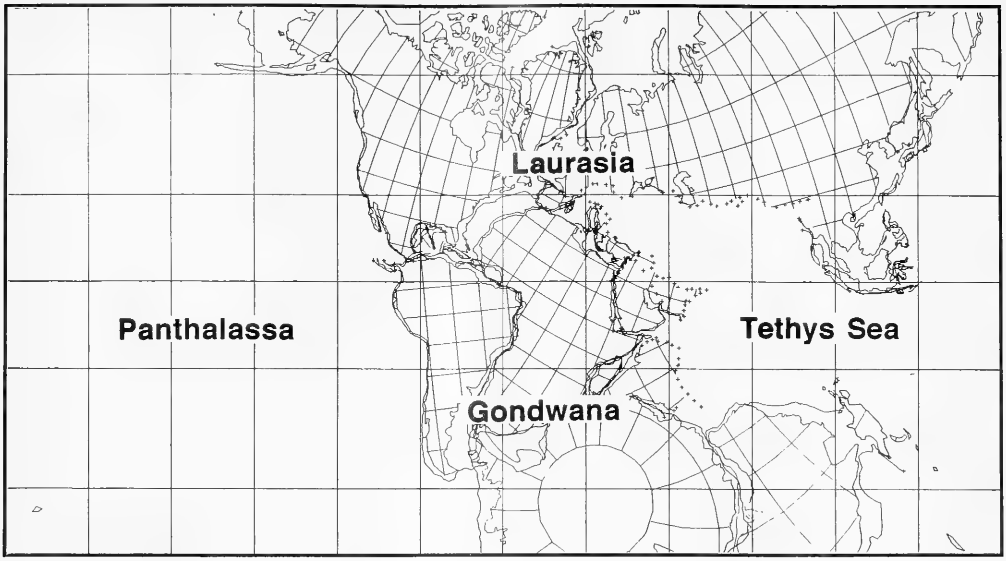


Fig. 2. Palaeogeographic reconstruction of 160 My ago, showing the break-up of Pangea into Laurasia and Gondwana by the Tethys sea. From Smith & Briden (1977).

gin of Sumatra, however, is poorly constrained from a longitudinal position and, as Pigram stated (pers. comm.) just were it originated is anyone's guess. During these rifting processes, the original Tethys Sea plate was consumed by subduction (the process in which one of two converging tectonic plates is forced to dip under the other) under Eurasia and replaced by the newly spreaded sea floor that caused all the aforementioned microcontinents to rift. The original Tethys was subsequently replaced by a Tethys II (or

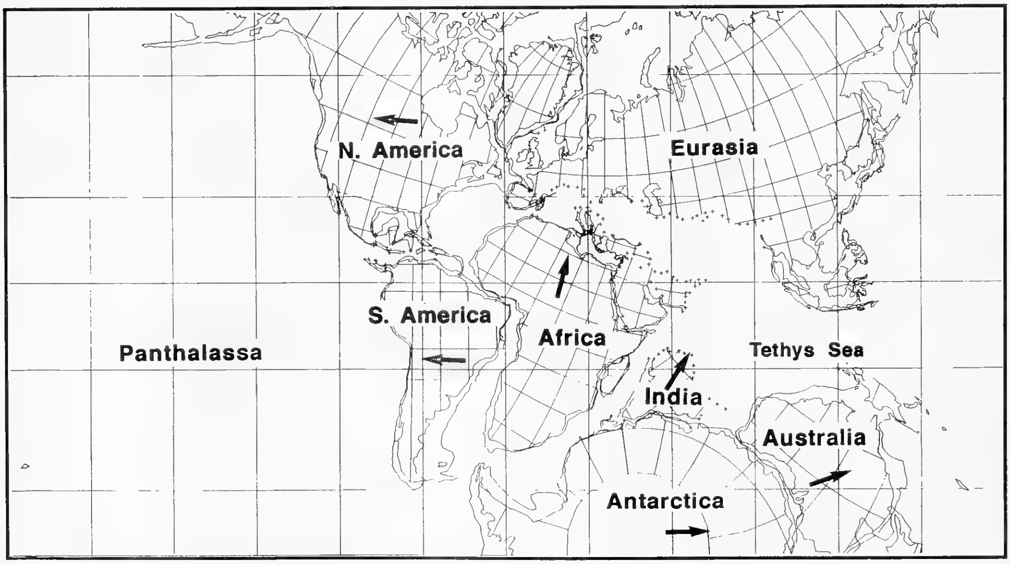


Fig. 3. Palaeogeographic reconstruction of 120 My ago, showing the break-up Gondwana (arrows indicating the direction of movement of the major Gondwana fragments). From Smith & Briden (1977).

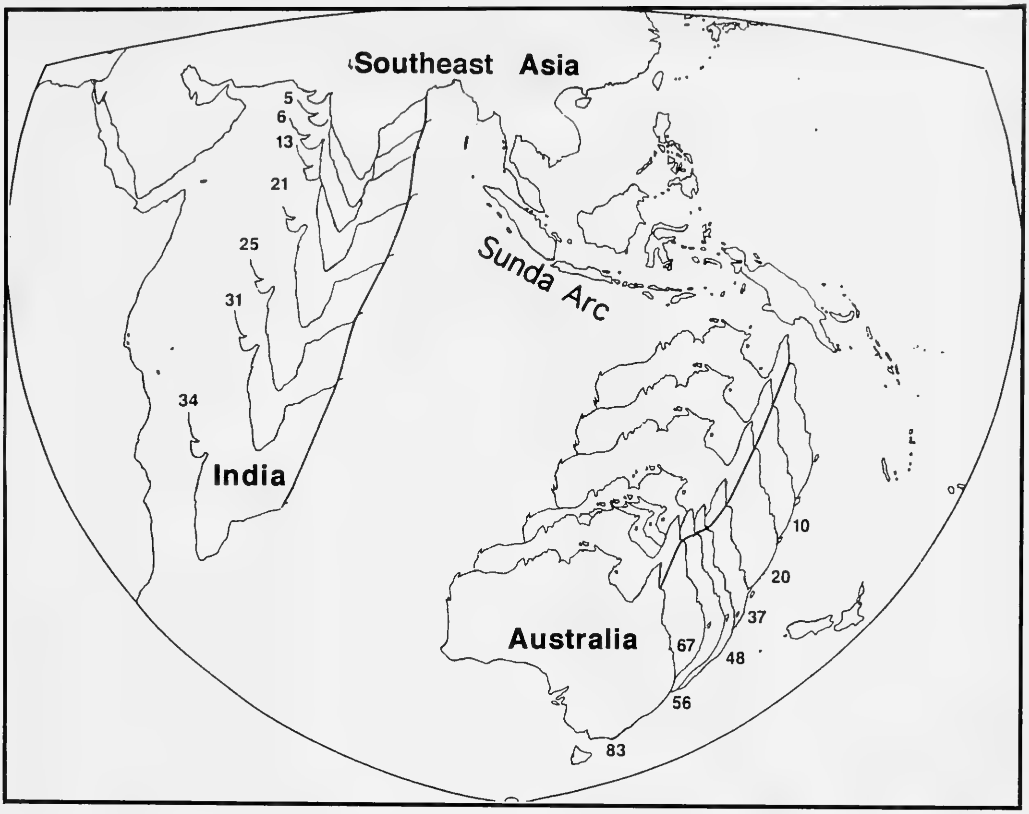


Fig. 4. Relative plate motions of India and Australia with respect to a fixed Eurasia (India positions in Chrons, Australia positions in My). From Daly et al. (1991).

neo-Tethys) and a Tethys III (or the proto Indian ocean) in the west and by the proto-Pacific ocean in the east (cf. fig 5). According to Pigram & Panggabean (1984) rifting along the eastern margins of Australia started as early as 230 Mya and propagated in a southwestern direction. This timing is consistent with the opening of the proto-Pacific Ocean, as suggested by Nur & Ben Avraham (1977). Pigram & Panggabean state that by the end of the Jurassic (approximately 160 Mya) the northern margin of Australia faced a newly formed ocean, which probably linked the proto-Indian Ocean (the Tethys iii of Audley-Charles 1987) to the proto-Pacific Ocean. These three new oceans were separated from the older oceans of neo-Tethys and Panthalassa (the ancestral ocean that surrounded the former single supercontinent Pangea) by a screen of continents and/or microcontinents, the chequered blocks in fig. 6.

This screen of continents and/or microcontinents is probably identical to the lost Pacifica continent of Nur & Ben Avraham (1977), which these authors consider to have been rifted off Gondwana, between 225 and 180 Mya. In their scenario, continued spreading in the proto-Pacific Ocean caused fragmentation of what is considered to have been a single land mass to the northeast of Australia, which they called Pacifica, into four major groups of continental fragments. These fragments were presumably carried along toward subduction zones and finally collided with the continental margins bordering the Pacific, thus forming the circum-Pacific Cordillera. Fragments of this Pacifica continent are supposed to have ended up in Alaska and eastern Siberia, North America, and South America, but the whole concept of a Pacifica continent has fallen out of favour and especially the idea of fragments of Pacifica in northern America and Asia is being questioned (Pigram pers. comm.). In addition the submerged platforms of Ontong-Java and Manihiki in the southwest Pacific were considered to be possible fragments of this lost Pacifica; these fragments show a remarkable conformity with continental crust (Nur & Ben Avraham

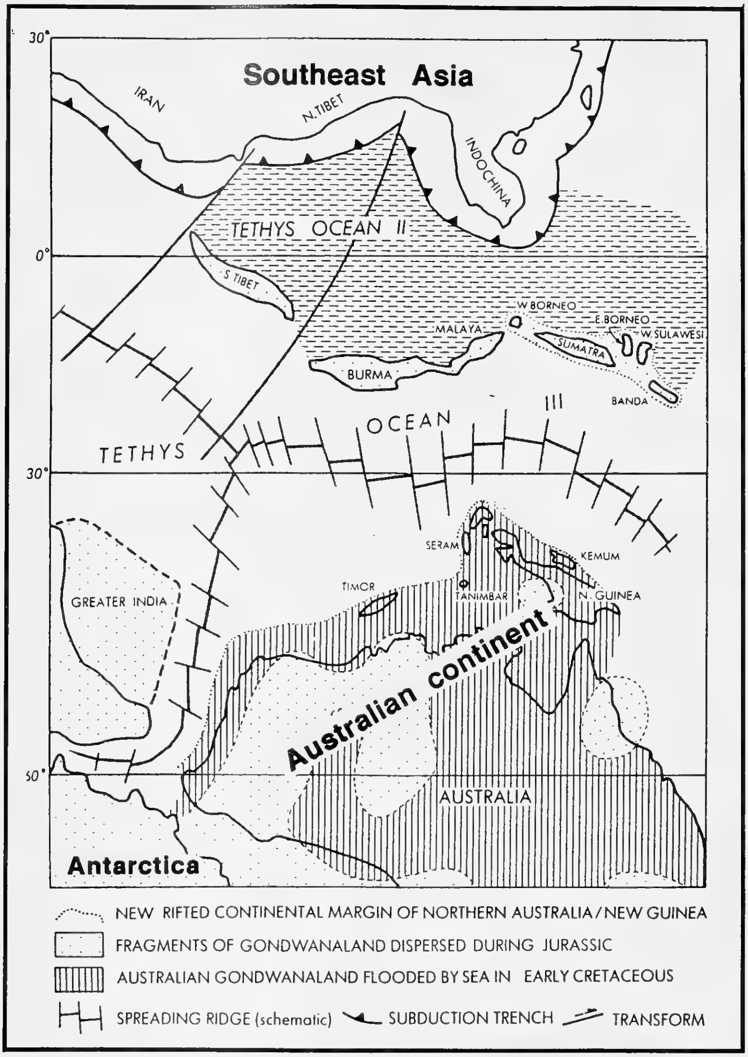


Fig. 5. The rifting of micro-continents from Gondwana by a successive Tethys II and Tethys III. From Audley-Charles (1987).

1981). Recent drilling showed that the Ontong-Java plateau consists of large buildups of basaltic volcanics, such platforms are now referred to as Large Igneous Provinces (Coffin & Eldholm 1993). The break-up of Pacifica is shown in four stages in fig. 7; for a complete list of presumed lost Pacifica remnants is referred to Nur & Ben Avraham (1981).

Some fragments that rifted from the more western parts of the northern margin of Gondwana reached subduction zones at the southern margin of Eurasia and became squashed between Eurasia and India when, about 50 Mya, India collided with the Eurasian continent (Nishimura & Suparka 1990; Rangin et al. 1990a; 1990b; Daly et al. 1991; Veevers 1991). Such parts, like the Kohistan arc, are now incorporated in the Himalaya mountains.

The collision between India and Eurasia had an enormous impact on the further development of New Guinea and adjacent areas by triggering a train of events. The force of the collision caused an indentation of the former southern margin of Eurasia, as a result of which Indo-China and Sumatra started to rotate clockwise to the south (Hamilton 1979; 1986). This rotation forced the opening of the Gulf of Thailand Basin and the Andaman Sea. Somewhat later, between 32 and 17 Mya, the South China Sea

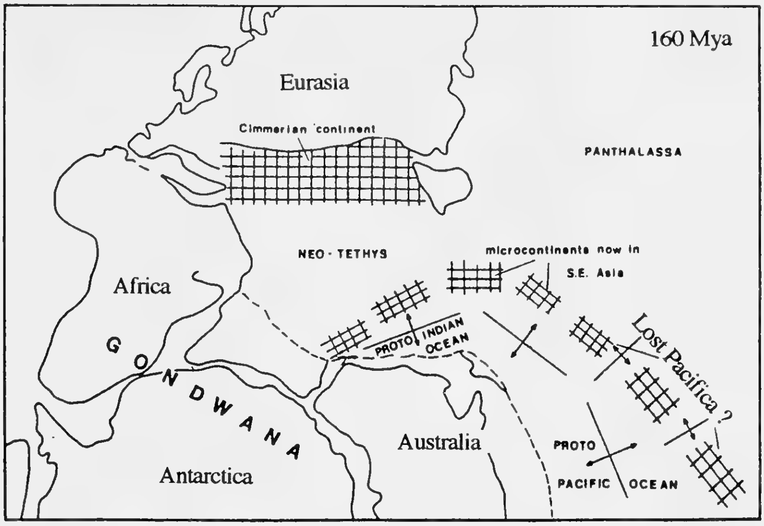


Fig. 6. The screen of continents and/or microcontinents (chequered blocks) that separated (160 My ago) the proto-Indian- and proto-Pacific oceans from the Neo-Tethys and Panthalassa. From Pigram & Panggabean (1984).

opened, which again was accompanied by the rifting and southward migration of Reed Bank, Macklesfield Bank, and north Palawan from the Chinese coast. Reed Bank and Palawan collided with Borneo at about 17 Mya (Lee & McCabe 1986; Daly et al. 1991). Because of this collision a part of oceanic crust became isolated and now forms the Celebes Sea. Probably induced by all these changes in southeast Asia, the Pacific plate changed its course, from initially NNW to almost westward, at about 42-43 Mya (Daly et al. 1991). This sub-perpendicular change of direction can be easily read from the angle between the Emperor Seamount chain and the Hawaii chain; these chains result from one single volcanic 'hot spot'. The volcanos evolved at the same, stationary, mantle location and were carried away on the tectonic plate, which slides over that 'spot', so leaving a trace reflecting the plate motion, with the oldest volcano farthest removed from the 'hot spot' or the place of origin. This change in plate motion, as part of a global plate readjustment, caused a fracture in the Pacific plate at about the same time (42 Mya) and, as a result, the Philippine plate was separated (Nishimura & Suparka 1990). This, more or less triangle-shaped, Philippine plate possibly moved northward until about 3 Mya, but then started rotating clockwise around a rotation pole near its northern edge (see also Hall & Nichols 1990; Daly et al. 1991), and is now being subducted at the Philippine Trench. Along the western margin of this plate, eastward subduction gave rise to volcanic islands that now form part of the Philippines and West (error? on the accompanying maps of that publication northren and eastern Sulawesi are indicated) Sulawesi (Daly et al. 1991). Lee & McCabe (1986) and Hamilton (1986) consider the latter (= west Sulawesi) to have rifted from eastern Borneo.

Development of an island arc system

The Australian continent, comprising Australia, the Arafura Sea, and southern New Guinea (see fig. 9), had changed its course from eastward to northward even before the collision (50 Mya) between India and Eurasia (fig. 4). This change of direction was part of the above mentioned global plate readjustment and was accompanied by the opening of the Tasman Sea (82-60 Mya), which separated Australia from Antarctica (Daly et al. 1991; Honza 1991). It might have caused an episode of rapid sea floor spreading in the Tasman Sea, which occurred coincidently with the onset of the collision between India and Eurasia (Nishimura & Suparka 1990). As a result of these changes and the changes in movement of the Pacific plate from northward to westward, Australia rapidly advanced on the Philippine and Pacific plates and the older and heavier Tethys Sea floor to the north of Australia was forced to subduct at the western and southern margins of the Philippine – Pacific plates. The volcanism accompanying this subduction gave rise to an oceanic island arc on the southern and western edges of these two oceanic plates. This Indo-Melanesian arc formed part of a much larger Tertiary island arc complex, that extended all along the western margins of the Pacific ocean. A compilation of these Pacific island arc systems is presented in fig. 8. The Indo-Melanesian arc was possibly continuous with the Bonin, Mariana, Yap, and Palau arcs (Honza 1991).

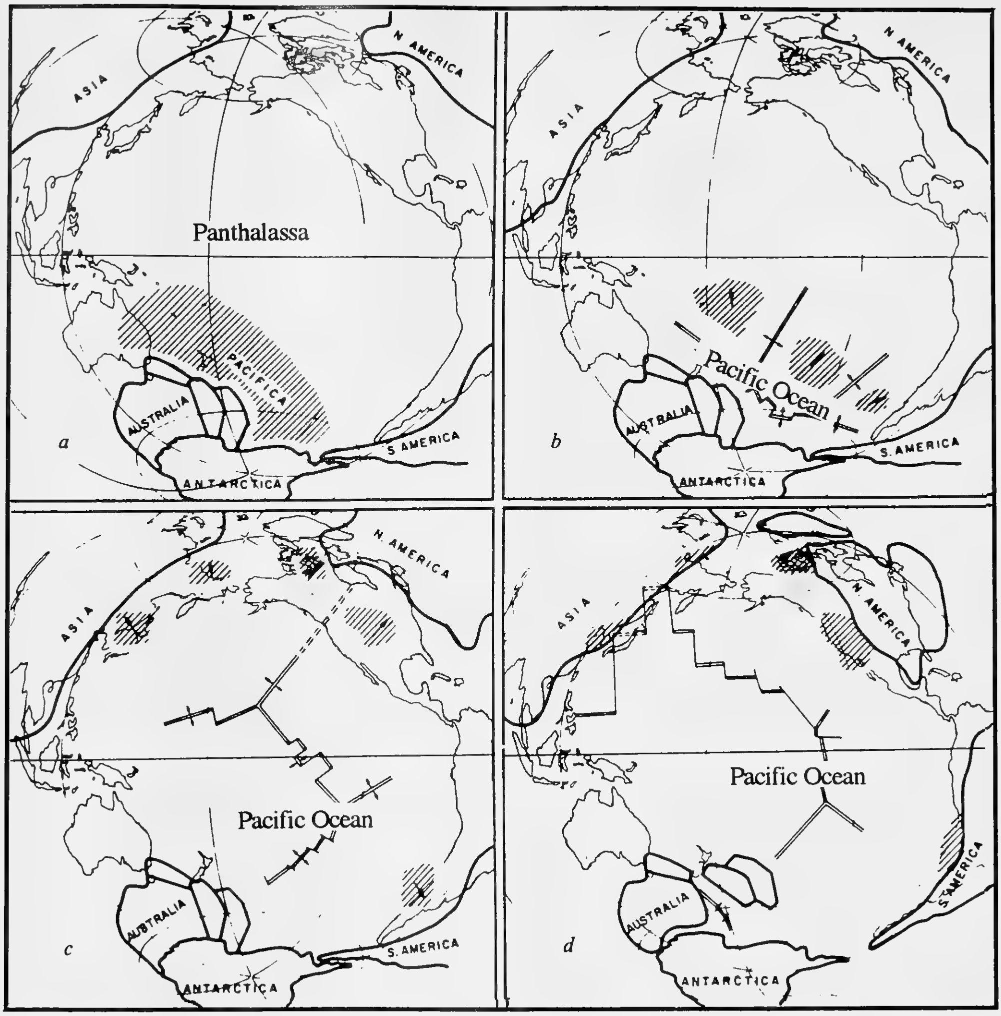


Fig. 7. Schematic model of the break-up of the Pacifica continent and the destination of its fragments in the circum Pacific cordillera. Possible ages of the various palaeogeographic reconstructions: a. 225 Mya, b. 180 Mya, c. 135 Mya, d. 65 Mya. From Nur & Ben Avraham (1977).

Alternatively, it may have been, or may also have been, connected to the earlier Daito arc and the Ryukyu Islands. Honza (1991) states that 'the Daito arc most likely faced southward as a western trace of the North New Guinea arc', which formed a part of what was called above the Indo-Melanesian arc. The Indo-Melanesian part of this large Pacific arc system started to develop at about 40 Mya (Hamilton 1979; Rangin et al. 1990a; 1990b; Daly et al. 1991). The arc developed most rapidly in the west where the Australian and Pacific plates were advancing at almost right angles and subduction of the intermediate Tethys Sea floor was maximal. Its development gradually slowed down to the east where the advancement between Tethys and Pacific was oblique and thus less material was subducted per time span. Land masses that represent the present-day remnants of this Indo-Melanesian island arc are, in order from west to east: the central parts of the Philippines, parts of northwestern and eastern Sulawesi, the northern parts of the central mountain ranges of New Guinea, the greater part of northern and eastern New Guinea, and the Bismarck Archipelago. Explicit statements about the origin of the various parts of Sulawesi are rare in the literature,

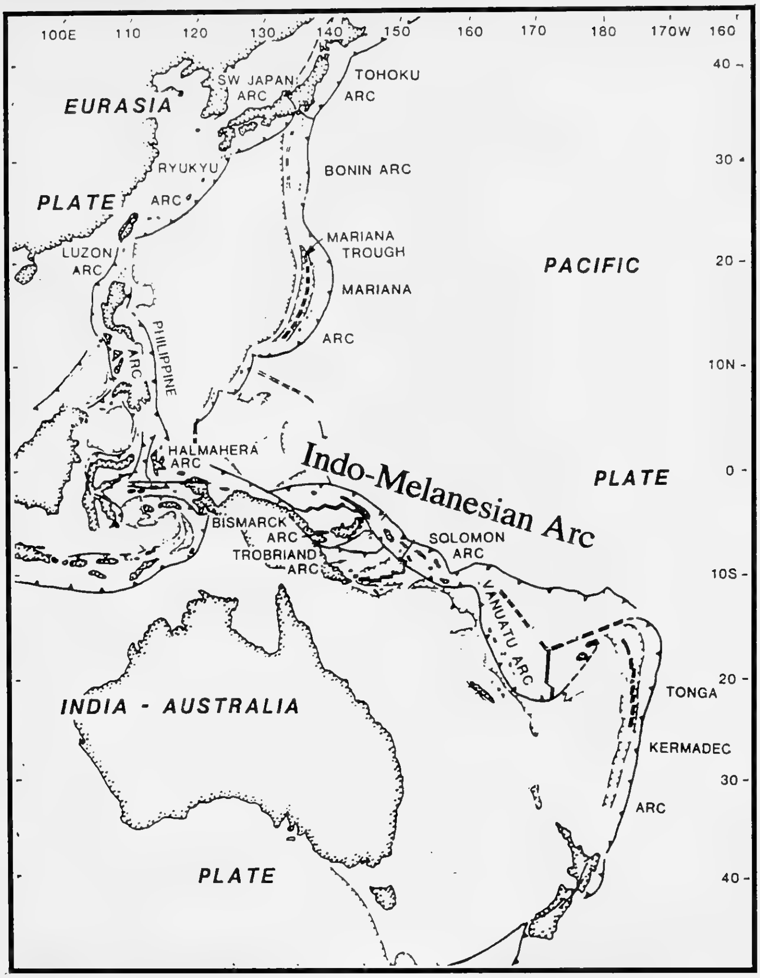


Fig. 8. The Tertiary island arc systems along the southern and western margins of the Pacific plate in their present-day setting. From Honza (1991).

their possible partial island arc origin was inferred from figures given by Daly et al. (1991) (see figs. 9-10). This island arc seemingly continues to the Solomon Islands, Vanuatu, Fiji and Tonga, but these latter island groups appear to have a fundamentally different origin (see below). Only the northeastern parts of the Solomons might be a continuation of the arc discussed here. The Indo-Melanesian part of the island arc system is known by several names (e.g., Outer Melanesian Arc, or Sepik Arc, or Vitiaz Arc), but the various authors usually confine any of these names to certain parts of the arc system only. The Outer Melanesian Arc (OMA), as it is generally termed in biogeographic studies (Duffels 1986; Holloway 1979), has been of paramount importance for the development of the Melanesian biota since it served as a route of dispersal for southeast Asian, and possibly Australian, animals and plants invading Melanesia and Micronesia. Furthermore, as will be discussed in the next chapter, the ensuing fragmentation of the arc may have caused vicariant speciation events.

The continuing westward movement of the Pacific plate carried the OMA towards southeast Asia and somewhere between 40 and 30 Mya the most western part of the arc collided with the Asian continent. This collision is supposed to have enabled the Asiatic biota to migrate eastward into the island arc. It is not clear yet, where the first contact between the OMA and southeast Asia took place, but this possibly happened either in the Philippine region or just south of the

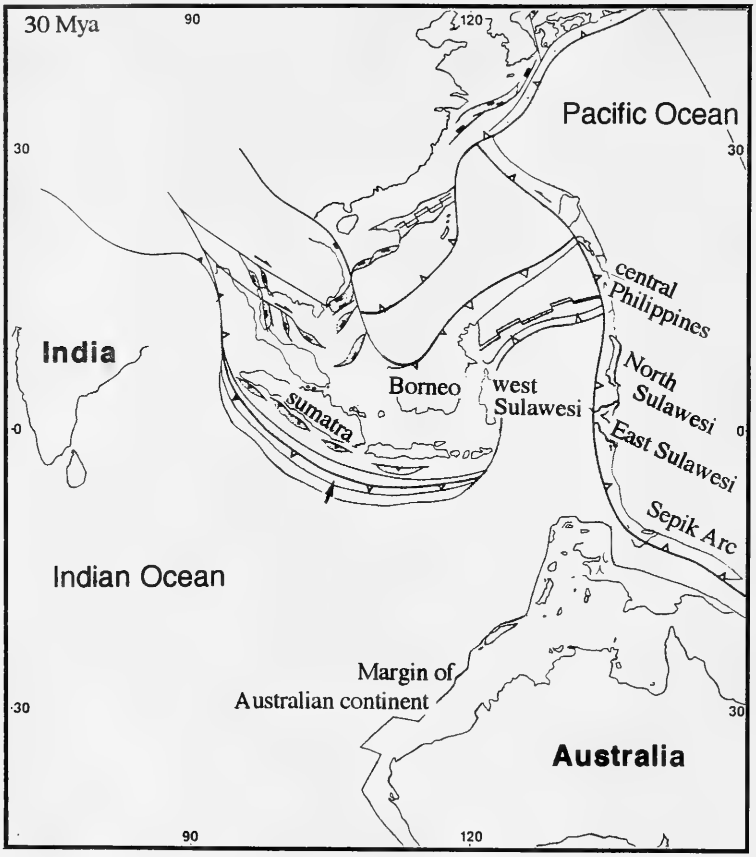


Fig. 9. Palaeogeographic reconstruction of 30 My ago, showing the approaching collision between an island arc containing fragments of the central Philippines and northern and east Sulawesi with southeast Asia and Sunda land. From Daly et al. (1991).

Philippines, that is somewhere near Borneo. Alternatively, the first contact with Asia could have been along the Bonin Arc or the Daito Arc, and then through Japan (cf. fig. 8) (Honza 1991). As a result of its collision with Asia, and the continued movement of the Pacific plate, the island arc started breaking up just east of those parts that are now supposed to form northwestern and eastern Sulawesi. The western part of the OMA, the central Philippine fragment and the Sulawesi fragments, started rotating clockwise, which led to a collision between the central Philippines and the continental western Philippines while northwestern and eastern Sulawesi swept past the northwestern edge of the Australian continent towards the Sunda Arc and Borneo (figs. 9-10) (Daly et al. 1991). The more eastern parts of the OMA, starting with a fragment known as the Sepik Arc (see below), continued their westward course and therefore obliquely advanced upon the northern craton of the continuously northward moving Australian continent (fig. 10).

The next decisive event in the formation of New Guinea occurred at about 30 Mya, when the original Tethys Sea was finally consumed by subduction and the Australian continent entered the subduction zone at the southern margins of the Philippine and Pacific plates (Pigram & Symonds 1991). This, as will presently be explained, resulted in a series of collisions with fragments of the OMA. However, the rifting of microcontinents from the northern margin of the Australian plate (= continental New Guinea) that began about 230 Mya, continued until after the genesis of the OMA. Some of these more recently rifted microcontinents preceded Australia in reaching the subduction zone of the former Tethys Sea and became incorporated in the OMA. Assuming that these microcontinents were not submerged, we must conclude that the Australian biota could have reached the OMA long before its various fragments collided with the Australian continent. The parts of the OMA that eventually accreted to New Guinea were thus already of composite geological origin. In fact, Pigram & Davies (1987) identified no less than 32 tectonostratigraphic terranes in the northern and eastern (i.e., the accreted) parts of New Guinea (fig. 16). They de-

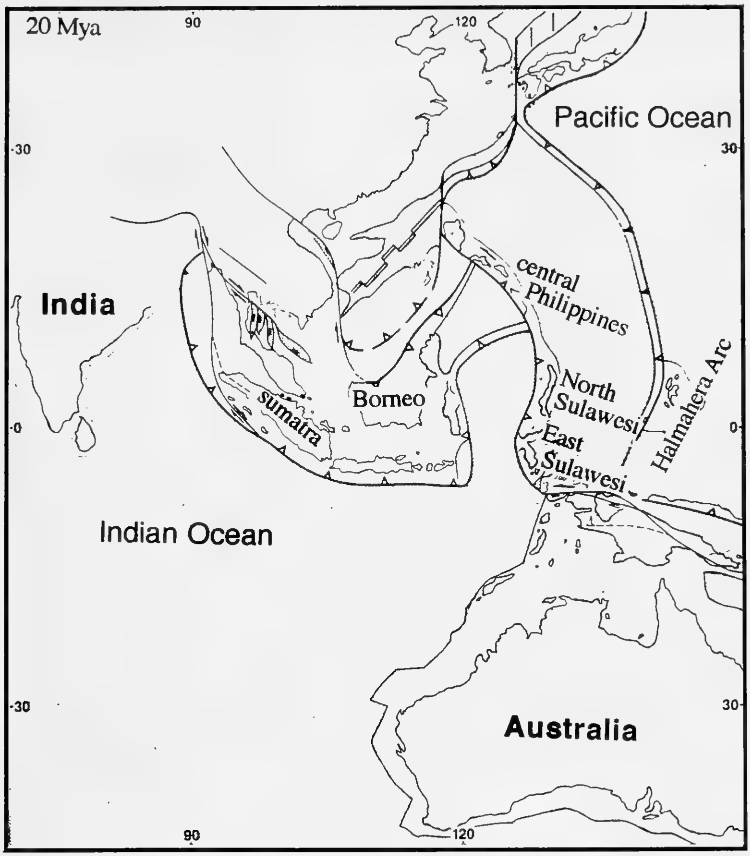


Fig. 10. Palaeogeographic reconstruction of 20 My ago, showing an island arc containing fragments of the central Philippines, northern and eastern Sulawesi, and central New Guinea (the Sepic Arc). The Sulawesi fragments approach western Sulawesi and Australia approaches the Sepic Arc. From Daly et al. (1991).

fine these terranes as 'internally homogenous geologic provinces, the stratigraphy, fauna, tectonic style, palaeomagnetic signature, and history of which contrasts with that of adjoining provinces [...] that lie outboard the craton margin'. Most of these terranes have oceanic (OMA) 'affinities', but in western New Guinea terranes with a continental 'affinity' (microcontinents rifted from Australia) dominate.

This illustrates the extreme complexity of the accretion history of New Guinea. The tectonic movements and the effects of the several collisions on the surrounding areas will from here onwards be discussed separately for the various areas, from west to east respectively and beginning with the Maluku-Banda Sea region.

Maluku and the Banda Sea

The Banda Sea presumably consists of two trapped parts of oceanic crust, the North and South Banda basins, that are separated by submerged continental fragments, the Banda ridges. The southern Banda Sea is a fragment of the Indian Ocean, the northern Banda Sea is a part of the Molucca Sea (Silver et al. 1985). Hamilton (1986), on the other hand, assumes that the South Banda basin resulted from 'spreading behind a rapidly migrating Banda Arc', and expanded to fill the concavity between New Guinea and Australia. At present these seas are surrounded by the islands of the Moluccas and of the Banda Arcs. Formerly, the Banda basins were continuous with the Argo–Abyssal plain, which is the sea area to the north of Australia, the Arafura Sea (Hartono 1990; Lee & McCabe 1986). According to Lee & McCabe (1986) the Banda, Celebes, and Sulu basins were continuous until the Tertiary, probably forming a northern extension of the eastern Indian Ocean. The islands that have separated these basins either arrived by middle or late Tertiary, or were formed in place as a result of Neogene subduction. There is, however, much controversy about this timing.

As in western New Guinea, the terranes in the Moluccas are predominantly of continental (probably Australian) origin (fig. 11). Many of these continental fragments (e.g., Buton and the Tukang Besi plat-

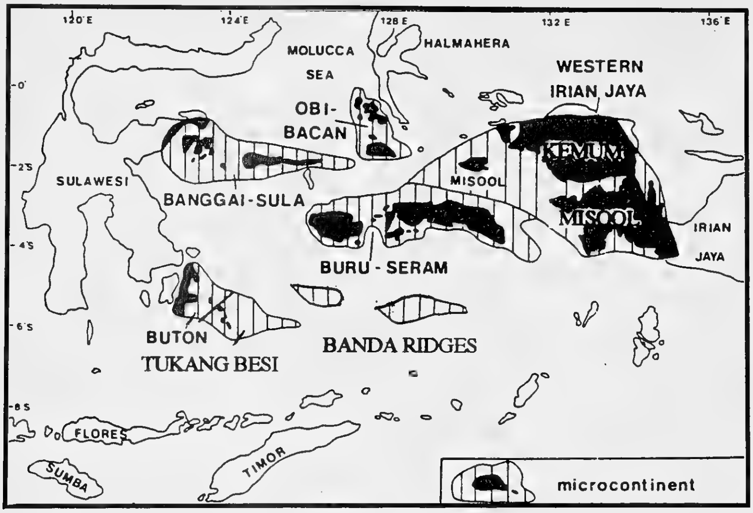


Fig. 11. Microcontinents in the Birds Head and the Maluku area. Reconstructed after Pigram & Pangabean (1984) and Silver et al. (1985).

form; the Banda ridges, which are submerged terranes in the centre of the Banda Sea; Bacan and Obi; Sula, Banggai, and small parts of eastern Sulawesi) are supposed to be slivers that have become detached from the northern craton of the Australian continent, in other words: from the continental part of New Guinea. It is generally assumed, that these slivers were sliced off the Birds Head and carried westward along the Sorong fault (a fault zone across northern New Guinea), forced by the westward movement of the Philippine – Pacific plate (Hamilton 1979; 1986; Silver & Smith 1983; Silver et al. 1985; Pigram et al. 1985; Lee & McCabe 1986; Hartono 1990; Daly et al. 1991; Smith & Silver 1991). Katili (1989) uses the term 'bacon slicer' for this process. Silver et al. (1985) found similarities between the Banda ridges, the Kemum and Tamrau terranes of the Birds Head and the Ligu metamorphics on Misool island. However, Pigram & Panggabean (1984) conclude from stratigraphic comparison that many of these continental fragments (including the Birds Head) come from far more eastward. These authors suppose that Sula and Banggai, Buton, and Obi and Bacan all originate from as far east as present-day central Papua New Guinea and suggest that these fragments became detached in early Jurassic time (approximately 180-195 Mya). Later Pigram & Symonds (1991) realized, that if these riftings had occurred that early in time, the fragments in question would by now have reached southeast Asia. They hypothesized rather that the riftings were related to the opening of the Coral Sea (50-60 Mya) and to an oblique spreading centre that must have existed along the northern edge of the Australian craton. They state that, since spreading in the Coral Sea was of short duration and ended in middle Eocene, these microcontinents could not have been far removed from the Australian craton before they were forced to move westward by the approaching oceanic island arc fragments. Pigram et al. (1985) locate the origin of the Sula platform in Papua New Guinea, between 141° and 145° E., basing this hypothesis on the almost identical pre-Cretaceous stratigraphic sequences found for these two areas. Daly et al. (1991) suppose that these continental slivers or 'tectonic flakes' (as they call them) were chiselled off the northern craton of Australia, and pushed westward, by the obliquely colliding Sepik Arc, which is the first part of the OMA that became accreted to the Australian continent by 20 Mya. This timing seems in agreement with the timing of the collision between the Buton/Tukang Besi fragment and Sulawesi in middle Miocene (± 17 Mya), and between the Sula/Banggai fragment and Sulawesi in late Miocene (8-9 Mya) (Smith & Silver 1991). In a palaeogeographic computer reconstruction of the middle to late Triassic Struckmeyer et al. (1993) placed the Moluccan and Birds Head (see below) microcontinents all together as a single continental mass bordering the present-day northern and northeastern margin of the Australian plate, similar to the 'lost Pacifica' block of fig 7a, but much smaller.

Silver et al. (1985) proposed that the first fragments that became detached from the Australian plate and were pushed westward can be found in the southern parts of the Banda Sea. More recently detached fragments are presumed to have ended up north of earlier fragments since, due to the continuous northward movement of the Australian conti-

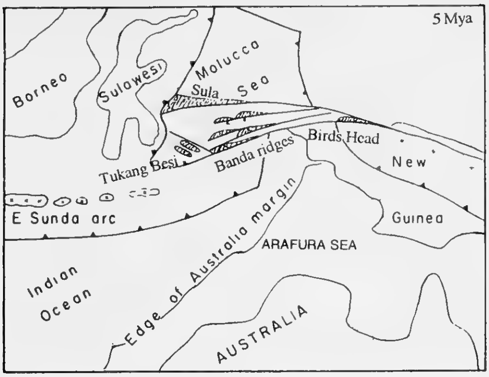


Fig. 12. Reconstruction of the Banda Sea region at 5 My ago, showing the order in which microcontinents (shaded blocks) are supposed to have invaded the area. Heavy lines = faults (teeths on upper plate of subduction zones). From Silver et al. (1985).

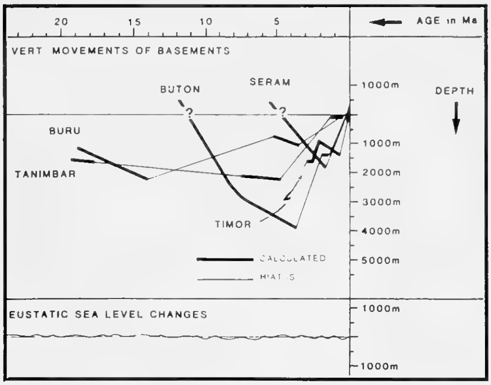


Fig. 13. Graphs showing the sea level changes and the vertical movements of Buru, Buton, Seram, Tanimbar, and Timor over the last 20 My. From Fortuin & De Smet (1991).

nent, the northern craton had reached a position farther north when they became detached. In this way, Australia overtook its own rifted fragments (see also Silver et al. 1985; Silver & Smith 1983; Smith & Silver 1991). The following order in the rifting of these Moluccan microcontinents is suggested 1) the Banda ridges, 2) parts of Buru and Seram, 3) Buton and Tukang Besi, 4) Sula and Banggai (fig. 12). Silver et al. (1985) do not discuss the origin and nature of Bacan and Obi as a possible Australian microcontinent. Smith & Silver (1991) propose an alternative, in which Tukang Besi and Sula formed a single microcontinent that fragmented during its oblique collision with southeastern Sulawesi (or with Buton (Fortuin et al. 1990)) in middle Miocene, after which the Sula platform slid farther northward until its late Miocene collision with central eastern Sulawesi. The collision between Sula and Sulawesi is held responsible for the clockwise rotation of the Sulawesi north arm of about 90° (Hamilton 1979), though part of this rotation might have been caused by 'earlier events' (Silver et al. 1985).

The origin of Buru and Seram, though certainly Australian, is still subject to controversy. Hamilton (1979) suggests that these islands rifted in late Cenozoic time from present-day northwestern Irian Jaya (see also Lee & McCabe 1986). Pigram and Panggabean (1984), however, suppose that they rifted in Jurassic time as a single block from the Australian continent, somewhere east of Joseph Bonaparte Gulf, and possibly (based on similarities with the island of Misool) from as far east as central Papua New Guinea (see also Struckmeyer et al. 1993). Several other authors again suggest that the Buru – Seram microcontinent originates from northwestern Australia, and that it rotated anticlockwise for about 90° (starting at about 10 Mya) to its present position (Silver & Smith 1983; De Smet 1989; Hartono 1990; Daly et al. 1991). De Smet (1989) has construed a mechanical model, showing that this rotation could have been accomplished with a mininum of deformation and sea floor spreading.

The outer Banda Arc islands emerged as a result of uplift when, about 3 Mya, the northern margin of the Australian continent entered the subduction complex bordering the Banda Sea (Hartono 1990; Fortuin & De Smet 1991). Both Sumba and Timor are generally regarded as being of (Australian) continental origin, while continental 'basement' is also assumed under Tanimbar (Hartono 1990). These islands are supposed to have rifted from Australia in Jurassic time (Hartono 1990). This leaves only the volcanic islands of the Inner Banda Arc, such as Alor, Wetar, Damar, and Teun, as islands that were actually formed in place. These islands are the result of subduction of the Banda Sea (Lee & McCabe 1986) and were formed since 12 Mya, though the maximum age of the subduction is put down to 82 My (Hartono 1990). De Smet (1989) supposes that the Kai islands were formed in late Miocene (8-9 Mya) and Tanimbar in the Pliocene (2-7 Mya) as a result of a subduction under the Banda Sea.

However, all the movements of these various terranes have probably no, or very limited, significance for the biogeography of Indo-Melanesian cicadas since most of the islands only very recently emerged. Fortuin & De Smet (1991) discuss the vertical movements of Buton, Buru, Kai, Seram, Tanimbar, and Timor. These movements over the past 20 My are characterized by long periods of subsidence alternated

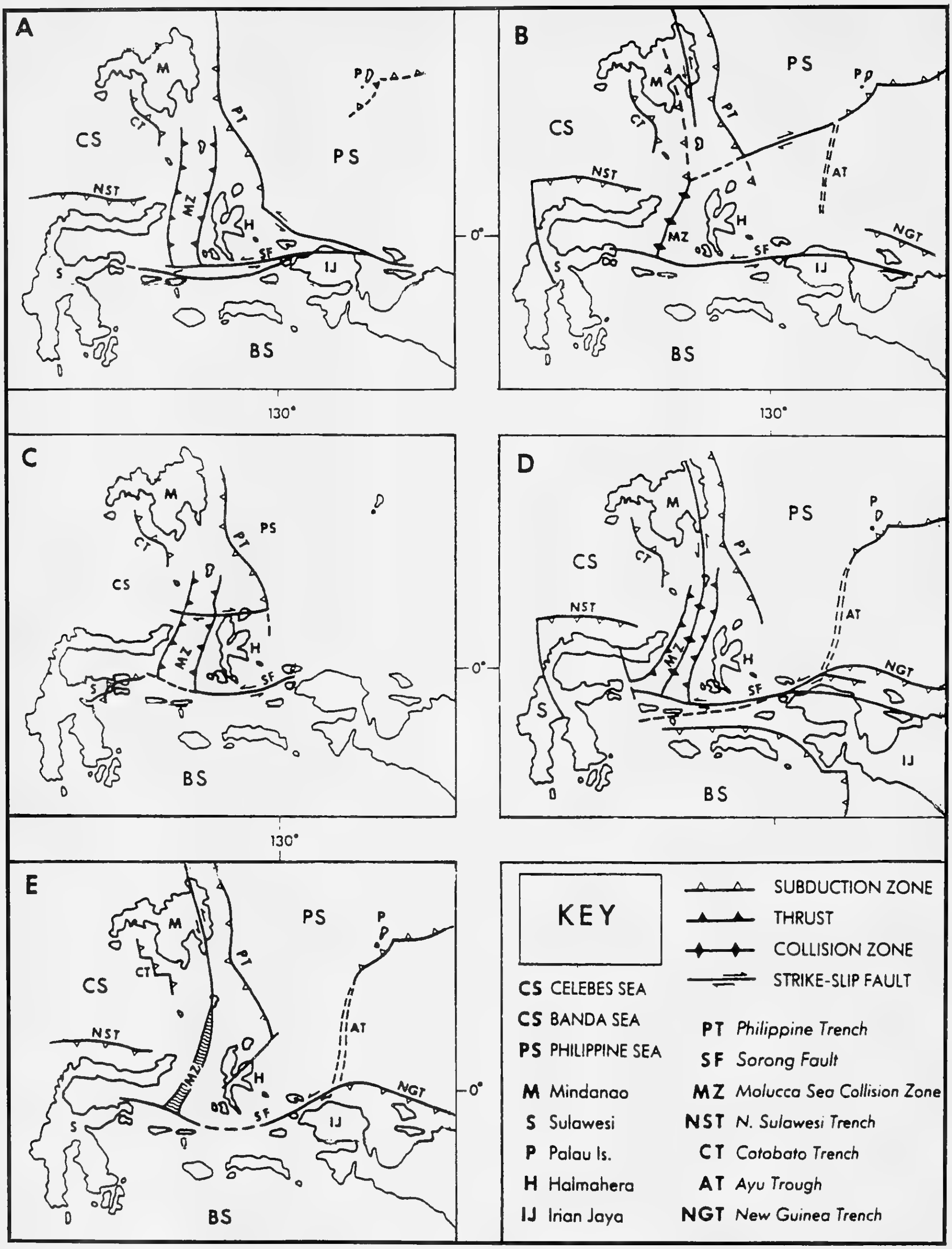


Fig. 14. Alternative tectonic models concerning the southward propagation of the Philippine Trench in relation to Halmahera. The Philippine Trench either continuing east of Halmahera (A), or west of Halmahera (B, C), or ending near Halmahera (D), or continuing through Halmahera (E). From Nichols et al. (1989).

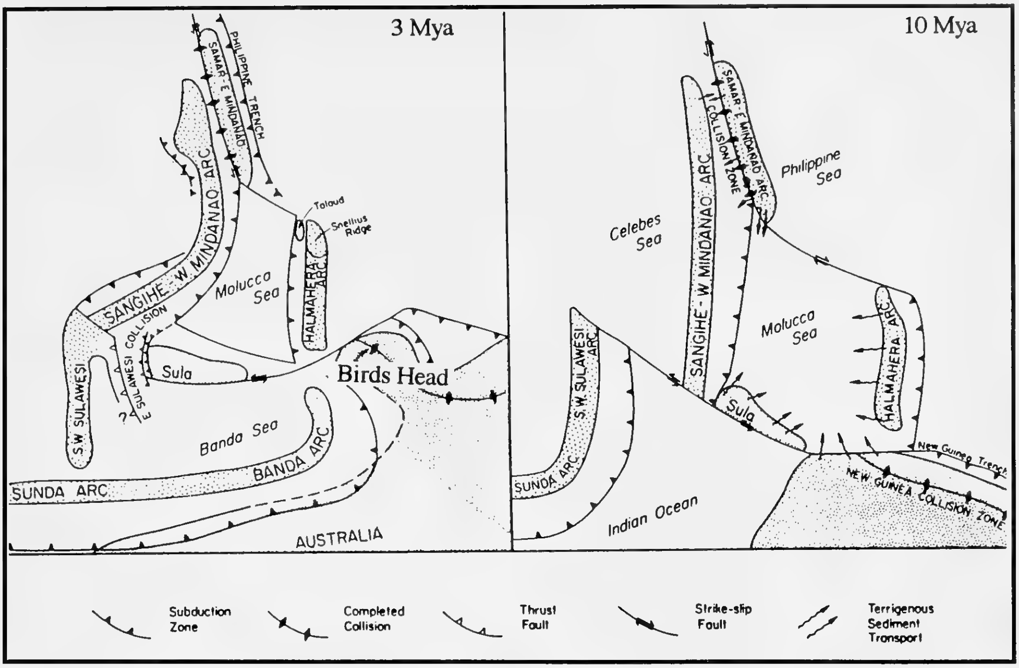


Fig. 15. Schematic tectonic reconstruction of the arc-arc collisions in the Molucca Sea area. From Moore & Silver (1982).

by short periods of uplift (fig. 13). The two final pulses of uplift in Timor, of 2.2-2.0 and 0.2 Mya, are interpreted as the beginning of the introduction of respectively the main slope area and the shelf area of the Australian continental margin into the Banda arc subduction zone (De Smet et al. 1990), while the final uplift and emergence of Buton is related to its collision with the Tukang Besi platform (Fortuin et al. 1990). For other islands the most important, final, uplift started no longer than about 5 Mya, and emergence of all these islands occurred less than 1 Mya. Only Buton (11 Mya) and Seram (5 Mya) might have been emergent during an earlier period (Fortuin & De Smet 1991).

Only a part of the northern Moluccas, the Halmahera arc, is associated with or directly derived from the OMA. Honza (1991) proposed that the Halmahera arc was possibly part of a larger arc complex, including the Mariana, Yap, and Palau Arcs, that was connected to parts of what now forms New Guinea. He states that 'the Eocene basement in the eastern belt of New Guinea is possibly the same sequence as is seen in the Yap and Mariana Arcs' and that the 'older basement in the southwestern portion of the Halmahera Arc, which is considered to be the same sequence as those in New Guinea, migrated westward along the left lateral Sorong Faults.' Hall & Nichols (1990) found a similarity in age and lithology between Halmahera, the East Mindanao – Samar fragment and the Daito Ridge province plateaus, although they presume that these terranes have not formed a continuous arc. However, the geology of the northern Moluccas is extremely complex and subject to much controversy. Eastern Halmahera presumably forms a continuous terrane with Gebe, Gag, and Waigeu Islands, and possibly also with the Tamrau Mountains of the northern Birds Head (Hall & Nichols 1990), while the island of Morotai is an eastern extension of the northwestern arm of Halmahera (Nichols et al. 1990). The controversy about the origin of the Halmahera terranes arises from the fact that no southward extension of the Philippine Trench can be traced in the Halmahera area. The Philippine Trench, which is a fault system to the east of Mindanao, seems to come to a dead end at the East Morotai Plateau, a submarine microcontinent to the east of Morotai island that might be another remnant of Nur & Ben Avraham's lost Pacifica. Hall & Nichols (1990) and Nichols et al. (1990) present a revision of the several ideas developed in attempts to link the Philippine Trench to the Sorong or other fault systems in the Molucca Sea collision zone (fig. 14) with the Philippine Trench as a southward propagating fault system, continuing either east of

Halmahera, or west of Halmahera, or through Halmahera. Halmahera is thus either completely or partly placed on the western edge of the Philippine sea plate, or placed on a separate plate. It is clear that Halmahera is moving westward, presumably forced by a spreading centre in the Ayu Trough (cf. figs. 14d, e) since early or middle Miocene (Honza 1991), and approaching the Sangihe Arc. The Molucca Sea dips westward under Sangihe and eastward under Halmahera (Moore & Silver 1982; Hamilton 1986; Hall & Nichols 1990; Nichols et al. 1990; Honza 1991). The volcanic arc of west Halmahera results from this subduction and so do some of the small islands west of Halmahera, (Mayu, Talaud, and Tifore), which represent emerged parts of 'compressed forearc sediment wedges, with slivers of Sangihe forearc basement' (Hall & Nichols 1990). Moore & Silver (1982) and Hamilton (1986) regard this future Halmahera – Sangihe collision as the southward propagation of the middle Tertiary collision that took place between central Mindanao and east Mindanao including the Samar block. Moore & Silver (1982) describe this collision as a southward scissoring between the Sangihe Arc (continuous with the west Mindanao Arc) and one of the following options: either 1) a long continuous Mindanao – Halmahera Arc, or 2) a double Mindanao – Talaud and a Halmahera Arc, or 3) a double Mindanao and a Talaud – Halmahera Arc, or 4) a series of small and unconnected arc segments (fig. 15). They prefer the third option. The Philippine fault (the north-south fault across Mindanao) is thus regarded as the northern, closed, continuation of the Molucca Sea. This would mean that the Molucca Sea plate has extended northward and was possibly originally part of the West Philippine Basin (Honza 1991). However, since there is no proof of subduction of the Molucca Sea to the north of Talaud island, Hall & Nichols (1990) conclude that the Halmahera – Sangihe collision is not a simple continuation of earlier collisions in Mindanao, but an effect of these very collisions. They think that the Moluccan Sea has continued north as the part of East Mindanao which lies between the Philippine Trench and the Philippine Fault. However this may be, it is generally agreed that Halmahera originates from a position far to the east of its present one. Moore & Silver (1982) and Rangin et al. (1990a, 1990b) presume that 10 Mya Halmahera lay approximately 800 km to the southeast of its present position. Daly et al. (1991) suppose that Halmahera originates from far to the east in the OMA, while Honza (1991) concludes that Halmahera has been part of, or was attached to, arc fragments which now form part of New Guinea.

Western New Guinea, the Birds Head peninsula

The greater part of the Birds Head of New Guinea is of continental (Australian) origin. Only the Waigeu, Arfak, and Tamrau terranes originate from the oceanic island arc systems (figs. 11, 16). The Waigeu terrane includes Waigeu Island, numerous small islands as Batanta, Gebe, Gag, and Kofiau, and

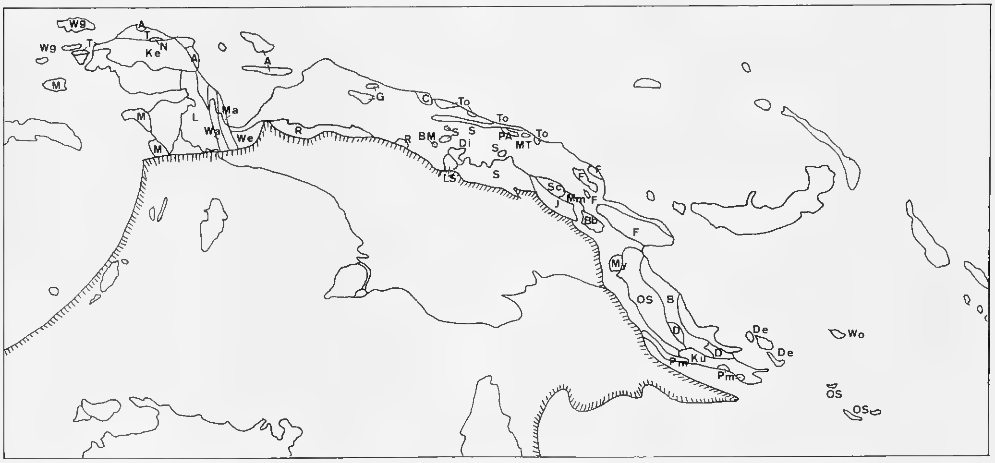


Fig. 16. The allochtonous terranes in New Guinea, which successively accreted to the northern craton of the Australian plate. Lettering: A = Arfak, B = Bowutu, Bb = Benabena, BM = Border Mountains, C= Cyclops, D = Dayman, De = D'Entrecasteaux, Di = Dimaie, F = Finisterre, G = Gauttier, J = Jimi, Ke = Kemum, Ku = Kutu, L = Lengguru, LS = landslip, M = Misool, Ma = Maransabadi, Mm = Marum, MT = Mount Turu, My = Menyamya, OS = Owen Stanley, PA = Prince Alexander, Pm = Port Moresby, R = Rouffaer, S = Sepik, Sc = Schrader, T = Tamrau, To = Torricelli, Wa = Wandammen, We = Weyland, Wg = Waigeu, Wo = Woodlark. From Pigram & Davies (1987), for a description of these terranes see that publication.

a small sliver of the Birds Head to the east of Sorong (Pigram & Davies 1987). This terrane is supposed to form a single block with Halmahera and, possibly, the Tamrau mountains (see above), although Pigram & Davies (1987) regard the latter as of continental origin. The Arfak terrane consists of the Arfak mountains in the northeastern Birds Head, the Tosem mountains of the northern Birds Head, Num and Japen Islands, and a part of Biak Island. The Arfak elements probably are part of the OMA system, and might be a western continuation of the terranes that form the northern mountain ranges of New Guinea (e.g., the Gauttier, Cyclops, and Torricelli terranes) (cf. fig. 16). The Arfak terrane is supposed to have accreted recently (2 Mya) to New Guinea (Pigram & Davies 1987). The main part and nucleus of the Birds Head, however, is of Australian origin. One has regarded it either as an integral part of the Australian craton or one has tried to explain its present position by rotation rather than accretion. Hamilton (1979) suggested that the Birds Head rotated clockwise northward in the Neogene, from a position near the west coast of Australia, but an anticlockwise rotation resulting from a presumed spreading centre in the Geelvink Bay has also been considered (Daly et al. 1991). None of these rotations, however, can explain the north-south directed mountain chains on Lengguru, the Birds Neck. The presence of these mountains can be explained, however, by supposing that a collision occurred between the Birds Head and Lengguru. Realising this, Pigram and Panggabean (1984) argued that the continental part of the Birds Head consists of two microcontinents (figs. 11, 16): the northern half of the Birds Head, of which the nucleus is formed by the continental Kemum terrane; and the southern half, formed by the Misool microcontinent. The latter includes Misool Island and the Onin and Kumaua peninsulas. On the basis of stratigraphic comparison, it was concluded that the Misool microcontinent rifted in late Lias (approximately 175

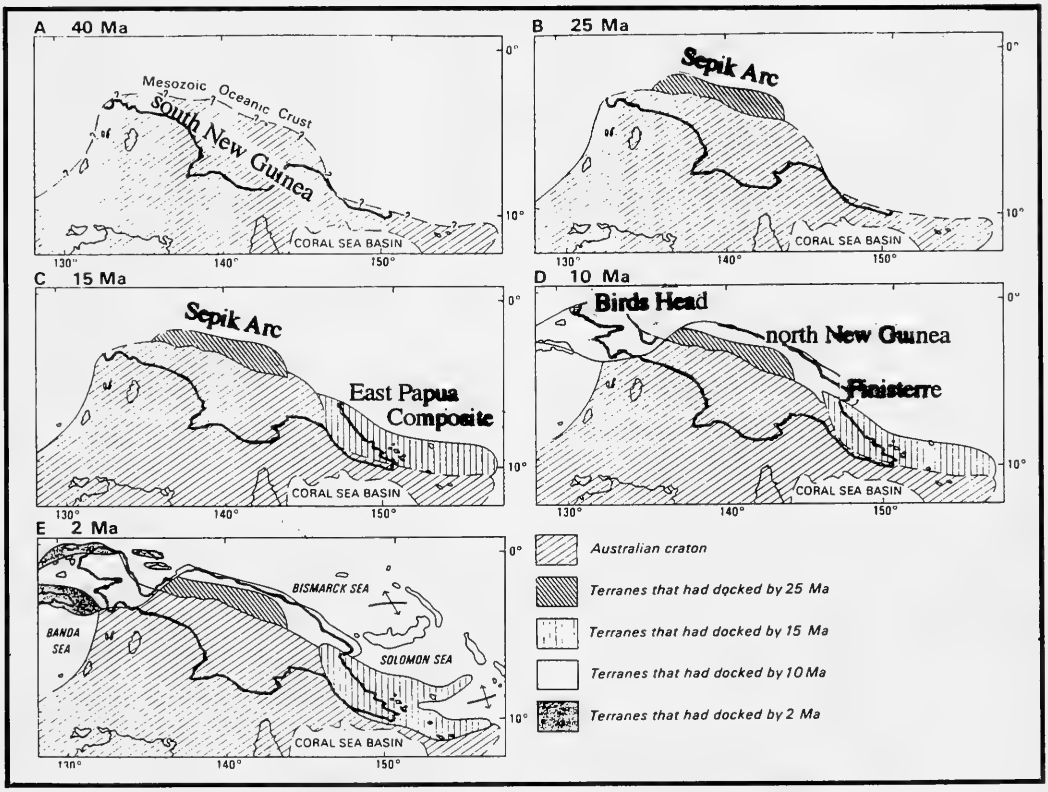


Fig. 17. The accretion history of New Guinea after Pigram & Davies (1987). A. 40 Mya, the pre-accretion outline of the Australian plate; B. 25 Mya, accretion of the composite Sepic Arc terrane; C. 15 Mya, accretion of the East Papua Composite terrane; D. accretion of the Birds Head microcontinents, the northern New Guinea terranes, and the Finisterre terrane; E. 2 Mya, accretion of the Arfak, Tamrau, and Waigeu terranes to the Birds Head, and the Cyclops mountens to northern New Guinea, and the arrival of the Bismarck terrane at New Guinea.

Mya) from central Papua New Guinea, while the Kemum microcontinent rifted in Aptian times (approximately 135 Mya), possibly from as far east as present-day northern Queensland (see also the palaeogeographic reconstructions in Struckmeyer et al. 1993). Palaeomagnetic data from the Kemum terrane show that a large-scale Neogene clockwise rotation can be ruled out for that microcontinent and support the theory that Kemum derived from the northeastern margin of the Australian craton (Giddings et al. 1993). Instead, Kemum underwent a 55° anticlockwise rotation between Triassic – Early Jurassic and Middle – late Eocene, which these authors relate to its rifting off the Australian margin. The two Birds Head microcontinents were carried westward by the Pacific plate and joined by the end of the Oligocene (26 Mya). The composite Misool – Kemum terrane then amalgamated with the Lengguru terrane by late Miocene (10 Mya), which may or may not have involved the accretion of these terranes to the Australian craton since it is not clear whether Lengguru formed an integral part of that craton or has a history of displacement of its own (Pigram & Davies 1987).

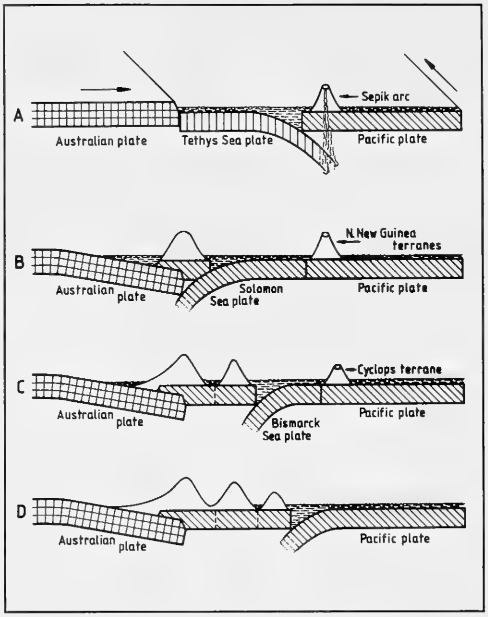


Fig. 18. The accretion history of New Guinea in cross sections. A. 30 Mya, the Tethys Sea is being subducted under the Pacific plate and Australia approaches the Sepic Arc; B. 25 Mya, the Sepic Arc has colided to Australia, the subduction has reversed and the Pacific plate (the Solomon Sea) is being subducted under under the Australian plate, Australia approaches the northern New Guinea terranes; C. 10 Mya, the northern New Guinea terranes have colided to Australia Australia approaches the Cyclops terrane; D. present, the Cyclops terrane has collided to northern New Guinea.

New Guinea

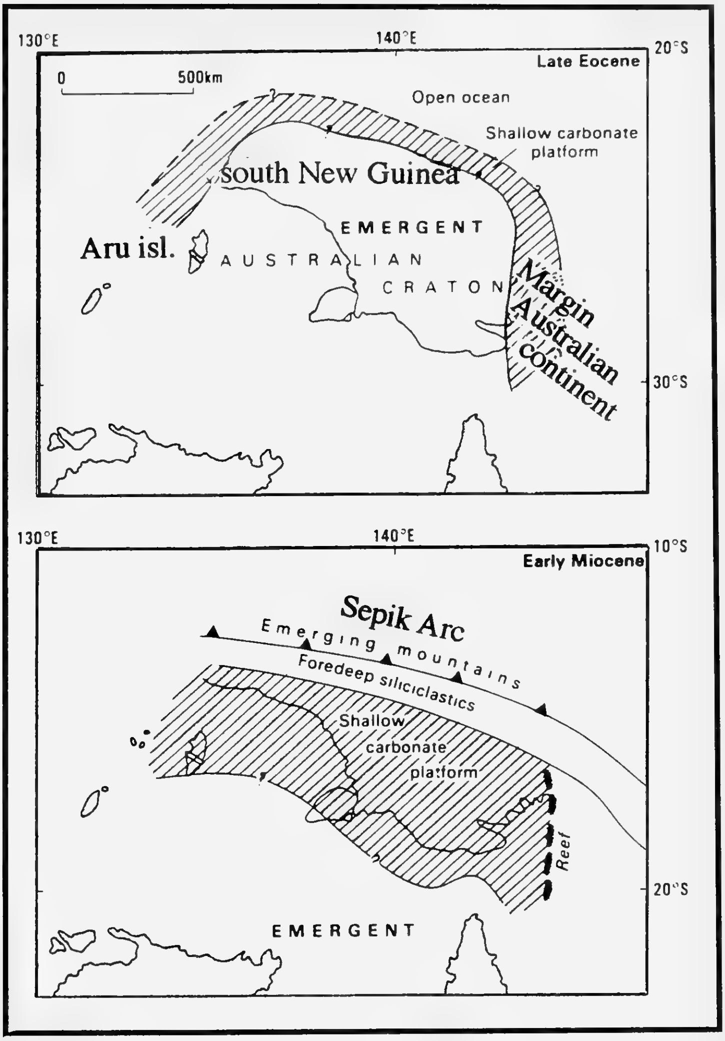
By 25 Mya Australia entered the subduction zone at the southern margin of the Pacific and Philippine plates, where composite terranes had been assembled (Pigram & Davies 1987). These terranes were composite since fragments that had rifted from the Australian continent had preceded that continent in reaching the subduction zone where they had collided with parts of the oceanic OMA. When Australia reached this subduction zone, its northern craton collided in the first of a series of collisions with the part of the composite OMA that is known as the Sepik Arc (fig. 17b). To this arc fragment belonged the Sepik terrane in Papua New Guinea, and presumably the Rouffaer terrane in Irian Jaya (cf. fig. 16). Volcanism in the Sepik terrane started possibly as early as late Cretaceous, but the terrane did not emerge until the Oligocene (38-26 Mya) (Dow 1977). The collision between the Australian plate and the Sepik Arc was oblique, started in the west of present-day New Guinea and propagated eastward (Daly et al. 1991). It had, apart from the above discussed rifting and displacement of the Moluccan microcontinents, three major effects.

First, the collision lead to an inversion of the subduction zone. Prior to the collision, the Tethys Sea was being subducted northward under the Pacific plate. After the accretion of the Sepik Arc to the Australian continent, when the Tethys Sea had been completely consumed by subduction and due to the continued northward movement of Australia, a part of the Pacific plate, the Solomon Sea, was forced to subduct southward under the Australian plate, or rather under the newly accreted Sepik Arc terranes (fig. 18).

Second, the collision initiated orogenesis in what is now central New Guinea, which resulted in the formation of the central mountain ranges. These central mountain ranges are thus for the greater part derived from the Australian craton, but along their northern slopes they contain parts of Sepik Arc origin. Pigram & Davies (1987) state that orogenesis started in the middle or late Oligocene. All older, Eocene, deformation found in New Guinea resulted from the afore mentioned island arc – microcontinent collisions that had preceded the Australia – Sepik Arc collision. These collisions occurred far away from the Australian craton.

Third, a foreland basin developed behind (south of) the collision zone (Pigram et al. 1989). The weight of the accreted Sepik Arc terranes pushed down the northern parts of the Australian continent (southern

Fig. 19. The development of a foreland basin between the New Guinea orogen (the Sepik Arc terrane) and Australia. A (top). Late Eocene, border of the Australian continent prior to the Sepik Arc collision; B (bottom). Early Miocene, an epicontinental sea covering present-day southern New Guinea. From Pigram et al. (1989).



New Guinea and northern Queensland), causing their submergence. Southern New Guinea had been emergent before the development of that basin, during Eocene and Oligocene (Dow 1977). Only a small area, the Kubor Range in the central mountains of Papua New Guinea, was not pushed down by the Sepik Arc terranes. This terrane is also of microcontinental origin and has a history of displacement (Struckmeyer et al. 1993), but comprises presumably the only part of continental New Guinea that has continuously been above sea level (Dow 1977). The foreland basin stretched as a shallow epicontinental sea over what is now southern New Guinea from the Coral Sea to the Indian Ocean. This basin was about 6-700 km across (figs. 18, 19) and existed for 18 million years (Pigram et al. 1989). The implications for biogeography are obvious. The foreland basin must have formed an important barrier for many animals and plants, separating the New Guinea orogen from the Australian continent. Sedimentation of erosion products from the developing mountain ranges in central New Guinea successively filled the foreland basin and since about 10 Mya (Pigram pers. comm.) the marshy lowland of southern New Guinea (re)emerged. During the last glacial period of about 18 thousand years ago a global sea level drop of 100-150 m occurred during which southern New Guinea was continuous with the Australian mainland (Veevers 1991).

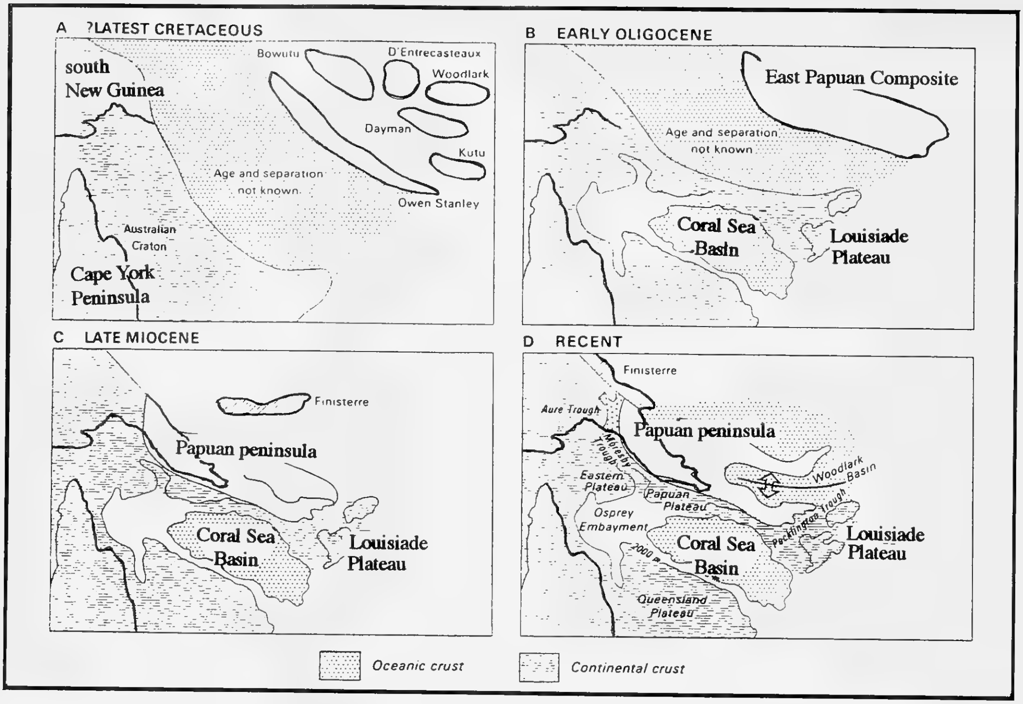


Fig. 20. The accretion history of the Papuan peninsula according to Pigram & Davies (1987). A. Late Cretaceous (70 Mya), the East Papuan terranes form an archipelago; B. late Oligocene (26 Mya), the islands of the archipelago have amalgamated to a single block, the East Papua Composite terrane; C. late Miocene (± 10 Mya), the East Papua Composite terrane has accreted to New Guinea and Finisterre approaches on New Guinea; D. recent, the East Papua Composite terrane is being dismembered by the opening of the Woodlark Basin.

To the east of the Sepik Arc a large composite block was formed by the amalgamation of several terranes of diverse origin (fig. 20). Volcanism in this area started in late Cretaceous (appr. 70 Mya) (Dow 1977). The amalgamation of this block may have started as early as 52 Mya when the Owen Stanley, Dayman, and Bowutu terranes collided. In fact, here we find an example of the older Eocene orogen in New Guinea, as mentioned above. By late Oligocene the Menyama terrane had amalgamated with this composite terrane (Pigram & Davies 1987). Parts of this composite block are emergent since the Oligocene (Dow 1977). The formation of this East Papua Composite terrane, as it is called by Pigram & Davies, which also comprised the D'Entrecasteaux Islands, the Woodlark Plateau and the Port Moresby and Kutu Terranes (cf. fig. 16), was completed by the end of the Oligocene (26 Mya) and was then separated from the Australian craton by an oceanic basin. The Menyamya, Port Moresby, and Kutu terranes (cf. fig. 16) are possible remnants of this oceanic basin. This basin was separated from the Coral Sea by a long salient of the Australian craton, which was made up by the Eastern, Papuan, and possibly the Louisiade Plateaus (Pigram & Davies 1987). The Eastern and Papuan plateaus were formed together with the Queensland Plateau during 'cretaceous margin extension' and became detached from the Queensland Plateau by sea floor spreading (Pigram & Symonds 1991). In middle or late Miocene (appr. 15 Mya), the East Papua Composite terrane, which was carried westward by the Pacific Plate as part of the OMA, collided with the aforementioned salient of the northward moving Australian continent to form the Papuan peninsula (figs. 16, 17c, 20c). This area remained long separated from the other parts of New Guinea by the north-south tending Aure Trough (fig. 20d, 21) (Dow 1977). This Aure Trough, which marks the eastern edge of the Australian continental plate, became slowly filled with sediments from the adjoining developing mountains, but may have existed until the Finisterre terrane joined New Guinea (about 2 Mya see below). Dow (1977), however, states that a connection between the Bismarck Range of central Papua New Guinea and the Owen Stanley Range of the Papuan peninsula may have existed since late Miocene. The eastern part of the East Papua Composite terrane is currently being dismembered by the opening of the Woodlark Basin as a result of sea floor spreading, which incidentally explains why no other arc terranes have accreted here since (Pigram & Davies 1987). Instead of approaching, terranes are at present being pushed away from the Papuan peninsula.

Next, the terranes that now form the northern mountain ranges of New Guinea (viz., the Torricelli, Prince Alexander, and Mt. Turu terranes in Papua New Guinea and the Gauttier terrane, which possibly is a dismembered portion of the Torricelli terrane, in Irian Jaya (cf. fig. 16)), accreted to New Guinea after the consumption of the western part of the Solomon Sea Basin under the Sepik Arc (figs. 17d, 18b) (Pigram & Davies 1987; Honza 1991). These terranes reached New Guinea approximately 10 Mya, at about the same time that the microcontinents of the Birds Head collided with western New Guinea. It is not clear what the exact position of these northern New Guinea terranes was within the historic island arc. Since they reached New Guinea later, they may have come from farther east than the components of the East Papua Composite, which means that they must have passed north of that block. In this respect, a remark of Packham (1973) about northern New Guinea might be significant. He states that: 'the deposition of clastics (in northern New Guinea) after the Oligocene orogenesis took place to the north of the large mafic and ultramafic bodies such as those that occur in the western Central and Bismarck Ranges.' The mechanism of this passing is not well understood, but the suggestion of Pigram & Davies (1987) that the opening of the Woodlark Basin prevented further accretion to eastern Papua New Guinea, may be relevant here. Seafloor spreading in the Woodlark Basin might well have influenced the direction of the OMA fragments, leading them around the Papuan peninsula towards northern New Guinea. As a matter of fact, at present we might see a similar mechanism at work in the Bismarck Archipelago, where the Admiralty Islands, New Hanover, New Ireland and in their rear the Solomon Islands, apparently curve around New Britain on their way to the north coast of New Guinea. In their palaeogeographic reconstruction of the late Eocene, Struckmeyer et al. (1993) situate the northern New Guinea terranes, the Finisterre terrane, and part of the Bismarck terrane already to the north of the East Papua Composite terrane (fig. 56). The northern New Guinea terranes are doubtlessly younger than the Sepik Arc and the East

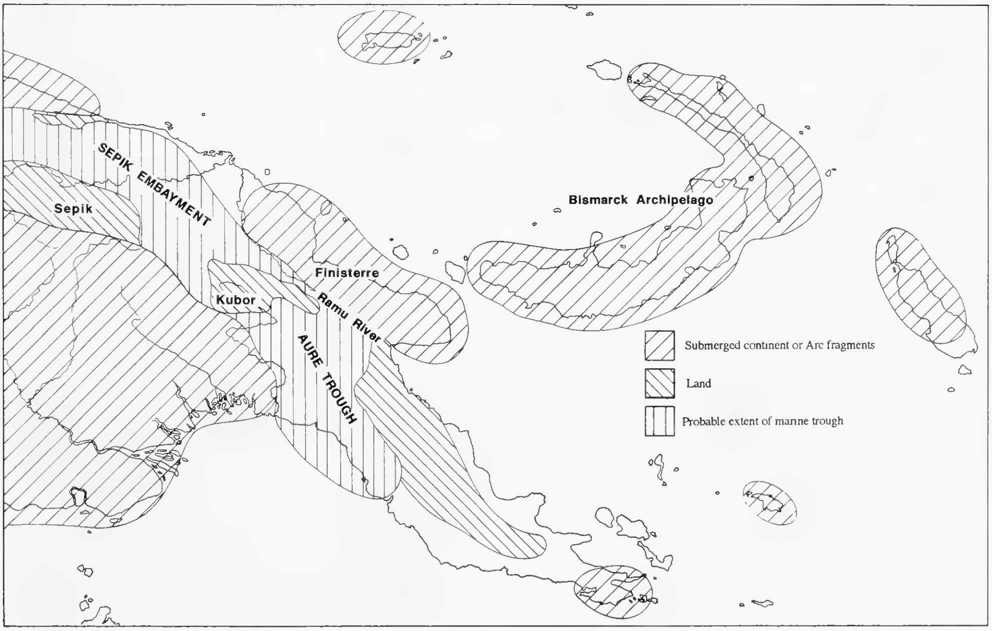


Fig. 21. Early Miocene reconstruction of dry land in Papua New Guinea, showing the position of the Aure Trough. From Dow (1970). The emerged or submarine state of land masses is indicated in their present-day locations. Of course, the actual location of terranes like the Bismarck Archipelago and Finisterre was still far removed from New Guinea in Early Miocene.

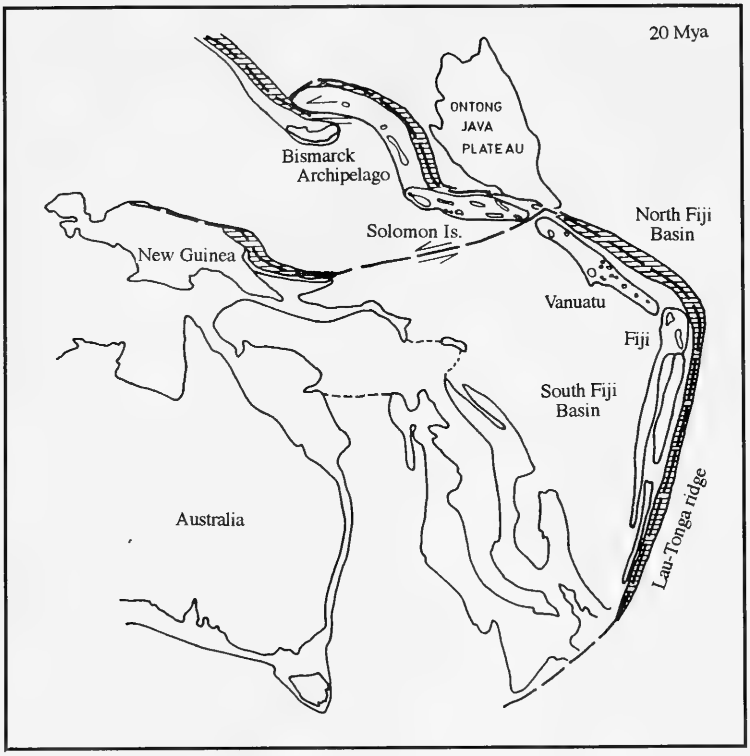


Fig. 22. Palaeogeographic reconstruction of a continuous East-Melanesian Arc (20 Mya), showing Vanuatu linking the Solomon Islands to Fiji, and the approaching collision between the Solomon Islands and the Ontong Java plateau. From Packham (1973).

Papuan block; the first volcanism in the Bewani and Torricelli mountains originates from the Eocene, while these terranes emerged in early Miocene (Dow 1977). After the northern New Guinea terranes had accreted they broke off the Pacific plate and the sea floor to the northeast of these terranes, the Bismarck Sea, started to subduct (fig. 18c)

Soon after or simultaneously with the accretion of the northern New Guinea terranes, the Finisterre terrane, which comprises the Finisterre range and the Huon peninsula of New Guinea (fig. 16), arrived at the New Guinean coast. This Finisterre terrane might earlier have formed a single linear island arc segment with New Britain, New Ireland, Manus island, and the Solomon Islands (Pigram & Davies 1987). Accretion of the Finisterre terrane to New Guinea, along the Ramu – Markham Fault zone, may have started about 10 Mya in the west (which would mean at the same time as the other north New Guinea terranes), propagated eastward, and was completed by approximately 2 Mya (fig. 17d, e) (Pigram & Davies 1987). However, Silver et al. (1991) presume that the accretion of Finisterre started much later, less than 3 Mya. Abbot & Silver (1991) state that the southern part of the Finisterre region was at bathyal depths at this time and remained so until at least 1.1-1.3 Mya, when the continuing collision caused its uplift. The Finisterre terrane is again younger than the terranes of northern New Guinea. Although volcanism also started in Eocene, it suddenly ceased in early Miocene, and the Finisterre terrane did not emerge until after Miocene (Dow 1977).

When the accretion of Finisterre was completed, some smaller terranes had likewise been added to northern New Guinea after parts of the Bismarck Sea had been consumed by subduction (Biak and Japen Islands, and presumably the Cyclops Mountains) (fig. 18d) and to the northern Birds Head (Arfak and Waigeu cf. fig. 16) (Pigram & Davies 1987). The Finisterre terrane, being the last of the larger blocks that became accreted to New Guinea does, in this respect, an honour to its name that has never been thought of.

The Bismarck Archipelago presumably reached New Guinea in the rear of the Finisterre terrane.

East-Melanesian Archipelagos

To the east of the Bismarck Archipelago, the OMA apparently continues in the Solomon Islands, Vanuatu (the New Hebrides), Fiji, and in the Lau and Tonga ridges. The Samoan islands are presumably hot-spot related, as their westward increasing age and subparallelism to other chains of hot-spot origin

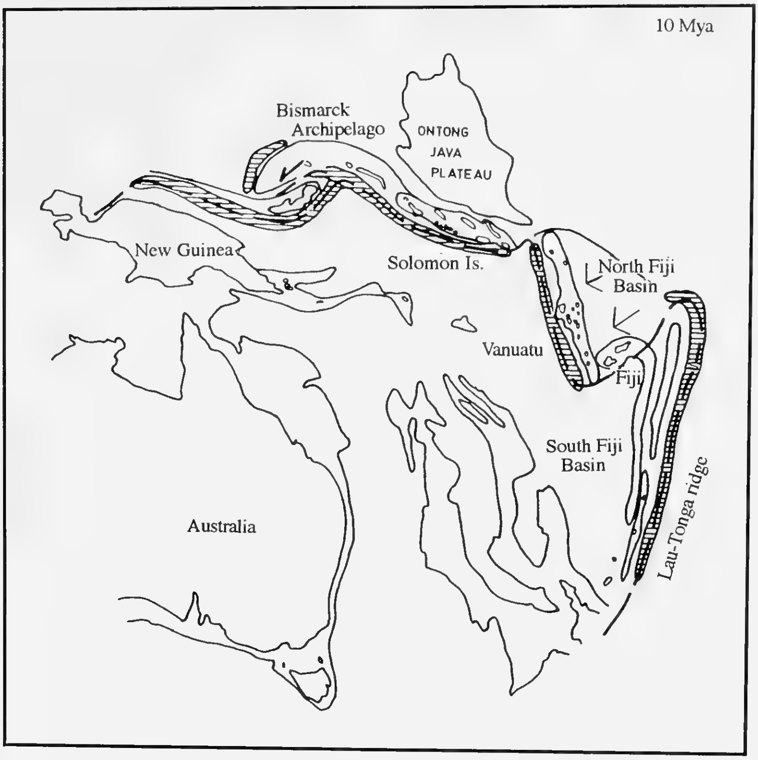


Fig. 23. Palaeogeographic reconstruction of the disrupted East-Melanesian Arc (10 Mya) after the collision between the Solomon Islands and the Ontong Java plateau. Vanuatu rotates clockwise to the south, Fiji becomes isolated, and the Lau and Tonga ridges separate. From Packham (1973).

suggest (Ewart 1988). The Samoan chain, however, shows active volcanism at both its northwestern and southeastern ends, which apparently opposes the 'hot spot' hypothesis. Furthermore, there are indications that, for the last 13.5 My, the Samoan shield volcanos were formed at approximately the same distance from the eastward migrating Tonga trench, which indicates that Samoa could, at least partly, be related to the OMA system (Ewart 1988).

The eastern parts of the OMA developed during Eocene as a continuous island chain, with Vanuatu linking the Solomon Islands to Fiji and Tonga (fig. 22) (Packham 1973; Ewart 1988), but remained mainly submarine until early Miocene (Gill & Gorton 1973). Similar to the western parts of the OMA, these eastern parts arose along the margins of the Pacific plate. Yet, there is a fundamental difference between these two parts of the arc. The OMA west of the Solomons, which possibly includes the northeastern part of the Solomon chain, evolved as the result of an initially northward subduction of the Tethys Sea under the Pacific plate. The polarity of this subduction was reversed after the collision of a part of the OMA (the Sepik Arc fragment) with the Australian continent (see above and fig. 18). From the Solomons eastward, the subduction was initially south- and westward directed, where the Pacific plate was being subducted under the South Fiji Basin (fig. 22) (Gill & Gorton 1973; Ewart 1988) and reversed in the Solomon and Vanuatu region after collision of the Solomon chain with the Ontong Java Plateau in the middle or late Miocene (cf. fig. 23) (Packham 1973; Honza 1991). The Ontong Java Plateau, which is about two thirds the size of Australia, consists of volcanic rocks and is supposed to have formed about 120 Mya in a very short time (less than 3 million years). This and similar oceanic plateaus represent upwellings of magma which erupted as tremendous floods of lava, they are referred to as Large Igneous Provinces (Coffin & Eldholm 1993). Before the collision between the Solomon chain and the Ontong Java Plateau, as Packham (1973) specifically states: 'the New Hebrides would have behaved as part of the Australian plate, while now they form part of the Pacific plate', and we may conclude that that would then also have been the case for the (southeastern) Solomon Islands and Fiji. The initially single Lau/Tonga ridge also developed in association with the Australian continent, and rifted eastward since the late Oligocene opening of the South Fiji Basin

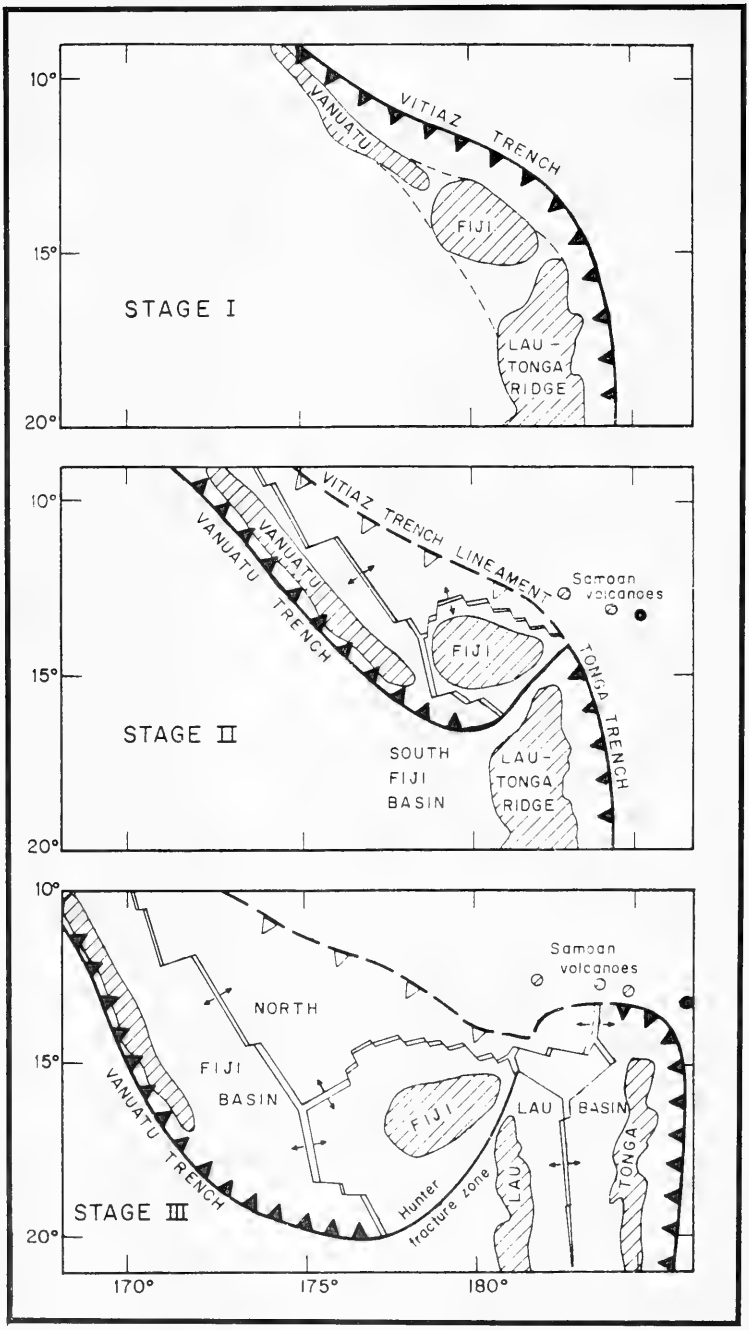


Fig. 24. Schematic reconstruction of the Break-up of the East-Melanesian Arc. Stage I, late Eocene-Oligocene, Vanuatu, Fiji, and Tonga form a continuous chain; Stage II, Miocene, Vanuatu starts rotating clockwise to the south; Stage III, Pliocene-Pleistocene, Fiji gets isolated and the Lau and Tonga ridges separate by the opening of the Lau Basin. From Ewart (1988).

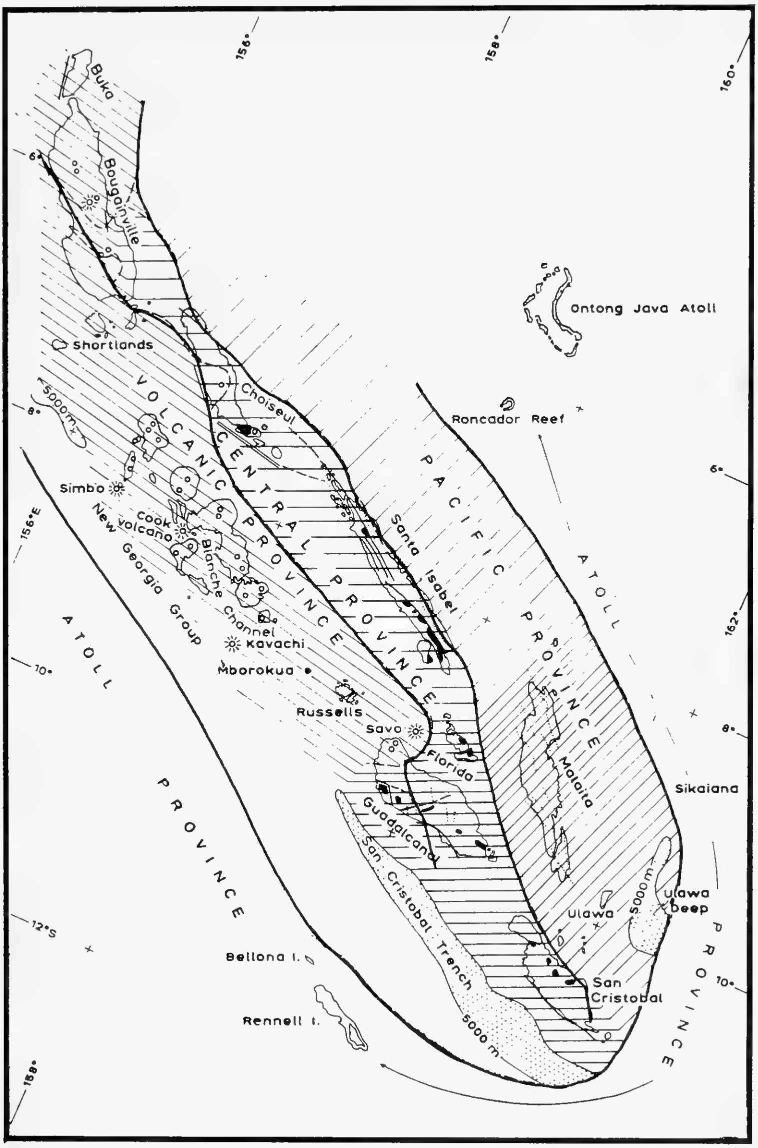


Fig. 25. The geological provinces of the Solomon Islands. From Hackman (1973).

(Ewart 1988). Burrett et al. (1991) also recognize this relationship with Australia and assume that the eastern parts of the OMA, notably the Fiji islands, contain rifted parts of Gondwana origin. The Vitiaz Trench Lineament, marked by the volcanic Rotuma and Wallis islands, and the Cape Johnson Trough might be the remnants of the original, southward directed, subduction site (Gill & Gorton 1973; Ewart 1988). At present the Pacific plate is being subducted westward at the Tonga – Kermadec Trench (Ewart 1988).

The collision of the Solomon chain with the Ontong Java Plateau (approximately 9-12.5 Mya), which resulted in the reversal of subduction, and the simultaneous collisions in northern New Guinea, or collisions with Pacific seamounts (as suggested by Ewart 1988) may all have caused the disruption of the eastern part of the OMA (Gill & Gorton 1973). This disruption may have started directly following these events, with the clockwise rotation of the New Hebrides by the opening of the North Fiji Basin and the subduction of an ancestral North Fiji Basin (cf. fig. 24). Dating the onset of the rotation of the New Hebrides as early as middle Miocene is consistent with the age of faulting in the New Hebrides (see also Honza 1991) and of an uplift in Fiji. On the other hand, a change of volcanism on Fiji and in the New Hebrides suggests that this rotation and disruption started much later, less than 5.5 Mya (Gill & Gorton 1973). In that case, the rifting between Fiji and the New Hebrides would have started simultaneously with the opening of the Lau – Havre Basin at about 5 Mya (Ewart 1988; Honza 1991), which caused the rifting of the Tonga – Kermadeck ridge from the Lau – Colville ridge and an anticlockwise rotation of Fiji. By 3 Mya these rifting and rotation events had caused a complete isolation of Fiji relative to other parts of the OMA (fig. 24) (Ewart 1988).

Solomon Islands

The Solomon Islands can be divided into four geological provinces (fig. 25) (Hackman 1973). The Central province, of Oligocene – Miocene age comprises Buka, Bougainville, Choiseul, Santa Isabel, Florida, Guadalcanal, and San Cristobal. This central province is flanked in the northeast by the Pacific province (Malaita and Ulava) and in the southwest by the Volcanic province (part of Bougainville, the New Georgia group, and part of Guadalcanal); these two provinces are both of Pliocene age. The Atoll province, finally, includes the atolls on the Ontong Java Plateau to the north of Malaita, and Bellona and Rennell Islands, south of Guadalcanal. This latter province does not form a geological entity. According to Silver & Smith (1983) Malaita contains a slice of the Ontong Java Plateau, while Honza (1991) states that the whole Eastern, Pacific, province is a marginal part of that plateau.

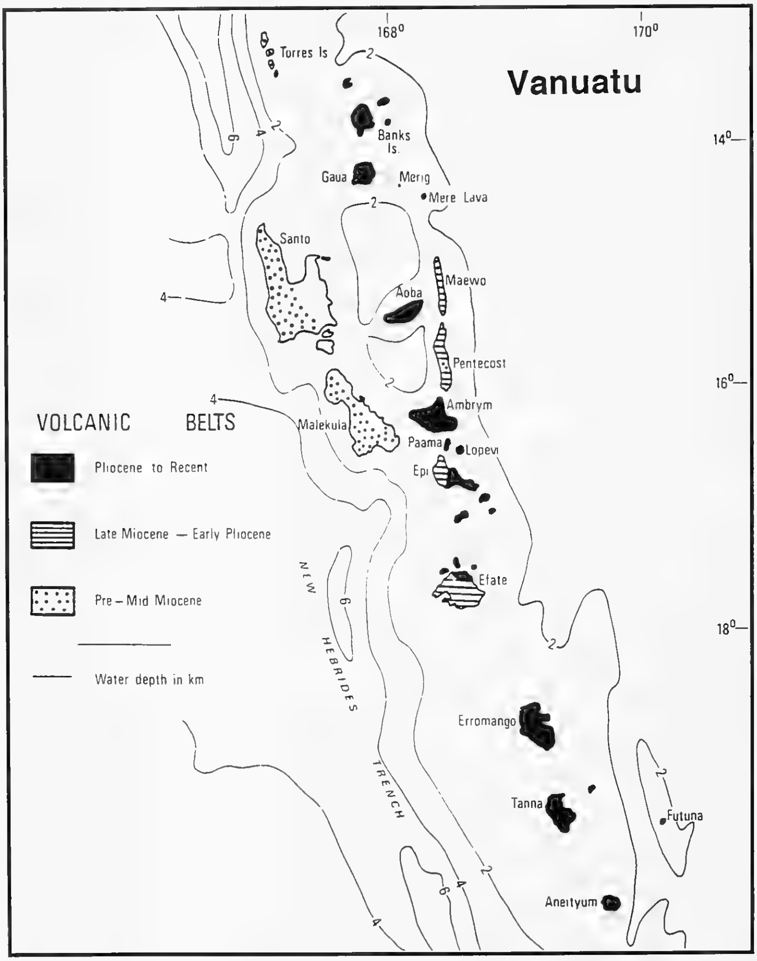


Fig. 26. The distribution of three volcanic belts in Vanuatu. From Mallick (1973).

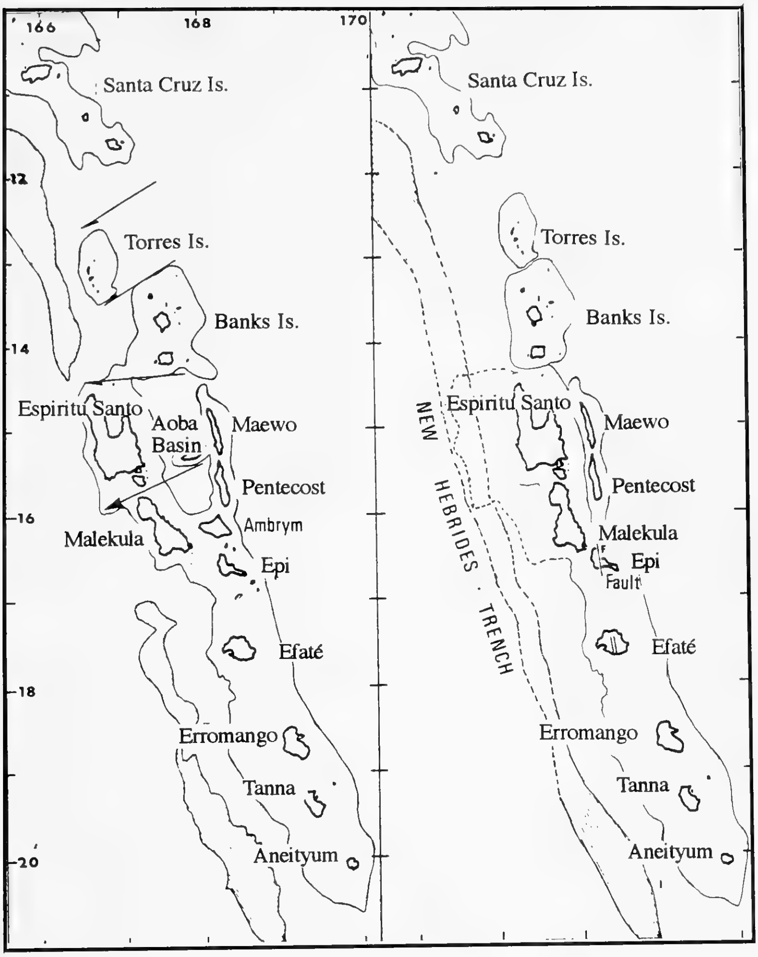


Fig. 27. The Break-up of Vanuatu. A (left). Present-day Vanuatu, B (right). pre Break-up Vanuatu. From Gill & Gorton (1973).

The basement of the Central province is similar to the ultramafic belt of eastern New Guinea; this province apparently continues to the Santa Cruz group, north of the New Hebrides (Hackman 1973). The parallel and younger Pacific and Volcanic provinces possibly developed and emerged as a result of the collision with the Ontong Java Plateau, and the ensuing reversal of subduction. The presumed continuity between the Finisterre terrane of New Guinea, New Britain, New Ireland, Manus, and the Solomon Islands that was mentioned above might be restricted to these younger provinces, but that is not explicitly stated in the literature.

Vanuatu (New Hebrides)

Mallick (1973) and Honza (1991) recognize three volcanic belts in the New Hebrides, linked to three periods of volcanism: a pre-middle Miocene Western belt (Espiritu Santo and Malekula), a late Miocene – early Pliocene Eastern belt (Maewo, Pentecost and parts of Epi and Efaté), and a Pliocene to Recent Central belt consisting of the remainder of the archipelago (fig. 26). The formation of the Eastern belt is possibly related to the reversal of subduction and to the onset of rotation of the New Hebrides that followed on the Ontong Java collision. The Central belt results from the fact that the New Hebrides ridge is currently being split in two. This splitting is expressed by the Y-shaped configuration of the island group and by the fault zones across Epi and Efaté (Mallick 1973; Gill & Gorton 1973) and is analogue to the splitting of the Lau and Tonga ridges, that occurred in late Miocene. Maewo and Pentecost islands move eastward, Espiritu Santo and Malekula westward (fig.

27). The subduction zone to the west of the New Hebrides is interrupted at Espiritu Santo and Malekula, where the east-west lineations of the D'Entracasteaux zone of the Coral Sea Basin abut against the New Hebrides ridge (Mallick 1973). These westward moving islands possibly overrode the subduction zone and filled the trench belonging to that zone with detritus. The deep Aoba Basin to the east of Espiritu Santo and Malekula resulted from this collision with the D'Entrecasteaux ridge (Honza 1991).

Fiji

Seismic activity on Fiji is less intense than in the surrounding Tonga and New Hebrides arc-trench systems. The development of Fiji as a landmass appears to have begun with submarine volcanic eruptions upon a segment of 'quasi-continental' crust, 'along structurally determined lines; critical zones of weakness incepted in the primordial oceanic crust' (Green & Cullen 1973). The oldest rocks on Fiji are of Eocene age, which is older than on surrounding island chains. Middle to late Eocene volcanism on the island of Viti Levu may predate the OMA and be related to the Norfolk – New Caledonia – D'Entrecasteaux ridges (Ewart 1988). Burrett et al. (1991) suppose that part of the Fiji islands rifted from the Australian part of Gondwana. However, a well evolved OMA, including the Fiji group, existed by middle Oligocene (Ewart 1988).

Since the opening of the Lau Basin (5 Mya) and the break-up of the island arc Fiji has rotated anticlockwise out of the OMA for 21-60°, and so became separated from the Tonga – Kermadec ridge (Ewart 1988). The presence of post rotational fractures suggests that this rotation has ceased some considerable time ago (Green & Cullen 1973). The greater part of Fiji has probably been emerged since middle Miocene (Ewart 1988).

Lau islands

The Lau islands include atoll reefs and islands surrounded by barrier and fringing reefs.

The northern islands of Yacata and Nayua are supposed to have formed an extension of the New Hebrides western volcanic belt during middle Miocene (Ewart 1988) until the Lau and New Hebrides ridges commenced to separate. A period of subsidence of the Lau islands evidently occurred following this separation, as is indicated by the reef growth, but the older, eroded, volcanos and reefs reemerged in late Pliocene to Quarternary (Ewart 1988).

Tonga

The Tonga ridge comprises two parallel chains of islands: a western arc of active volcanos (the Tofua arc), and an eastern, volcanically inactive, arc comprising the Vava'u, central Ha'apai, Nomuka, and Tongatapu island groups.

The Tonga chains evolved in middle Eocene as part of a single Lau – Tonga ridge (fig. 24), possibly near, or attached to, the Norfolk – New Caledonia ridge, as the middle Eocene volcanism on the island of 'Eua suggests; this volcanism predates the age of the South Fiji Basin. The Lau – Tonga ridge did not emerge until late Oligocene, after the opening of the South Fiji Basin. Most of the Tonga ridge was submerged again during the Miocene until the opening of the Lau Basin, which separated Lau and Tonga (fig. 24), initiated a new uplift by the end of the Miocene (Ewart 1988). The Tonga ridge currently collides in the east with the Louisville ridge. The Tofua arc volcanism is of Plio – Holocene age and is possibly related to this collision and to the subduction of the Louisville ridge (Ewart 1988).

BIOGEOGRAPHY OF THE CICADAS OF SULAWESI, NEW GUINEA AND THE WEST PACIFIC

New Guinean cicadas

The cicadas of New Guinea can be classified into four major groups: 1) the subtribe Cosmopsaltriaria Kato, 1932 (sensu Duffels 1983), 2) the tribe Chlorocystini Distant, 1905 (sensu stricto: De Boer 1995d), 3) the oriental Prasiini (sensu De Jong 1985) of the tribe Prasiini Matsumura, 1917, and 4) the tribe Cicadettini Buckton, 1890. The Cosmopsaltriaria belong to the family Cicadidae, the other three groups to the family Tibicinidae; these families are easily distinguished by the presence or absence of tymbal coverings, sclerotized plates derived from the second tergite that cover the tymbal organs.

Within New Guinea the Cosmopsaltriaria and the Chlorocystini are by far the most speciose groups of cicadas. Both these groups are widely distributed in New Guinea and the western Pacific, while the Cosmopsaltriaria extend westward to Sulawesi (compare figs 28 & 29). The oriental Prasiini, the presumed sister group of the Chlorocystini, are represented on New Guinea by the small genus *Arfaka* Distant, 1905 (3 species in the Birds Head area); by about ten undescribed and three described species of the genus *Lembeja* Distant, 1892; and by some undescribed species with uncertain relationships; but most species of the oriental Prasiini are endemics of Sulawesi (fig. 29). The Cicadettini form a large tribe with an almost world-wide distribution, they are especially numerous in Australia and New Zealand, and, in fact, all New Zealand cicadas belong to that tribe. The phylogenetic relationships within the

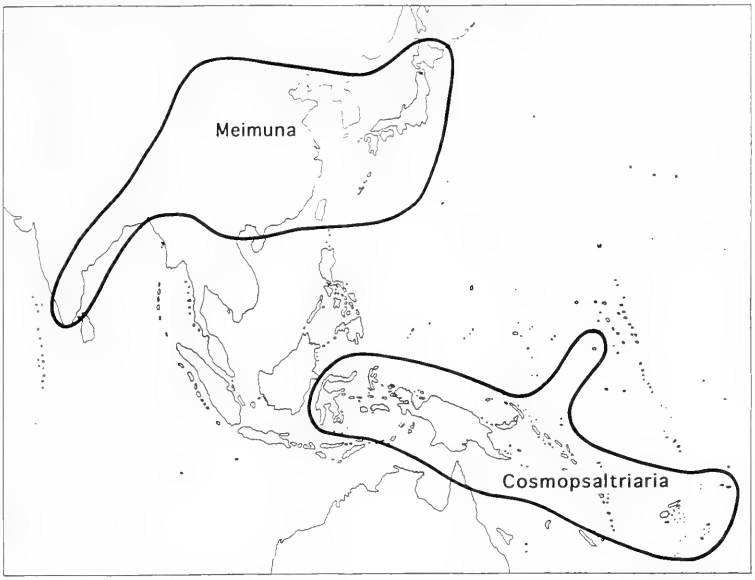


Fig. 28. Distribution of the subtribe Cosmopsaltriaria and its presumed sister group the genus *Meimuna* (sensu stricto, De Boer & Duffels in prep).

Cicadettini are very uncertain, and their monophyletic origin must be considered doubtful. The Cicadettini are represented on New Guinea by a small number of species assigned to three genera: the genus *Toxopeusella* Schmidt, 1926 (with four species, see Boulard 1981); the monotypic genus *Auta* Distant, 1897; and presumably by the genus *Pauropsalta* Goding & Froggatt, 1904, which is based on one specimen of *P. eyrey* (Distant, 1882) from Sogeri in eastern Papua New Guinea.

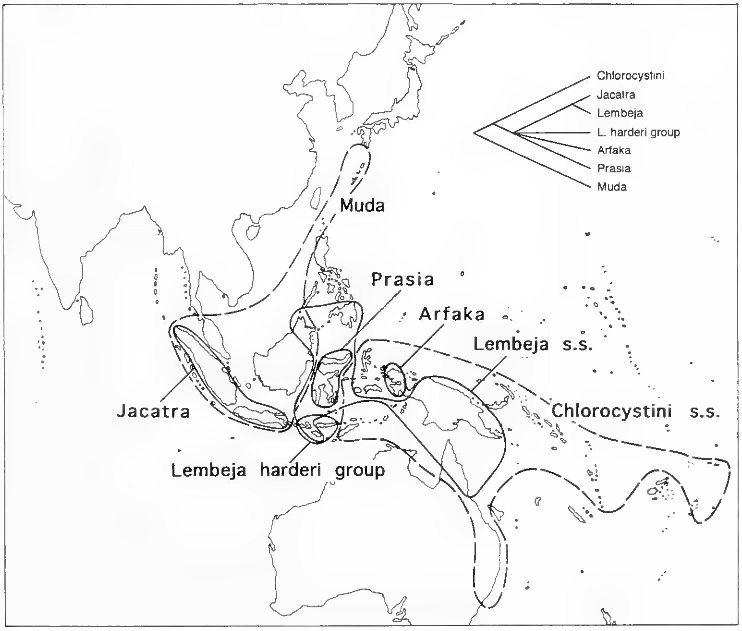


Fig. 29. Distribution of the sister tribes Chlorocystini and Prasiini and their presumed sister group the genus *Muda*.

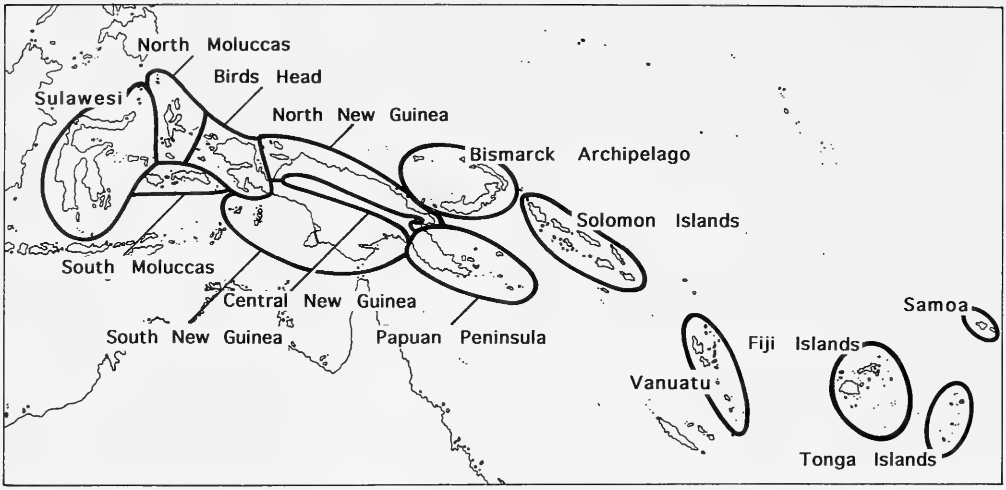


Fig. 30. Areas of endemism in the southwest Pacific

Furthermore, there are two or three undescribed species, that possibly belong to *Auta* and one that presumably belongs to *Pauropsalta*. The New Guinean Cicadettini presumably have their nearest relatives in Australia.

The present paper intends to make a comparison of biogeographical and area cladistic patterns found in the Cosmopsaltriaria, based on the revisionary work of Duffels (1977 and later works), and in the Chlorocystini, based on revisions by the present author (De Boer 1982 and later works). Revisionary work on the oriental Prasiini is not completed and, by lack of a reliable phylogenetic reconstruction, biogeographic and area cladistic reference to that group must be restricted to some provisional observations. Data concerning the oriental Prasiini are derived from revisionary work of De Jong and Duffels (1981), De Jong (1982 and later works), and unpublished data of the latter author (see De Boer 1995d). The oriental Prasiini are included in the phylogenetic and area-cladistic reconstructions as the presumed sister group of the Chlorocystini. The Cicadettini are not included in this study, since their distributional data are too incomplete and their phylogenetic relationships are too uncertain to allow any conclusions.

Vicariant patterns versus dispersal patterns

The distributional patterns of the cicada genera occurring on New Guinea show that these genera are not evenly distributed over the island. The various genera are, so to speak, differently orientated. They concentrate, often with endemic species, in different parts of the island. This can be illustrated best by comparing the distributions of three genera with a very similar distributional range over Maluku, New Guinea, and, in two instances, the Bismarck Archipelago. The patterns of species distribution of these genera, however, are very different: *Aedeastria* De Boer, 1990 (fig. 37) mainly occurs in western New Guinea, *Cosmopsaltria* Stål, 1866 (fig. 31) is most abundant in the central mountain ranges of New Guinea, and *Gymnotympana* Stål, 1861 (fig. 32) appears to be concentrated in Papua New Guinea. These patterns, and those of other genera from the same area, indicate the existence of several areas of endemism. Congruence between the distributions of endemic species(groups) led to the recognition of the following areas of endemism (fig. 30): Sulawesi, northern Maluku, southern Maluku, the Birds Head peninsula of New Guinea, northern, central, and southern New Guinea, the Papuan peninsula, the Bismarck Archipelago, and the East-Melanesian archipelagos. Many of these areas of endemism can be subdivided into areas of endemism of a lower rank; these are indicated by monophyletic subgroups of the groups that indicate the undivided area of endemism. These areas of endemism must have known a period of isolation in which their endemic biota could evolve. Keeping the geological knowledge discussed in the previous chapter in mind, one will realise that many of the areas of endemism recognized, coincide with geological entities like microcontinents or fragments of the Outer Melanesian Arc (OMA), areas indeed that have known a period of isolation.

It is postulated here, that the different patterns of distribution among the various New Guinean cicada genera, result from an origin of these genera on these different geological entities: the microcontinents or isolated fragments of the oceanic island arcs. Furthermore, it is postulated that the genera that are related to the New Guinean genera and that occur on Sulawesi, in the western Pacific, or in Australia also evolved in isolation on different fragments of the island arcs. Many of the vicariant events that separated the sister genera are apparently none others than the fragmentation events that occurred within the island arc systems. This paper aims to investigate the evidence for these postulations, and to reveal the links between the generic evolution of the two groups of Indo-Pacific cicadas under study and the palaeogeographic history of their area of distribution.

After the collision of the OMA with East Asia, at least two cicada species are supposed to have invaded that island arc: they were the ancestors of the Cosmopsaltriaria and of the oriental Prasiini plus the Chlorocystini (sensu stricto) together. How and from where these ancestors arrived in the arc will be discussed later. These ancestral species presumably dispersed over the entire area of the OMA emerged at that time. This dispersal was probably not an active colonisation on the part of the cicadas (the whole point of selecting cicadas for these biogeographic and area cladistic studies is, that life cycle and biology of cicadas oppose to such an active dispersal), but they were presumably merely carried along in 'waves' of vegetation, and possibly remained quite stationary relative to that vegetation, a phenomenon which was called biotic dispersal (Platnick & Nelson 1978). The OMA must not be regarded as a continuous stretch of dry land in the ocean, but as a chain of volcanic islands with continuously changing interconnections. The waves of biota that invaded this arc might thus have shifted up and down the arc, in response to the fluctuations that occurred in the connections between the various parts of the arc. Such fluctuations must already have caused some speciation and when the arc finally broke up, populations of various species became isolated on its fragments. These populations are supposed to be the ancestors of most of the genera now occurring on Sulawesi, New Guinea, and in the western Pacific. Others may have evolved on rifted microcontinents that had come into contact with fragments of the arc. As was outlined in the previous chapter, various fragments of the OMA collided at different times and at different locations with the northern craton of the Australian continent, finally shaping New Guinea as we know it today. It follows that, if our theory is correct, also the various genera of New Guinean cicadas arrived, travelling on these arc fragments, on New Guinea at different locations and in different times. And here presumably lies the reason why we see such marked differences among the distributional patterns of the various New Guinean genera.

After the accretion of a remnant of the OMA to New Guinea the biotas on that remnant and on the other, already amalgamated, parts of New Guinea could, of course, freely be exchanged by reciprocal dispersions and diffusions. It is not remarkable that such dispersals and diffusions also occurred among cicadas and that at present the New Guinean cicada genera are no longer confined to the historic OMA fragments on which they once evolved. What is remarkable is that due to some peculiar biological characteristics of cicadas this diffusion and dispersal remained limited to such an extent that the original patterns of distribution can still be recognized. Five major terranes are supposed to have accreted to form modern New Guinea. These are in chronological order: the Sepik Arc, the East Papua Composite terrane, the Birds Head microcontinents, northern New Guinea, and the Finisterre terrane (see the previous chapter). It is to be expected that the original areas of endemism of the New Guinean genera, their ancestral areas of distribution, coincide with these five terranes. However, the present-day distributions of the genera will prove to be the result of a combination of old vicariant events and more recent dispersal events. If the above outlined scenario is correct, it must be possible to recognize, up to a certain point, the areas of origin or 'source areas' of all New Guinean cicada genera, i.e., the ancestral areas of endemism as microcontinents or fragments of the OMA. For the non-New Guinea genera, furthermore, it must be possible to determine other parts of the island arc systems (e.g., Sulawesi, the Bismarck Archipelago or the East-Melanesian island chains) as ancestral areas of distribution. To recognize these ancestral areas of distribution we must decide what features in the present-day distributions are the result of recent diffusions; we must distinguish between the old vicariant patterns and the more recent dispersals.

Historical distributions of the genera

In the remaining part of this chapter the probable areas of origin of the genera of the Cosmopsaltriaria and the Chlorocystini (sensu stricto) will be discussed as far as these can be inferred from their present-day distribution patterns. First, the areas of origin of the New Guinean genera will be made plausible. Then the possible origin of the Australian genera of the Chlorocystini and the non-New Guinean genera of the Cosmopsaltriaria will be discussed. Finally, some remarks will be made on the distribution of the oriental Prasiini.

A concentration of species and especially of endemics of the New Guinean genera in any of the five possible areas of origin listed above is regarded as an indi-

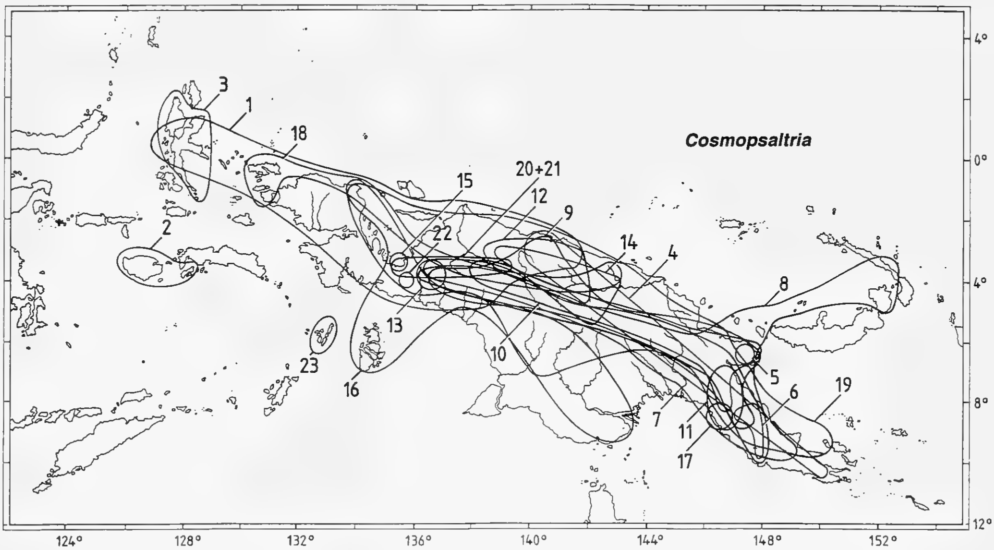


Fig. 31. Distribution of the species of *Cosmopsaltria*: *doryca* (1), *lata* (2), *halmaherae* (3), *gracilis* (4), *huonensis* (5), *gestroei* (6), *gigantea* (7), *mimika* (8), *aurata* (9), *signata* (10), *meeki* (11), *satyrus* (12), *personata* (13), *bloetei* (14), *emarginata* (15), *capitata* (16), *loriae* (17), *delfae* (18), *papuensis* (19), *retrorsa* (20), *toxopeusi* (21), *waine* (22), *kaiensis* (23).

cation that the genus in question originates from that particular area. Species with a relatively large distribution area are considered less informative, since they are obviously better dispersers. The occurrence of the genera outside their presumed area of origin can generally be explained by recent dispersals. It is not strange then that these occurrences generally concern species with a relatively wide distribution. Those genera of which the distributions most distinctly indicate a certain area of origin will be discussed first. For other genera where a concentration of endemic species is less obvious, a probable area of origin can often be inferred from a comparison of the similarities and differences in distribution patterns between these genera and those showing more lucid patterns. Such a comparison is allowed since genera that arrived on New Guinea on the same arc fragment must have had similar dispersal capacities and might therefore show similar dispersal patterns. Nevertheless, it will appear that genera which are supposed to originate from the same fragment can still show marked differences in distributions. Such differences must possibly partly be explained by the fact that these arc fragments themselves often are of a composite nature and that different parts of them might, at different times, have had different connections to other parts of the historic island arcs. Furthermore, the distribution patterns of several genera indicate more than one area as the area of origin, in that various monophyletic subgroups show a different area of concentration. In such cases, where the arbitrary classification in genera apparently does not coincide with the main fragmentation events of the island arcs, these areas together are regarded as the area of origin. This does not necessarily mean that these genera are non-monophyletic; the geological events merely caused vicariant speciation within species groups that are classified as genera.

The New Guinea orientated genera

Cosmopsaltria Stål

One of the most remarkable distribution patterns was found for the genus *Cosmopsaltria* Stål, 1866 (fig. 31). For exact data on the distribution of the species see Duffels (1983, 1988c, 1988d) and Duffels & Van Mastrigt (1991). The genus is, apart from a species incertae sedis from the Fiji islands (*C. vitiensis*), restricted to New Guinea, Maluku, and the Bismarck Archipelago and by far most of its species are restricted to the central mountain ranges of New Guinea. The distributions of these species often span the whole length of these mountain ranges, from the Wissel lakes area in the west to well into the Papuan peninsula. Only three species (*C. gestroei*, *C. meeki*, and *C. loriae*) are endemic to the Papuan peninsula. Several of the central mountain range species have a wider distribution, extending either to the northern parts of Cendrawasih (*C. papuensis*), or to northern

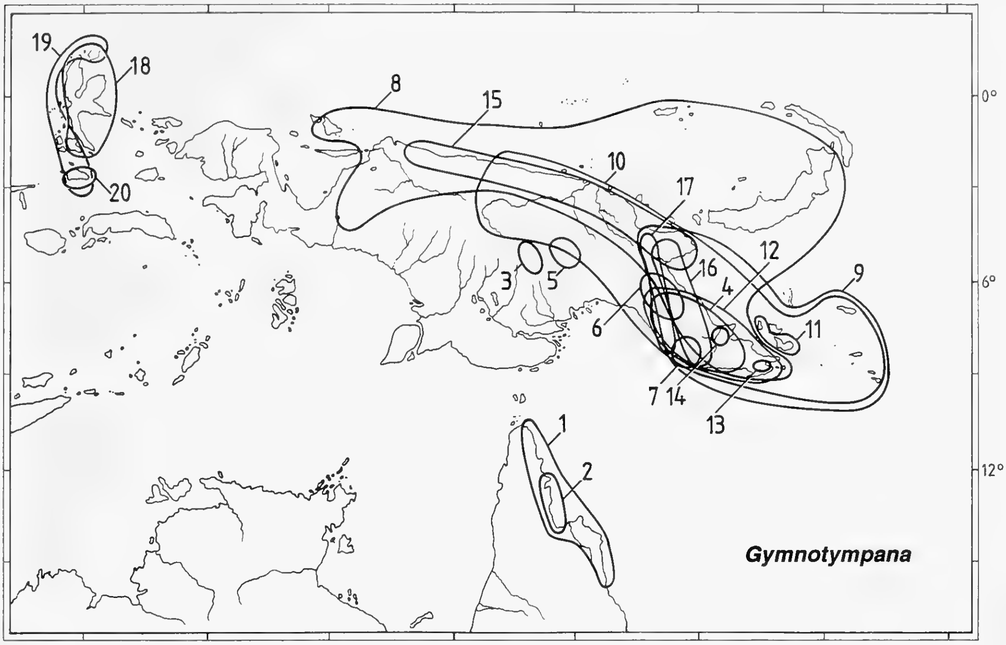


Fig. 32. Distribution of the species of *Gymnotympana*: *varicolor* (1), *rufa* (2), *hirsuta* (3), *olivacea* (4), *verlaani* (5), *montana* (6), *viridis* (7), *dahli* (8), *strepitans* (9), *rubricata* (10), *langeraki* (11), *nigravirgula* (12), *parvula* (13), *stenocephalis* (14), *membrana* (15), *minoramembrana* (16), *phyloglycera* (17), *stridens* (18), *subnotata* (19), *obiensis* (20).

New Guinea (*C. aurata*, *C. mimica*, *C. papuensis*), or to the Bismarck Archipelago (*C. mimica*). Two small species groups, the *doryca* group and the *gracilis* group, occur almost exclusively outside the central mountain ranges. The *C. doryca* group (*C. doryca*, *C. halmaherae*, and *C. lata*), being the sister group of all other *Cosmopsaltria* species has a western distribution. *C. doryca* has a wide distribution in western New Guinea (including the most western part of the central mountain ranges) and Halmahera, *C. lata* is endemic to Ambon, Buru, and possibly Timor, and *C. halmaherae* is endemic to Halmahera island. The *gracilis* group (*C. gestroei*, *C. gracilis*, and *C. huonensis*) is the sister group of the '*mimica* complex' (all *Cosmopsaltria* species minus the *doryca* and *gracilis* groups). *C. gestroei* is distributed in the Papuan peninsula, *C. gracilis* occurs in central northern New Guinea and is recorded with doubt from the eastern end of the Papuan peninsula, and *C. huonensis* is known from a single locality on the Huon peninsula. Finally, several species of the '*mimica* complex' are endemic to areas other than the central mountains. *C. kaiensis* is endemic to the Kai islands to the south of New Guinea and the three species of the *C. capitata* group almost encircle the central mountains. *C. capitata* is distributed in north New Guinea and the Birds Head, *C. delfae* occurs in southern New Guinea, on the Birds Head, and on Aru island, and *C. loriae* is known from a single locality on the Papuan peninsula.

The concentration of *Cosmopsaltria* species in the central mountain ranges of New Guinea, the small number of endemic species in the Papuan peninsula, and the fact that the number of co-occurring species decreases eastward in the Papuan peninsula suggest that *Cosmopsaltria* originates from that part of the OMA that is known as the Sepik Arc, notwithstanding the fact that only very few *Cosmopsaltria* species are actually endemic to the Sepik Arc terranes. The Sepik Arc was the first part of the OMA that collided with New Guinea (about 25 Mya); its collision resulted in the orogenesis of the central mountain ranges (Pigram & Davies 1987; Daly et al. 1991). The distribution of *Cosmopsaltria* in other parts of New Guinea, including the Papuan peninsula, and in the Bismarck Archipelago, Aru, and the Kai islands is presumably due to a later dispersal that occurred after these areas had either successively become accreted to New Guinea or had become available during periods of low sea levels. The occurrence of the basal *C. dory-*

ca group in Maluku might represent an older pattern, indicating a historical relationship between a part of Maluku with the Sepik Arc; but the wide distribution of *C. doryca* from the central mountains to Halmahera and the recent emergence of the south Moluccan islands makes a recent westward dispersal equally plausible. Moreover, the distribution of the *C. doryca* group shows much resemblance to that of the *Baeturia conviva* group (see below, fig. 39), which indicates that they may result from a similar dispersal event. Since *Baeturia*, as will be explained below, is supposed to have arrived on New Guinea about 15 My later than *Cosmopsaltria*, its occurrence in Maluku is almost certainly of a fairly recent date.

Gymnotympana Stål

Gymnotympana Stål, 1861 of the Chlorocystini shows a quite different distributional pattern than *Cosmopsaltria*. Apart from two endemic species (*G. hirsuta* and *G. verlaani*) in central Papua New Guinea, this genus is virtually absent in the central mountain ranges (fig. 32). For exact data on the distribution of the species see Moulds (1990) and De Boer (1995a). *Gymnotympana* is distinctly concentrated in eastern New Guinea, and more precisely on the Papuan peninsula. Of the 20 species of *Gymnotympana*, 15 occur in Papua New Guinea, 9 of which occur in the Papuan peninsula, while 6 are endemic there. Moreover, one species (*G. langeraki*) is endemic to the D'Entrecasteaux islands, which in geological sense form a part of the Papuan peninsula. A monophyletic subgroup of three species is restricted to northern Maluku and a monophyletic subgroup of two species is endemic to northern Queensland. The Australian species *Venustria superba* might belong to the latter group (see the section on the Australian genera below and De Boer 1995a, d). Three relatively widely distributed species (*G. dahli*, *G. membrana*, and *G. rubricata*) occur in northern New Guinea and the Papuan peninsula, while *G. dahli* extends even farther westward to Biak and to Manus and New Britain.

Gymnotympana presumably originates from the Papuan peninsula, the East Papua Composite terrane as defined by Pigram and Davies (1987), although part of northern Maluku presumably also formed part of the ancestral distribution area. A presumed origin on the East Papua Composite terrane seems to be corroborated by the occurrence of the genus on the D'Enterecasteaux islands, the Louisiade archipelago and on Woodlark island; these islands are supposed to have formed part of, or been related to, the East Papua Composite block. On the other hand the fact that two of the three species distributed on these islands (*G. rubricata* and *G. strepitans*) have a wider distribution in New Guinea, makes a dispersal into these islands, possibly during Pleistocene low sea levels, equally plausible.

The occurrence of *Gymnotympana* species (widespread or endemic) in northern New Guinea, central Papua New Guinea, the Bismarck Archipelago, and northern Queensland is presumably due to recent dispersals, that took place after the accretion of the Finisterre terrane and the termination of the isolation of the Papuan peninsula by the closure of the Aure Trough. The comparatively wide distributions of those species that occur in northern New Guinea and the Bismarck Archipelago suggest that they more easily disperse. The two endemics in the easternmost part of the central mountain ranges presumably got isolated after a westward diffusion of their ancestors, and the common ancestor of the two (or three, *V. superba*) endemic Queensland species possibly reached Australia during one of the glacial related Pliocene-Pleistocene sea level falls. In that case, one might expect to find a *Gymnotympana* species in southern New Guinea as well; since large parts of southern New Guinea are hardly accessible and definitely undercollected such a species might very well exist.

The distribution of *Gymnotympana* in northern Maluku did presumably not result from dispersal, but is supposed to indicate a historical proximity between the Halmahera arc and the terranes of the Papuan peninsula. This assumption is based on geological evidence for an eastern origin of Halmahera, the disjunction of the *Gymnotympana* distribution in the Birds Head area, and the fact that a very similar disjunct pattern was found for the genus *Diceropyga*. The latter argument indicates that there must be a common cause for these two distribution patterns rather than two independent chance disperals.

Diceropyga Stål

The distribution pattern of the genus *Diceropyga* Stål, 1870 of the Cosmopsaltriaria (fig. 33) is, as far as its New Guinean and Moluccan species are concerned, very similar to that of *Gymnotympana*; a similar origin on the Papuan peninsula (viz., the East Papua Composite terrane) and part of the northern Moluccas seems plausible. Within New Guinea, there is a distinct concentration of *Diceropyga* species in the Papuan peninsula; in fact all species that occur on New Guinea are recorded from the Papuan peninsula, and several of them are endemic there. For exact data on the distribution of the species of *Diceropyga* see Duffels (1977, 1988b). *Diceropyga*, just like *Gymnotympana*, is almost lacking in the central mountain ranges and absent in the northern part of the Birds Head, but reappears in Maluku with a monophyletic group of four endemic species, the *D. obtecta* group. The distribution in Maluku also includes Buru, Seram, and Sula (*D. obtecta*). *Diceropyga* has no

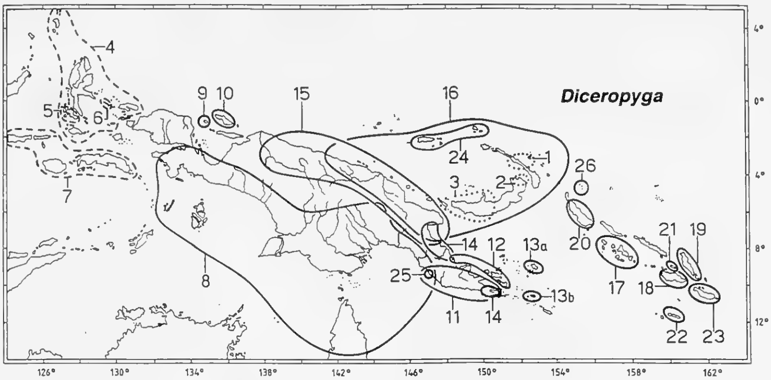


Fig. 33. Distribution of the species of *Diceropyga*: dotted line: *obliterans* group, *noonadani* (1), *novaebritannicae* (2), *obliterans* (3); interrupted line: *obtecta* group, *junctivitta* (4), *bacanensis* (5), *ochrothorax* (6), *obtecta* (7); uninterrupted line: *subapicalis* group, *subapicalis* (8), n.sp. Numfur (9), n. sp. Biak (10), *bicornis* (11), *auriculata* (12), *woodlarkensis* (13), *subjuga* (14), *bihamata* (15), *gravesteini* (16), *major* (17), *guadalcanensis* (18), *malaitensis* (19), *bougainvillensis* (20), *tortifer* (21), *rennellensis* (22), *aurita* (23), *triangulata* (24), *novaeguinae* (25), *didyma* (26).

endemic species in Australia, but *D. subapicalis* is widely distributed in southern New Guinea, the Aru islands, and northern Queensland. The fairly wide distribution of that species suggests dispersal. Two species (*D. bihamata* and *D. gravesteini*) have a fairly wide distribution in northern New Guinea, while *D. gravesteini* extends to the Bismarck Archipelago and Admiralty islands. Furthermore, like in *Gymnotympana*, the distribution area of *Diceropyga* includes the D'Entrecasteaux islands, Misima island of the Louisiade Archipelago, and Woodlark island, which all have formed part of the East Papua Composite terrane.

There are, however, also several differences between the distribution patterns of *Diceropyga* and *Gymnotympana*. *Diceropyga* has a monophyletic group of three species (the *obliterans* group) in the Bismarck Archipelago, an endemic species on the Admiralty islands, and no less than eight endemic species, often restricted to a single island, on the Solomon Islands. Furthermore, *Diceropyga* has undescribed endemic species on Biak and Numfur islands in the Geelvink Bay (Duffels pers. comm.).

The *obliterans* group is the sister group of all other *Diceropyga* species, which suggests that its occurrence on the Bismarck Archipelago is not due to recent dispersal but results from a historical relationship between the Bismarck Archipelago and the East Papua Composite terrane. This suggests that the Bismarck Archipelago should be included in a presumed ancestral area of distribution. The relatively wide distribution of *D. gravesteini* in the Bismarck Archipelago, however, should probably have to be explained by a more recent dispersal event.

The occurrence of the *obtecta* group on Maluku must presumably be explained by a historical proximity between the Halmahera arc and the East Papua Composite terrane, for the same reasons mentioned above for *Gymnotympana*, and the Halmahera arc should be included in the area of origin of *Diceropyga*.

The speciation of *Diceropyga* on the Solomon Islands too, cannot easily be explained by dispersal. The Solomon species, which do not form a monophyletic group as was suggested earlier (Duffels 1977) (Duffels, pers. comm.), are closer related to the New Guinean species of the *subapicalis* group than to the *obliterans* group of the Bismarck Archipelago. This suggests that there has been a historical contact between the East Papua Composite terrane and the Solomon Islands, in bypassing the Bismarck Archipelago. At least part of the Solomon Islands should be included in the area of origin of *Diceropyga*.

Diceropyga triangulata, a species endemic to the Admiralty islands, is presumably related to the *obliterans* group and might have dispersed from the Bismarck Archipelago. The phylogenetic relationships of the two undescribed endemics of Biak and Numfur are not known and speculations on their possible origin either due to dispersal or to a vicariant event are premature.

Thaumastopsaltria Kirkaldy

Thaumastopsaltria Kirkaldy, 1900 of the Chlorocystini is, with only seven species, much smaller than the foregoing genera. For exact data on the distribution of the species see Moulds (1990) and De Boer (1992a). Four of the seven species of *Thaumastopsaltria* occur on the Papuan peninsula (fig. 34), but

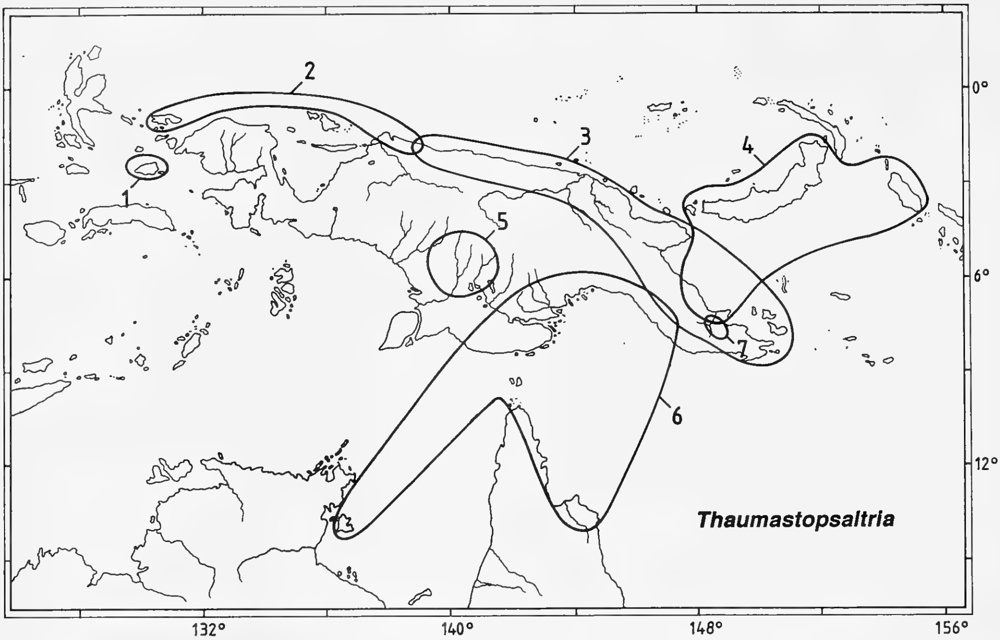


Fig. 34. Distribution f the species of *Thaumastopsaltria*: *adipata* (1), *sicula* (2), *lanceola* (3), *spelunca* (4), *sarissa* (5), *globosa* (6), *pneumatica* (7).

only one (*T. pneumatica*) is endemic there. The other three have a comparatively wide distribution, overlapping in the Papuan peninsula and extending to either southern New Guinea, northern Queensland and Grootte island (*T. globosa*), or to New Britain, Buka and Bougainville (*T. spelunca*), or along the northern mountain ranges to western New Guinea (*T. lanceola*). *Thaumastopsaltria* has one species restricted to southern New Guinea (*T. sarissa*) and one species occurring in northwestern New Guinea and on Waigeu island (*T. sicula*). The type-species of the genus (*T. adipata*) is presumed to come from the island of Misool, but this needs confirmation; the locality label 'M' on the only specimen known may also stand for Morotai (De Boer 1995a).

A weak concentration of species of *Thaumastopsaltria* on the Papuan peninsula, and a somewhat similar pattern of more or less widespread species in northern New Guinea as found for *Gymnotympana* and *Diceropyga*, and in southern New Guinea and Northern Queensland as found for *Diceropyga*, suggest that this genus also originates from the East Papua Composite terrane. The distribution of *Thaumastopsaltria* in other areas than the Papuan peninsula must probably be explained by recent dispersals that occurred since the closure of the Aure Trough. *T. globosa* could have reached Australia during the Pliocene-Pleistocene low sea levels. Only the occurrence of *T. adipata* on Misool, which is supposed to be most closely related to *T. pneumatica* from the eastern part of the Papuan peninsula, will presumably need another explanation. Should *T. adipata* come from Morotai, then *Thaumastopsaltria* shows the very same vicariant pattern between the Papuan peninsula and northern Maluku, as was found for *Diceropyga* and *Gymnotympana*. If so, the occurrence of *T. adipata* on Morotai could be explained by a historical proximity between the Halmahera arc, of which Morotai is supposed to form a part, and the East Papua Composite terrane. In this light it is interesting that also Waigeu where *T. sicula* occurs, is possibly a part of that Halmahera arc. *T. adipata* and *T. sicula*, however, are not sister species so that it can not be said that *Thaumastopsaltria* has a monophyletic group in the northern Maluku area.

Guineapsaltria De Boer

Guineapsaltria De Boer, 1993 of the Chlorocystini is more difficult to trace to its area of origin. For exact data on the distribution of the species of that genus see Moulds (1990) and De Boer (1993a). Six of the eight species of *Guineapsaltria* occur on the Papuan

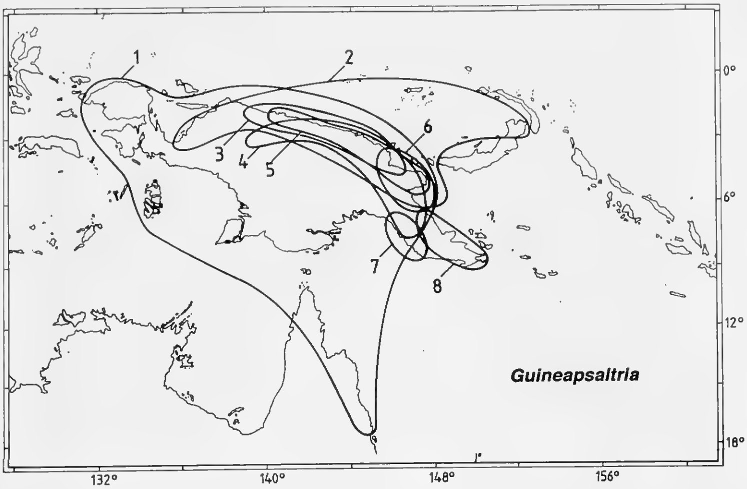


Fig. 35. Distribution of the species of *Guineapsaltria*: *flava* (1), *viridula* (2), *pallida* (3), *stylata* (4), *pallidula* (5), *pennyi* (6), *chinai* (7), *flaveola* (8).

peninsula (fig. 35), but only two (*G. chinai* and *G. flaveola*) are endemic there. However, apart from *G. flaveola*, which also occurs on Sideia island at the eastern tip of the Papuan peninsula, all these species seem confined to the western half of that peninsula only. Moreover *G. pennyi* and *G. viridula* are recorded only from the most northwestern corner of the Papuan peninsula.

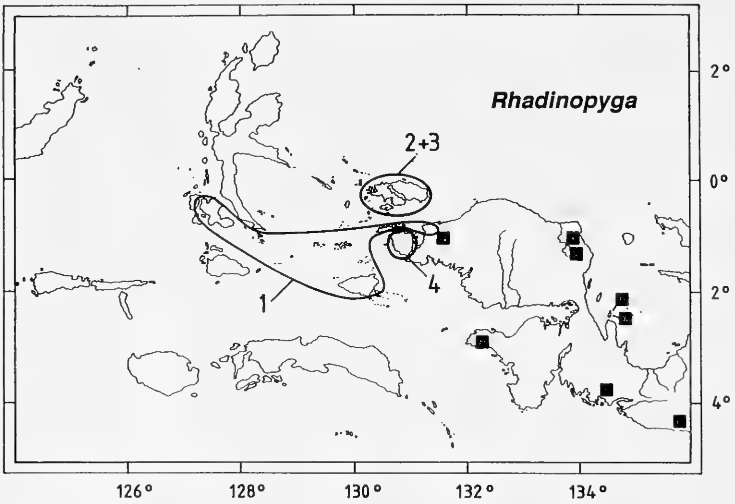
Five species have a fairly wide distribution in the northern mountain ranges of New Guinea, including the Huon peninsula, while two (*G. pallida* and *G. pallidula*) are endemic there. *G. viridula* extends over northern New Guinea to New Britain and Manus island, and *G. stylata* extends from northern New Guinea to half-way down the Papuan peninsula. *G. flava* has an extremely wide distribution compared to other New Guinean cicada species. That species is distributed all over New Guinea except for the central mountain ranges and the eastern part of the Papuan peninsula, and it also occurs on Aru island and along the east coast of northern Queensland. *G. pennyi*, finally, is restricted to the Huon peninsula and the northwestern corner of the Papuan peninsula.

Several areas seem equally plausible as area of origin for *Guineapsaltria*. Purely on account of the total number of species and endemics, one would favour the Papuan peninsula. The distribution of *G. flava* in Queensland, which is very similar to that of *Diceropyga subapicalis*, *Thaumastopsaltria globosa*, and *Gymnotympana rufa* and *G. varicolor* seems to corroborate this option, as it could represent a similar dispersal event. However, the extremely wide distribution of *G. flava* suggests that this species readily disperses, and the presumption of a similar dispersal event is therefore not strictly necessary. Furthermore, the fact that most of the *Guineapsaltria* species occurring on the Papuan peninsula are only present in the western half of the peninsula and continue in northern New Guinea, might indicate that they came there by dispersal, which makes an East Papua Composite terrane origin less likely. The only species occurring in the eastern part of the Papuan peninsula (*G. flaveola*) is the sister species of the widely distributed *G. flava* and might have reached these eastern parts also by dispersal. Alternatively, *Guineapsaltria* could originate from the terranes forming northern New Guinea, or from the Finisterre terrane. In the latter case one would expect a greater variety of species on New Britain and even on New Ireland, since the Finisterre terrane is supposed to have been connected to the Bismarck terranes. A supposed origin of *Guineapsaltria* on any of the terranes that now constitute northern New Guinea seems the best choice. This would mean, that *Guineapsaltria* arrived on New Guinea at about 10 Mya.

Rhadinopyga Duffels

Rhadinopyga Duffels, 1985 of the Cosmopsaltriaria is a fairly small genus with only four species described, but five other species that should be included in this genus still await their description. For exact data on the distribution of the species see Duffels (1985; 1986). *Rhadinopyga* is restricted to the Birds Head of New Guinea and some adjacent islands (fig. 36). *R. epiplatys* is recorded from the northwestern corner of the Birds Head, and from Misool and Bacan islands. *R. recedens* is endemic to Salawati, and *R. acuminata* and *R. impar* are endemic to Waigeu. The five undescribed species have an endemic distribution on the Birds Head and on Roon island (Duffels 1986).

Fig. 36. Distribution of the species of *Rhadinopyga*: *epiplatys* (1), *acuminata* (2), *impar* (3), *recedens* (4). Black squares represent localities of undescribed species.



This distribution area is of composite geological origin; the greater part of the Birds Head consists of two microcontinents, the Misool and Kemum terranes, that accreted about 10 Mya as a single block to New Guinea. Some terranes in the northern Birds Head are of OMA origin, they accreted fairly recently to New Guinea, about 2 Mya. The extensive speciation that occurred in and around the Birds Head suggests a long history of isolation on any of the two microcontinents rather than a recent dispersal and evolution since the accretion of the OMA fragments to the Birds Head. It is therefore supposed that *Rhadinopyga* is of microcontinental origin and evolved either on the Misool, or on the Kemum terrane, or on both after these terranes had fused. The occurrence of *R. epiplatys* on Bacan might be the result of a recent dispersal but could also result from the presumed historical proximity between the Bacan microcontinent and the Birds Head terranes. The latter possibility, however, implies that the Bacan microcontinent was emerged during its westward displacement, while it is supposed that many similar Moluccan microcontinents were submerged at that time (see chapter 2).

Aedeastria De Boer

Aedeastria De Boer, 1990 of the Chlorocystini is widely distributed in New Guinea and the northern Moluccas, but most of its twelve species are found in western New Guinea; the Birds Head and, especially, the islands adjacent to the Birds Head (fig. 37). For exact data on the distribution of the species see De Boer (1990; 1993b). Only two species actually occur on the Birds Head itself: *A. cobrops* is endemic there and *A. sepia* is known from one locality on the Birds Head, from Roon Island, and from one locality in the Torricelli mountains. The specimens from these three localities differ considerably, and it is quite possible that they represent three separate species (De Boer 1990). *Aedeastria* has several endemic species on the islands surrounding the Birds Head: *A. kaiensis* is endemic to the Kai Islands, *A. obiensis* is endemic to Obi, and *A. waigeuensis* is endemic to Waigeu Island. *A. cheesmanae* occurs only on Waigeu and Misool. Two species have a somewhat wider distribution in the northern Moluccas: *A. hastulata* is recorded from Bacan, Halmahera and Morotai, and *A. moluccensis* from Obi, Halmahera and Ternate. Only four species occur east of the Birds Head. *A. digitata* and *A. bullata* are endemics of northern New Guinea, both known from only one locality, and *A. dilobata* is known from one locality on the Papuan peninsula. *A. latifrons*, finally, has a fairly wide distribution in Irian Jaya, excluding the Birds Head but including the Aru Islands, and the western parts of Papua New Guinea. The species has apparently not been able to reach Queensland.

Considering the fact that most species of *Aedeastria* are found in western New Guinea, and that, just like the genus *Rhadinopyga*, several species are endemic to the islands adjacent to the Birds Head (*Aedeastria* and *Rhadinopyga* are the only two genera that have endemic species on these islands), it is plausible that *Aedeastria* also originates from one or both of the microcontinents that now form the greater part of the Birds Head peninsula. However, compared to *Rhadinopyga*, *Aedeastria* has notably less endemic species on the Birds Head itself.

The occurrence of *Aedeastria* in Maluku might,

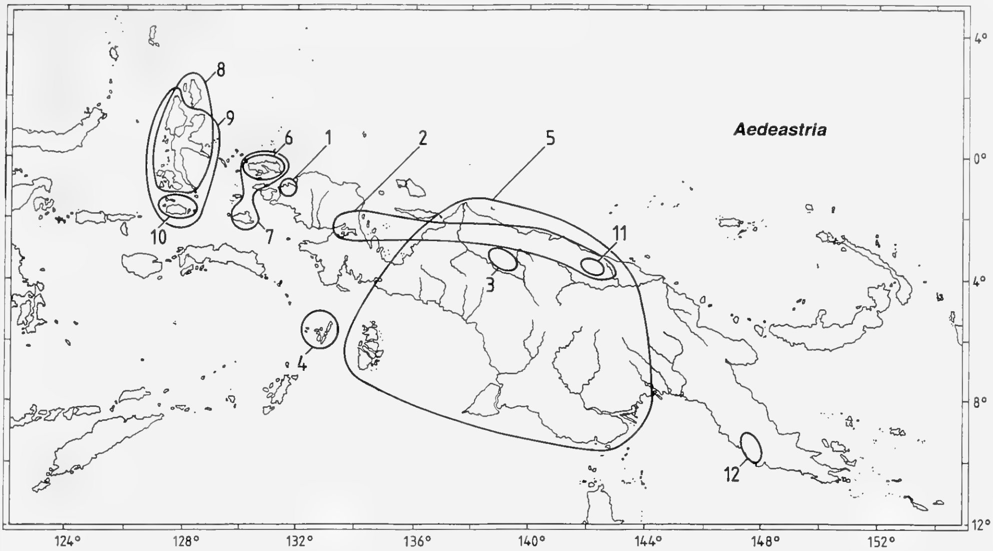


Fig. 37. Distribution of the species of *Aedeastria*: *cobrops* (1), *sepia* (2), *digitata* (3), *kaiensis* (4), *latifrons* (5), *waigeuensis* (6), *cheesmanae* (7), *hastulata* (8), *moluccensis* (9), *obiensis* (10), *bullata* (11), *dilobata* (12).

like in *Rhadinopyga* (fig. 36), either be due to dispersal or to the presumed historical proximity between the Bacan microcontinent and the Birds Head terranes. The latter possibility presupposes that the Bacan microcontinent had emerged before its westward displacement (see above). The apparent occurrence of two endemic species in Papua New Guinea is more difficult to explain. These two species strongly deviate and might be the sister group of all other *Aedeastria* species together.

Baeturia Stål

Baeturia Stål, 1866 of the Chlorocystini is with about 60 species by far the largest of the cicada genera occurring on New Guinea. The genus spans an extremely wide area of distribution, from Timor in the west, to Samoa and Tonga in the east. Most of the species of *Baeturia* are found on New Guinea, and all of the seven monophyletic species groups, that can be recognized within *Baeturia*, are represented on that island. For exact data on the distribution of the species see De Boer (1982, 1986, 1989, 1992b, 1994a, 1994b, 1994c, 1994d) and Duffels (1988a).

Only one of these monophyletic species groups of *Baeturia*, the *bloetei* group (fig. 38) occurs to the east of the Bismarck Archipelago, and is represented by eight species on the Solomon Islands, one on Vanuatu, one on Santa Cruz, one on Rotuma Island, and one on Samoa and Tonga.

Five species of *Baeturia* are recorded from west of New Guinea, and occur in the Maluku-Banda region. The *conviva* group (fig. 39) has a subgroup of three species that is presumed to be monophyletic and mainly distributed in northern Maluku (*B. conviva* is recorded from Bacan and Obi, *B. laureli* is endemic to Halmahera, and *B. schulzi* occurs on Buru, Seram and Sula). Both other species that occur in Maluku (*B. exhausta* and *B. macgillavryi*) are more widely distributed in southern Maluku, on the Banda Islands and on Timor. *B. macgillavryi* also occurs farther northward on Halmahera, Morotai, and Talaud (figs 38, 40).

Apart from the *conviva* and *bloetei* groups, all groups of *Baeturia* center on New Guinea and it is fairly certain that the genus originates from some part of that island. *Baeturia* species are found throughout New Guinea, but most species are recorded from its northern parts (the northern mountain ranges and the Huon peninsula) and a good amount of these species are endemic there. Six of the seven monophyletic species groups are represented by species in northern New Guinea and three such groups definitely center there: six of the eight species of the *exhausta* group (fig. 40) occur in northern New Guinea, two of them are endemic to the northern mountain ranges and two to the Huon peninsula; the *viridis* group (fig. 41) is represented by five of its seven species in northern New Guinea, four of them are endemics; and the *guttulinervis* group (fig. 39) is practically restricted to northern New Guinea.

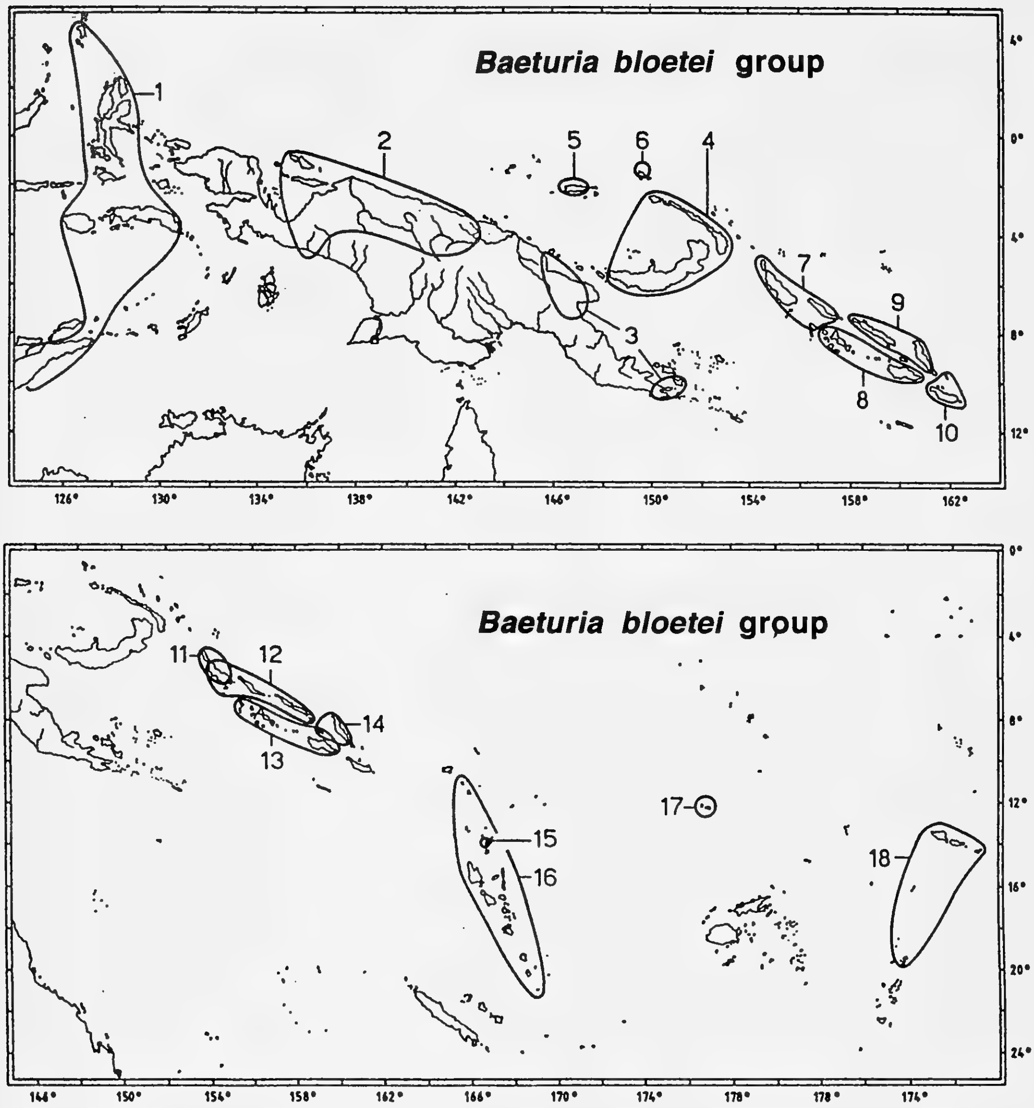


Fig. 38. Distribution of the species of the *Baeturia bloetei* group: *macgillavryi* (1), *bloetei* (2), *papuensis* (3), *bismarckensis* (4), *manusensis* (5), *mussauensis* (6), *brandti* (7), *sedlacekorum* (8), *reinhoudti* (9), *cristovalensis* (10), *gressitti* (11), *bilebanarai* (12), *mendanai* (13), *marginata* (14), *boulardi* (15), *edauberti* (16), *rotumae* (17), *maddisoni* (18).

This apparent concentration of *Baeturia* in northern New Guinea becomes the more clear when its distribution in other parts of the island is analysed. Only four or five species are known from the lowlands of southern New Guinea, while only two (*B. lorentzi* and *B. brongersmai*) are endemic there, although *B. hartonoi*, which is known from only one locality just south of the central mountain ranges, must possibly also be regarded as a southern New Guinea endemic. This small number of species is not remarkable considering the fact that these southern parts of the island are not of island arc origin and must have received their cicadas by dispersals. More remarkable are the comparatively low numbers of species on both the Birds Head and the Papuan peninsula. Four species (*B. bicolorata*, *B. parva*, *B. quadrifida*, and *B. viridis*)

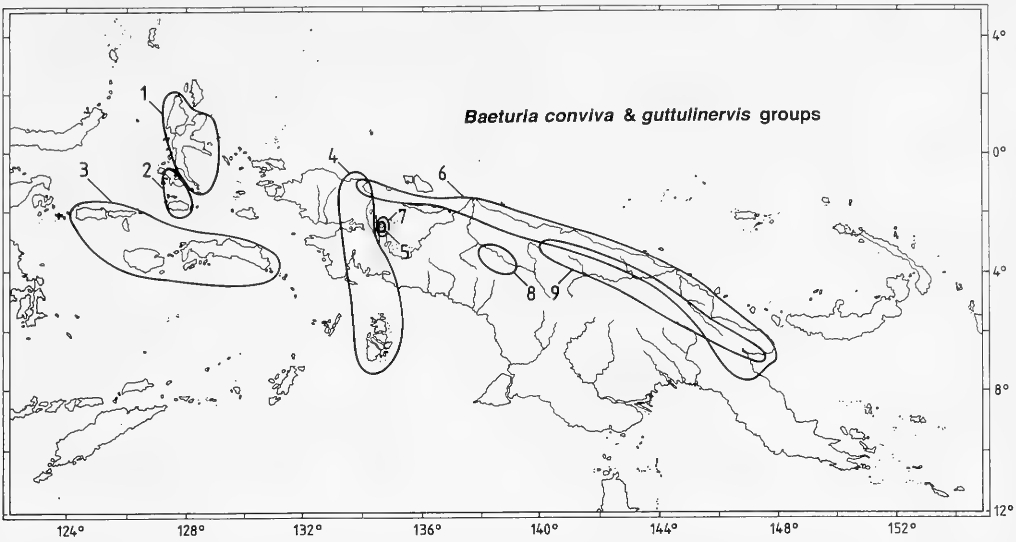


Fig. 39. Distribution of the species of the *Baeturia conviva* and *guttulinervis* groups: *laureli* (1), *conviva* (2), *schulzi* (3), *quadrifida* (4), *hardyi* (5), *inconstans* (6), *roonensis* (7), *guttulinervis* (8), *biroi* (9).

are recorded from the Birds Head, but none of them is endemic there. No less than fourteen species are recorded from the Papuan peninsula, but four of these (*B. fortuini*, *B. gigantea*, *B. inconstans*, and *B. wauensis*) are recorded from its most northwestern corner only. Three species, all of the *nasuta* group (*B. laminifer*, *B. mamillata*, and *B. nasuta*), are distributed in the Papuan peninsula and the central mountain ranges of New Guinea, while two species (*B. papuensis* and *B. vanderhammeni*) have a wide distribution in the peninsula and northern New Guinea. The record of *B. papuensis* from the Papuan peninsula is considered doubtful (De Boer 1989). Only five *Baeturia* species can be considered as endemic to the Papuan pe-

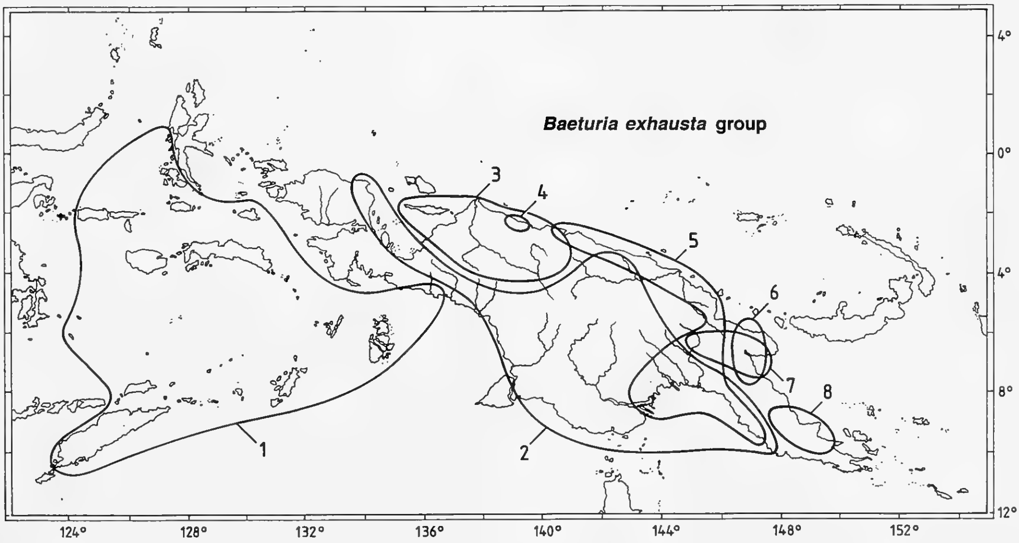


Fig. 40. Distribution of the species of the *Baeturia exhausta* group: *exhausta* (1), *bicolorata* (2), *rossi* (3), *maai* (4), *vanderhammeni* (5), *colossea* (6), *wauensis* (7), *versicolor* (8).

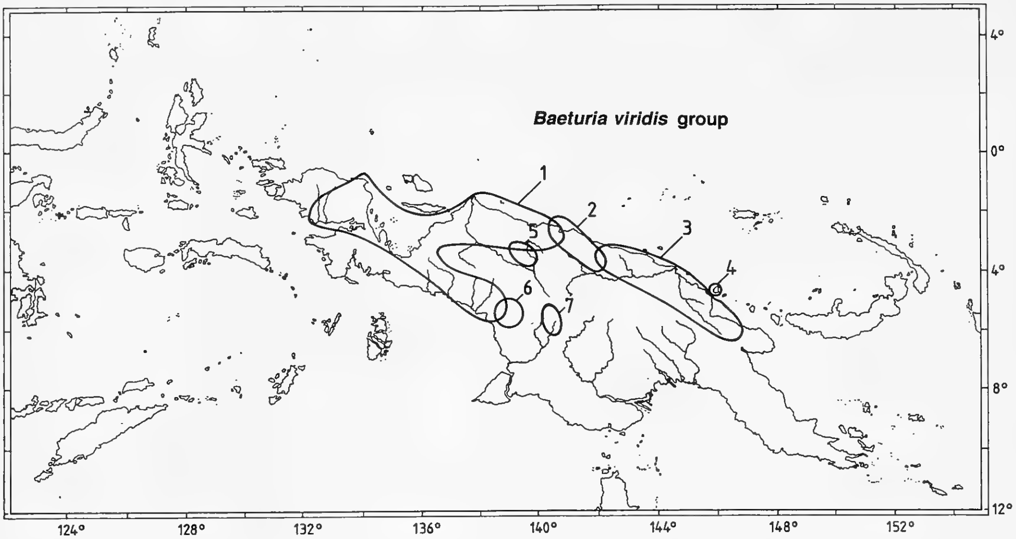


Fig. 41. Distribution of the species of the *Baeturia viridis* group: *viridis* (1), *furcillata* (2), *turgida* (3), *karkarensis* (4), *rufula* (5), *lorentzi* (6), *brongersmai* (7).

ninsula (*B. daviesi, B. gibberosa, B. loriae, B. tenuispina*, and *B. versicolor*), although *B. tenuispina* has a slightly wider distribution in the Huon peninsula and on Normanby Island. It is remarkable that two of these endemics (*B. daviesi* and *B. loriae*) belong to the *loriae* group (fig. 42), while a third (*B. tenuispina*) is supposed to be closely related to that group. The phylogenetic position of the *loriae* group is regarded doubtful, since its species share several characters with species of *Gymnotympana* (De Boer 1994a; 1995a), which genus seems to be a typical Papuan peninsula group, presumably originating from the East Papua Composite terrane (see above). It appears that the *loriae* group not only takes an intermediate position in a phylogenetic, but also in a biogeographic sense.

Two of the seven monophyletic species groups of *Baeturia* have species distributed in the central mountain ranges of New Guinea. Four species of the *loriae* group (fig. 42), the group with the dubious phylogenetic relationships, occur in or near the central mountains, and three of these (*B. pigrami, B. silveri*, and *B.*

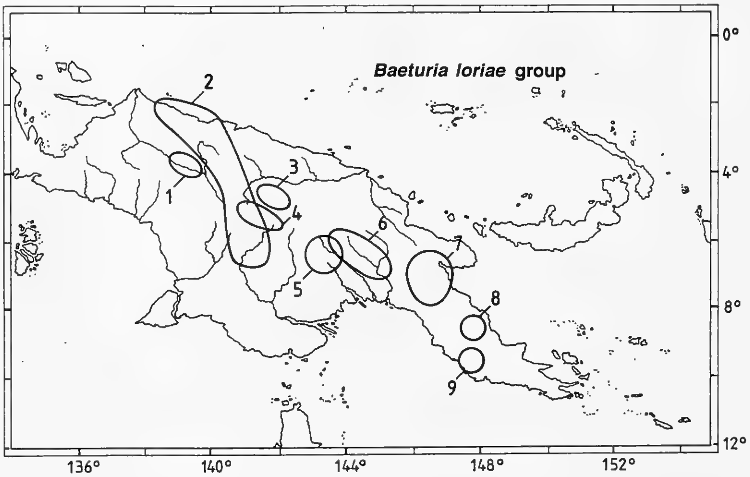


Fig. 42. Distribution of the species of the *Baeturia loriae* group: *hamiltoni* (1), *bemmeleni* (2), *wegeneri* (3), *pigrami* (4), *hartonoi* (5), *silveri* (6) *fortuini* (7), *daviesi* (8), *loriae* (9).

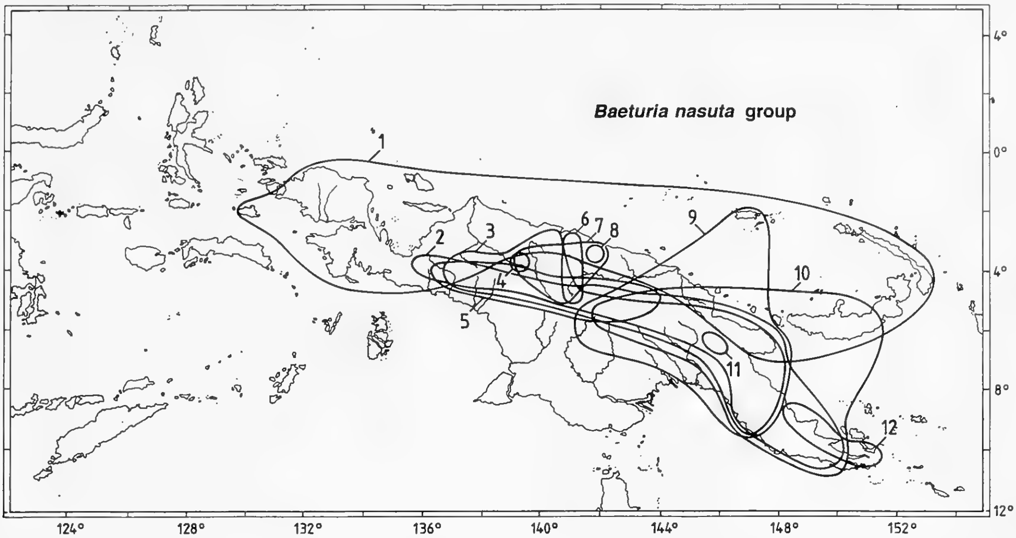


Fig. 43. Distribution of the species of the *Baeturia nasuta* group: *parva* (1), *mamillata* (2), *nasuta* (3), *bipunctata* (4), *arabuensis* (5), *guttulipennis* (6), *marmorata* (7), *splendida* (8), *retracta* (9), *laminifer* (10), *intermedia* (11), *gibberosa* (12).

wegeneri) seem endemic to part of that area. Other species of the *loriae* group occur in the Papuan peninsula (see above), northern New Guinea and the Huon peninsula, while *B. hartonoi* of that group occurs just south of the central mountains (fig. 42). The *nasuta* group (fig. 43) has been regarded as a typical central mountain range group and was discussed before in comparison with *Cosmopsaltria* (De Boer 1982; Duffels & De Boer 1990). However, four species that were recently added to this group (De Boer 1994d), and new biogeographical data on some of the other species, somewhat changed the general distribution pattern of the *nasuta* group. Furthermore, the area around Araucaria camp and Rattan camp, where two species of this group are endemic, and which apparently forms part of the Sepik terrane (fig. 16), should in a biogeographic sense possibly be regarded as part of northern, rather than central, New Guinea, or at least as a transition area. Most species from this area have their nearest relatives in northern New Guinea. Still, relatively many species of the *nasuta* group, six out of twelve, occur in the central mountain ranges,

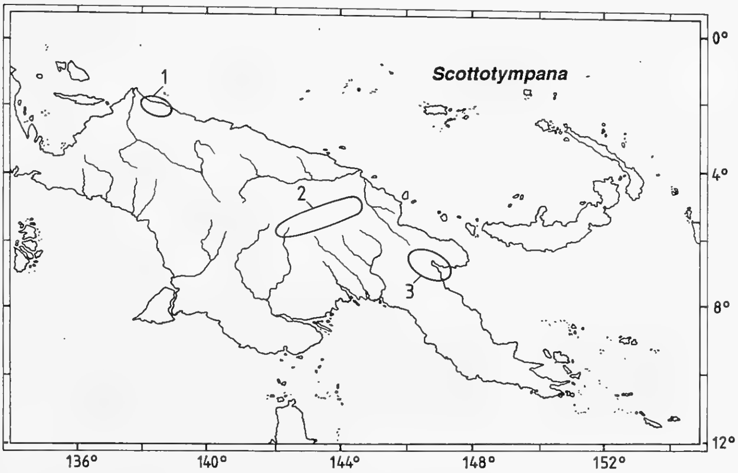


Fig. 44. Distribution of the species of *Scottotympana*: *sahebdivanii* (1), *biardae* (2), *huibregtsae* (3).

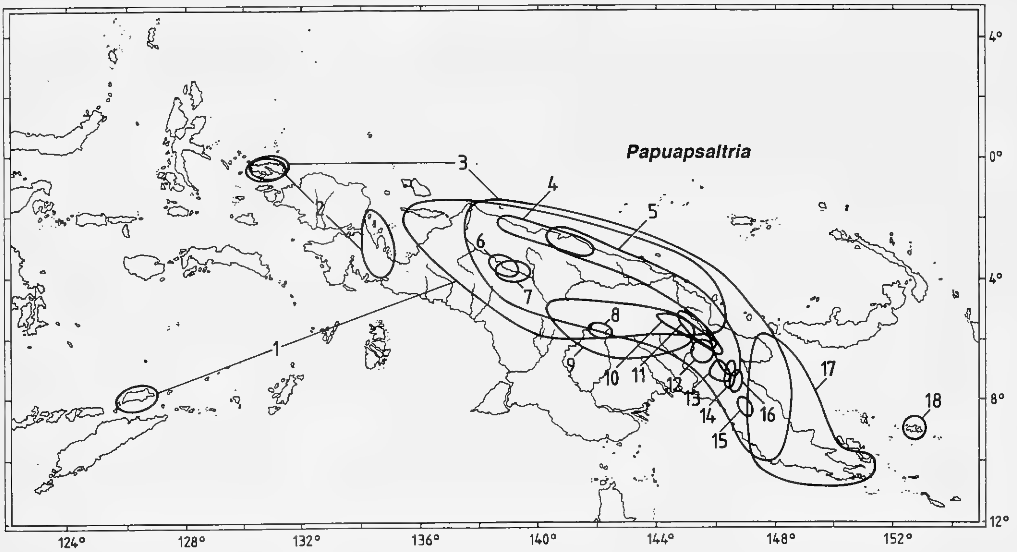


Fig. 45. Distribution of the species of *Papuapsaltria*: *bidigitula* (1), *dolabrata* (2), *phyllophora* (3), *baasi* (4), *lachlani* (5), *toxopei* (6), *ustulata* (7), *novariae* (8), *dioedes* (9), *goniodes* (10), *spinigera* (11), *brassi* (12), *plicata* (13), *stoliodes* (14), *ungula* (15), *angulata* (16), *nana* (17), *woodlarkensis* (18).

though only two (*B. arabuensis* and *B. intermedia*) appear to be actually endemic there. Others extend to the Huon and Papuan peninsulas (*B. nasuta* and *B. mamillata*), or have an even wider distribution reaching the Bismarck Archipelago and Admiralty islands (*B. laminifer* and *B. retracta*). The latter species also occurs in northern and southern New Guinea. Of the remaining six species of the *nasuta* group, one (*B. gibberosa*) is endemic to the Papuan peninsula, two are presumably endemic to northern New Guinea and one (*B. parva*) is widely distributed in Misool, the Birds Head, Biak, northern New Guinea, the Bismarck Archipelago, and the Admiralty islands. The *nasuta* group has thus as many species, and endemics, in northern as in central New Guinea.

The fact that *Baeturia* has most of its endemic species in northern New Guinea and that six out of its seven monophyletic groups have species in that area, suggests that *Baeturia* originates from one of the OMA fragments that now form the mountain ranges of northern New Guinea, viz., the Torricelli, Prince Alexander, Mt. Turu, and Gauttier terranes (fig. 16). It seems that the Finisterre terrane has to be ruled out as a possible source area of *Baeturia*, since if it, as is suggested, has formed a geological entity with the Bismarck Archipelago, one would expect a comparatively high rate of endemism in the Bismarck Archipelago as well, but only *B. bismarckensis* is endemic there.

An origin of *Baeturia* on one of the northern New Guinea terranes would mean that *Baeturia* arrived fairly recently (10 Mya) on New Guinea, and that the occurrence of *Baeturia* in other parts of that island is the result of dispersal since the amalgamation of these terranes. This might explain why the otherwise widely distributed genus *Baeturia* is absent in Australia. When *Baeturia* reached New Guinea, its southward dispersal was blocked by the central mountains, and by the time species of the genus had moved around this barrier and reached southern New Guinea, the Torres Straight prevented their crossing to Queensland. Only some species of the *nasuta* and *loriae* groups apparently had the opportunity to disperse into the central mountains.

Scottotympana De Boer

Scottotympana De Boer, 1991 of the Chlorocystini is a very small genus of four species, three of which are described (fig. 44). For exact data on the distribution of these species see De Boer (1991). Since all these species are known of only one or two localities, it is very difficult to recognize a pattern of distribution. Nevertheless, the genus seems to be concentrated in the northern parts of New Guinea; *S. sahebdivanii* is recorded from the northwestern corner of Irian Jaya, *S. biardae* from northern and central Papua New Guinea, and *S. huibregtsae* from a locality just south of the Huon peninsula and, possibly, New Britain.

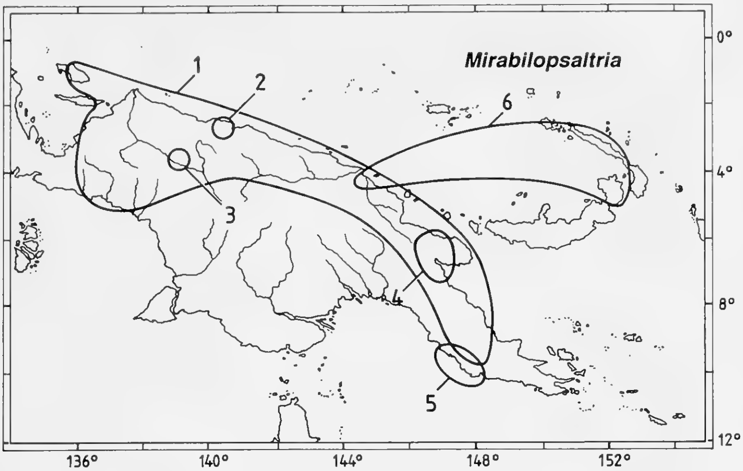


Fig. 46. Distribution of the species of *Mirabilopsaltria*: *humilis* (1), *inconspicua* (2), *toxopeusi* (3), *globulata* (4), *viridicata* (5), *inflata* (6).

The undescribed species concerns one specimen from Humboldt Bay in northern New Guinea. It seems most plausible that the genus originates from any of the terranes of northern New Guinea.

Papuapsaltria De Boer

Of the last two New Guinean genera to be discussed, *Papuapsaltria* De Boer, 1995 and *Mirabilopsaltria* De Boer, both of the Chlorocystini, a monophyletic origin is considered far from certain. And, curiously enough, these genera are most difficult to trace to an area of origin. *Papuapsaltria* De Boer (fig. 45) is distributed throughout the greater part of New Guinea and is also recorded from the islands of Normanby, Roon, Waigeu, Woodlark, and Japen. The record of one of its species from Wetar Island is considered doubtful. For exact data on the distribution of the species of this genus see De Boer (1995c). *Papuapsaltria* is presumably absent from the Birds Head peninsula (though several species occur in various adjacent areas), from the southern parts of central New Guinea, and from the western parts of the central mountain ranges. Most species of *Papuapsaltria* are found in Papua New Guinea: of its 18 species, 11 occur in Papua New Guinea, and nine are endemic there. Four of these endemic species are restricted, or practically restricted, to the Papuan peninsula, while *P. woodlarkensis* is endemic to Woodlark Island, which has formed a geological entity with the Papuan peninsula. Furthermore three species are endemic to the mountain ranges just south of the Huon peninsula, bordering on the Papuan peninsula. These numbers of endemics seem to indicate an origin of the genus on the East Papua Composite terrane. Similar to *Guineapsaltria*, most of the species that actually occur on the Papuan peninsula are restricted only to the western half of that peninsula, which for *Guineapsaltria* was regarded as an indication that that genus originated from the northern New Guinea terranes. However, compared to *Guineapsaltria, Papuapsaltria* shows quite a different pattern of distribution. The Papuan peninsula species of *Papuapsaltria* are all species with a very restricted area of distribution. An East Papua Composite terrane origin of *Papuapsaltria*, as proposed here, is also suggested by the fact that a similarly wide distribution from the Papuan peninsula to northern New Guinea, as found for *P. phyllophora* and *P. lachlani*, resembles that of several species of *Diceropyga*, *Gymnotympana*, and *Thaumastopsaltria* (the three other genera for which an East Papua Composite terrane origin was proposed). Such distributions can be explained by recent dispersals from the Papuan peninsula into northern New Guinea.

However, *Papuapsaltria* has no less than five endemic species (*P. baasi*, *P. dolabrata*, *P. novariae*, *P. toxopei*, and *P. ustulata*) in northwestern New Guinea, which presumably form a monophyletic group. Furthermore, *P. bidigitula* might also be endemic to (north)western New Guinea (its record from Wetar is questionable, the species is not known from any of the intermediate Moluccan and Banda islands). These endemics cannot easily be explained by a dispersal from the Papuan peninsula and the origin, of at least the ancestor of the above mentioned monophyletic group, on the Gauttier, Prince Alexander, Mt Turu, and/or Torricelli terranes of northern New Guinea (fig, 16) must be seriously considered. In this light it is interesting that some of the most parsimonious phylogenetic reconstructions do not recognize the monophyly of *Papuapsaltria* and regard its northwestern subgroup as a sister group of *Guineapsaltria* (De Boer 1995d). Since *Guineapsaltria* supposedly is of northern New Guinea origin (see above), a subdivision between a monophyletic group containing *Guineapsaltria* and this northwestern subgroup of *Papuapsaltria*, and a monophyletic group containing the remaining species of *Papuapsaltria* would even more clearly indicate a subdivision between an East Papua Composite terrane group and a northern New Guinea group.

Mirabilopsaltria De Boer

The monophyly of *Mirabilopsaltria* De Boer, 1995, just like that of *Papuapsaltria* (see above), is considered fairly uncertain, and is not based on sound apomorphic characters. Most species of *Mirabilopsaltria* are certainly closely related, of others the generic allocation is somewhat doubtful. The most parsimonious computer analysis shows *Mirabilopsaltria* as a paraphyletic group, but it depends on the homology of a certain clasper character whether this solution is acceptable (De Boer 1995d).

Mirabilopsaltria of the Chlorocystini is distributed along northern New Guinea including Biak island, the Huon peninsula, and the western half of the Papuan peninsula (fig. 46). For exact data on the distribution of the species see De Boer (1995b). One species (*M. inflata*) is possibly endemic to the Bismarck Archipelago, though a female from northern New Guinea might belong to that same species. *M. humilis* spans the whole length of the distribution area of the genus, from Biak Island and the south coast of western New Guinea to half-way down the Papuan peninsula. All other species have much more restricted areas of distribution. Their distribution ranges apparently do not overlap; the species are fairly evenly distributed over the area covered by the genus: *M. viridicata* is endemic to the Papuan peninsula, *M. globulata* to the Huon peninsula and adjacent areas, and *M. inconspicua* and *M. toxopeusi* are known (both from one locality) from northwestern New Guinea. Consequently, there is no concentration whatsoever of numbers of species in any particular part of the distribution area. However, three, possibly four, of the six species occur in northern New Guinea and an origin of *Mirabilopsaltria* in the Gauttier and/or the Torricelli terranes seems therefore the most plausible.

Should *Mirabilopsaltria* in fact turn out to be polyphyletic, as appears to be the most parsimonious solution (De Boer 1995d), then the Papuan species of the genus (*M. globulata* and *M. viridicata*) most probably form a monophyletic group together with the, presumably Papuan peninsula genus *Thaumastopsaltria*, which would even more clearly indicate a subdivision in an east Papuan group (*Thaumastopsaltria* and these two species), and a northern New Guinea group which extends to the Bismarck Archipelago (the remaining four species of *Mirabilopsaltria*).

The Australian genera of the Chlorocystini

There are six genera which are assigned to the the Chlorocystini (sensu stricto), and do not occur on New Guinea. These genera (*Chlorocysta* Westwood, 1851, *Cystopsaltria* Goding & Froggatt, 1904, *Cystosoma* Westwood, 1842, *Glaucopsaltria* Goding & Froggatt, 1904, *Owra* Ashton, 1912, and *Venustria* Goding & Froggatt, 1904) are all endemic to northeastern or eastern Australia. For more exact data on the distribution of the species of these genera see Moulds (1990).

The monotypic genus *Venustria* is endemic to the southeastern corner of the Cape York Peninsula of northern Queensland. The systematic status of *Venustria* is uncertain, *V. superba* shares several characters with the two Australian species of the genus *Gymnotympana*, but the species is not included in that genus since it does not share the supposedly apomorphic sexual dimorphism in wing venation of *Gymnotympana* (De Boer 1995a). Should *V. superba* form a monophyletic group with *G. rufa* and *G. varicolor*, then their common ancestor (as explained above) presumably dispersed during Pleistocene low sea levels, from the Papuan peninsula of New Guinea to Australia. However, should *Venustria*, which is certainly closely related to *Gymnotympana*, not be part of that genus, its presence in Australia must either precede the arrival of the ancestor of the Australian *Gymnotympana* species, or an ancestral *Venustria* species must have occurred on New Guinea before its dispersal to Australia.

Chlorocysta, *Glaucopsaltria*, and *Owra* form a monophyletic group (De Boer 1995d) of which five species are described: *Chlorocysta* has three described and one or two undescribed species, both other genera are monotypic. These three genera are discussed here as a single group. The distribution of this group, along the eastern coast of Queensland, resembles that of the Australian species of *Diceropyga*, *Guineapsaltria*, *Gymnotympana*, and *Thaumastopsaltria*, but the group reaches farther southward, into New South Wales, with *C. vitripennis* and *G. viridis* (fig. 47 after Moulds 1990). As explained above, the Australian distribution of *Diceropyga*, *Guineapsaltria*, *Gymnotympana*, and *Thaumastopsaltria* presumably results from a dispersal from New Guinea, possibly during the ice age related Pliocene-Pleistocene low sea levels. The similarity in distribution patterns between the Australian species of these genera and the group discussed here does not necessarily have to be explained by a similar dispersal event; their distributions simply coincide with the distribution of tropical rain forest

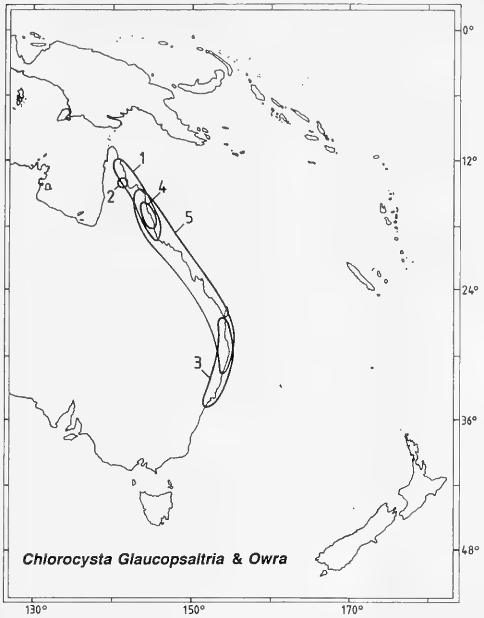


Fig. 47. Distribution of the species of *Chlorocysta*, *Glaucopsaltria*, and *Owra*: *C. suffusa* (1), *C. fumea* (2), *C. vitripennis* (3), *O. insignis* (4), *G. viridis* (5).

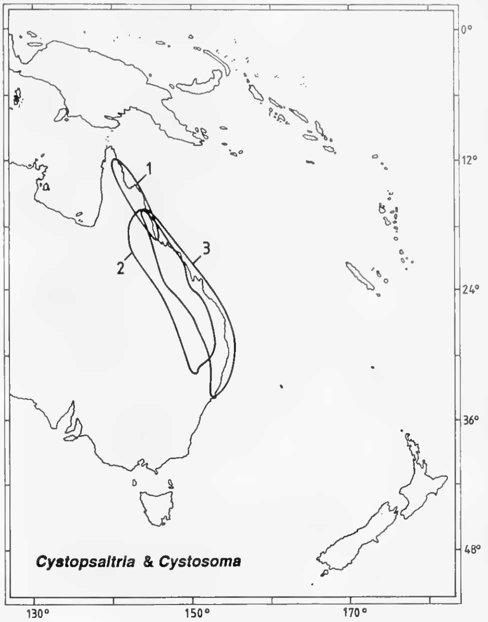


Fig. 48. Distribution of the species of *Cystopsaltria* and *Cystosoma*: *Cystopsaltria immaculata* (1), *Cystosoma schmeltzi* (2), *Cystosoma saundersii* (3).

in Australia. The speciation that occurred within this monophyletic group of Australian genera, the fact that the group has no representatives on New Guinea, and possibly also its larger distribution area, suggest that its common ancestor either arrived in Australia by an earlier dispersal event, or that the group has always been there. In the latter case, it would mean that the Chlorocystini are of Australian origin, and that its species entered the OMA from Australia. The geological literature does not contradict this possibility, since rifted microcontinents of Australian origin are supposed to have become incorporated in the OMA, long before the OMA broke up and its fragments collided with the Australian coninent. However, the fact that the sister group of the Chlorocystini is found on Sulawesi and the nearest outgroup in southeast Asia, strongly contradicts such an Australian origin and it seems more plausible that the common ancestor of *Chlorocysta*, *Glaucopsaltria*, and *Owra* entered Australia from one of the OMA terranes.

Cystosoma (two species) and *Cystopsaltria* (one species) also form a monophyletic group (De Boer 1995d). The distribution of this group is very similar to that of the group of three genera discussed above. *Cystopsaltria* follows the eastern coast of the Cape York Peninsula and *Cystosoma* is distributed in eastern Australia, from the southeastern corner of the Cape York Peninsula into northern New South Wales (fig. 48 after Moulds 1990).

The distribution of *Cystosoma* and *Cystopsaltria* must presumably be explained along similar lines as the distribution of the monophyletic group consisting of *Chlorocysta*, *Glaucopsaltria* and *Owra*: either their common ancestor dispersed from New Guinea, preceding the dispersals to Australia found for *Diceropyga*, *Gymnotympana*, *Guineapsaltria*, and *Thaumastopsaltria*, or that ancestor has always been in Australia.

The non-New Guinean genera of the Cosmopsaltriaria

Five genera of the Cosmopsaltriaria are absent from New Guinea: *Aceropyga* Duffels, 1977, *Brachylobopyga* Duffels, 1982, *Dilobopyga* Duffels, 1977, *Moana* Myers, 1928, and a new genus from the Solomon Islands recently recognized by Duffels (in prep.), henceforth referred to as new genus *'I.'* *Brachylobopyga* and its sister genus *Dilobopyga* are endemics of Sulawesi, the new genus *'I.'* is endemic to the Solomon Islands, and *Aceropyga* and its sister genus *Moana* are restricted to the eastern parts of the OMA.

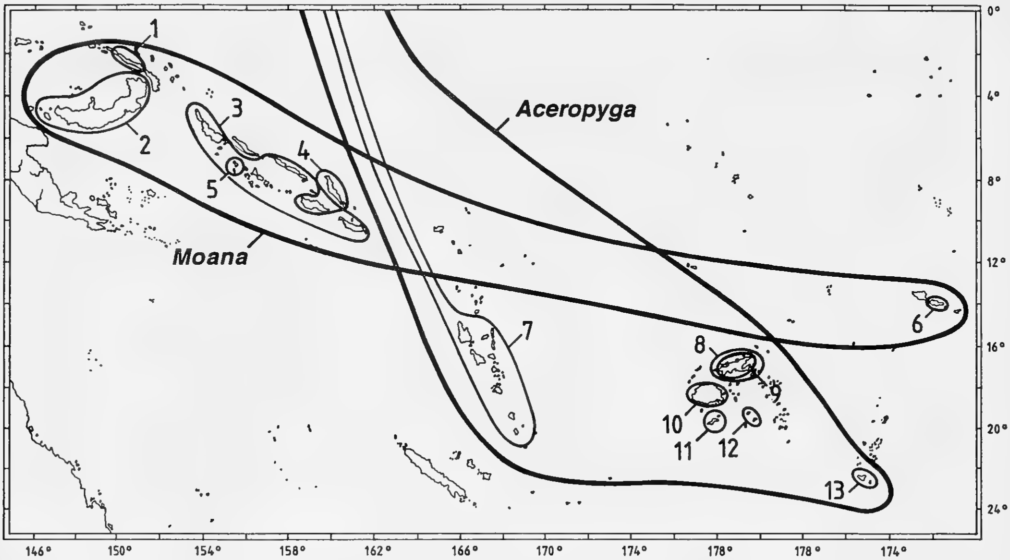


Fig. 49. Distribution of the species of *Moana* and *Aceropyga*: *M. novaeirelandicae* (1), *M. obliqua* (2), *M. aluana aluana* (3), *M. aluana torquata* (4), *M. aluana minima* (5), *M. expansa* (6), *A. poecilochlora* (7), *A. corynetus ungulata, A. distans taveuniensis, A. stuarti pallens* (8), *A. huireka* (9), *A. acuta, A. corynetus corynetus, A. distans distans, A. egmondae, A. macracantha, A. philorites, A. pterophon, A. stuarti stuarti,* (10), *A. corynetus monacantha* (11), *A. distans lineifera* (12), *A. albostriata* (13).

Aceropyga Duffels

Aceropyga Duffels, 1977 (fig. 49) is recorded from Vanuatu and Kusaie Island of the Caroline Islands (1 species), Fiji (14 (sub)species), and Tonga (1 species). For exact data on the distribution of the species of this genus see Duffels (1977, 1988a). Kusaie Island is not a part of the OMA. The extensive speciation that took place on Fiji, suggests that *Aceropyga* evolved in isolation on the Fiji islands. Taking into account that its sister genus, *Moana*, is distributed in other parts of the eastern OMA, *Aceropyga* must have reached Fiji through this arc before its break-up of about 5 Mya (Duffels 1988a; De Boer 1989). It is supposed that the geological event that separated Fiji from the OMA, also separated the ancestors of *Aceropyga* and *Moana*. The occurrence of *Aceropyga* outside the Fiji group might be due to recent dispersals. The wide distribution of *A. poecilochlora* in Vanuatu and Kusaie Island, compared to the strict island endemism of the Fiji (sub)species, certainly suggests dispersal. On the other hand, since southern Vanuatu was adjacent to Fiji before the break-up of the eastern OMA, this distribution in Vanuatu might also represent an older vicariant pattern.

Moana Myers

Moana Myers, 1928 was recently identified as the sister genus of *Aceropyga* and three species, formerly forming the *Aceropyga aluana* group, were added to this previously monotypic genus. *Moana* is now recorded from the Bismarck Archipelago (2 species), the Solomon Islands (1 species with 3 subspecies), and western Samoa (1 species) (fig. 49). For exact data on the distribution of the species of this genus see Duffels (1977, 1993). This distribution does not readily suggest an origin in any particular part of the distribution area since there are no concentrations of cooccurring species. It is supposed though, that *Moana* and *Aceropyga* evolved within the eastern parts of the OMA, at a time when these parts still formed a more or less continuous island chain, with the Vanuatu chain linking the Solomons to Fiji (fig. 22). The question is, along which route the ancestor of these two genera reached the eastern parts of the island chain. The most obvious route, along the Bismarck Archipelago, becomes doubtful, when the proximity between the Bismarck Archipelago and the Solomon Islands is, as supposed, of a fairly recent date (the Solomons evolved in connection with the margin of the Australian plate and advanced from the south, while the Bismarck islands are supposed to be part of the Pacific plate and came from the east, see the previous chapter). It is possible therefore, that the occurrence of *Moana* on New Britain and New Ireland represents a recent westward dispersal from the Solomon Islands. The distribution of *Moana*, reaching to Samoa in bypassing the Fiji group, resembles that of the *Baeturia bloetei* group (fig. 38), although that group also occurs on Vanuatu and Rotuma island (see Duffels 1988a; De Boer 1989). The west Pacific distribution of the *B. bloetei* group is presumably of fairly recent date. This group might have reached Samoa and Tonga along a Vitiaz arc, which included the island of Rotuma, at a time when Fiji had already become isolated from the arc (Duffels & De Boer 1990). *Moana* might have reached Samoa by a similar dispersal event, but when *Moana* had the same dispersal possibilities as the *bloetei* group it is strange that the genus is absent from Vanuatu.

New genus *'T'*

Duffels recently recognised a new genus of six undescribed species. This genus belongs to the Cosmopsaltriaria and is probably the sister genus of *Rhadinopyga*. The genus, here referred to as new genus *'T'*, is endemic to the Solomon Islands and presumably evolved on the Solomon arc. Its six species are mainly island endemics.

Dilobopyga Duffels

Dilobopyga Duffels, 1977 of the Cosmopsaltriaria is a fairly large genus, with at least 36 species, of which only 10 are at present described. Most of these species are endemic to Sulawesi, though the distribution area includes nearby islands as Banggai, Buton, Muna, Sangihe, Salayar and Sula, often with endemic species. One species (*D. gemina*) occurs with two subspecies in southern Maluku, on Buru, Gorong, Sapurua, Seram and presumably on Misool. For exact data on the distribution of the species see Duffels (1977, 1990).

Within Sulawesi, the genus seems concentrated in the northern arm and the central part of the island. Eight species are endemic to the northern arm of Sulawesi, nine to central Sulawesi, and five are restricted to northern + central Sulawesi, whereas only three are endemic to eastern Sulawesi. The apparent concentration of species in northern and central Sulawesi could well be influenced by undercollecting in eastern Sulawesi (Duffels 1990).

Duffels (1990) discussed two possible routes for the invasion of Sulawesi; *Dilobopyga* either entered Sulawesi along the western arc and dispersed into the eastern arc, or the genus first reached the eastern arc and dispersed into the western arc. If we suppose that *Dilobopyga* originates from the OMA, just as all other genera of the Cosmopsaltriaria seem to do, then these two routes appear equally plausible. The northern arm of Sulawesi, which is part of the western arc, as well as parts of eastern Sulawesi are supposed to be fragments of the OMA. The apparent concentration in the northern arm suggests that the genus originates from that part of the OMA. The occurrence of *D. gemina* in Maluku is presumably due to a recent eastward dispersal.

Brachylobopyga Duffels

Brachylobopyga Duffels, 1982 of the Cosmopsaltriaria is a very small genus, of which only two species are known: *B. montana* from central Sulawesi, and *B. toradja* from southwestern Sulawesi. For exact data on the distribution of these species see Duffels (1982, 1989, 1990). These sparse biogeographical data give no information as to a possible origin of the genus, but, since *Brachylobopyga* is the presumed sister genus of *Dilobopyga*, its ancestor, or the common ancestor of these two genera will, as explained above, probably originate from the OMA fragments of northern, or possibly eastern, Sulawesi.

The oriental Prasiini

The oriental Prasiini form a monophyletic group of about 50 species, attributed to four genera (*Arfaka* Distant, 1905, *Jacatra* Distant, 1905, *Lembeja* Distant, 1892, and *Prasia* Stål, 1863). A taxonomic revision of this group was started by De Jong in the early 1980s, but was unfortunately not finished. Revisions have been published for the genus *Prasia* (De Jong 1985) and for three monophyletic groups of the genus *Lembeja*: the *foliata* group (De Jong 1986) and the *fatiloqua* and *parvula* groups (De Jong 1987). Two other subgroups of *Lembeja* were indicated: the *harderi* group and the *robusta* group. The genus *Lembeja* is not monophyletic in its present concept; the *harderi* group is presumably more closely related to *Prasia* and *Arfaka* than to the other subgroups of *Lembeja*. A tentative cladogram of the genera and subgroups of the Prasiini can be made (fig. 54, see De Boer 1995d), but the phylogenetic position of many species and the relationships between several of the established groups remain uncertain. A well-argumented discussion on the historical biogeography of the oriental Prasiini is therefore not possible, but some remarks can certainly be made. The exact biogeographical data of most of the species here discussed can be found in De Jong (1982, 1985, 1986, 1987) and De Jong & Duffels (1981).

The oriental Prasiini are definitely concentrated on Sulawesi, where most of its species (28) are endemic. The small genus *Jacatra* (*J. typica* and one undescribed species) is endemic to Java and Sumatra, and *Arfaka* (*A. fulva*, *A. hariola*, and one undescribed species) is endemic to the Birds Head peninsula of New Guinea and some adjacent islands. *Lembeja* extends from Sulawesi to Borneo and Mindanao (*L. fatiloqua*), to some of the Lesser Sunda islands (*L. roehli*, *L. sumbawensis*, and the *harderi* group consisting of *L.*

harderi, and several undescribed species), to New Guinea (the *robusta* group consisting of *L. papuensis*, *L. robusta*, and at least four undescribed species), and Queensland (*L. paradoxa* and *L. vitticollis*).

Most of the Sulawesi endemics occur in the northern and western part of the island. Furthermore, the genus *Prasia*, which is possibly the sister group of all other Prasiini, is restricted to Sulawesi and the nearby Muna island. It is presumed therefore, that, similarly as in *Brachylobopyga* and *Dilobopyga*, the ancestor of the Prasiini originates from those parts of the OMA, that now form part of Sulawesi.

The occurrences of several species on the Lesser Sunda islands and of a species on Borneo and Mindanao presumably result from dispersals, and also the distribution of the genus *Jacatra* on Java and Sumatra might be the result of an early dispersal event. These dispersals, or some of them, possibly occurred during one of the Pliocene–Pleistocene glacial periods. The occurrence of the Prasiini in New Guinea and Australia is more difficult to explain, especially since their distributional patterns often show similarities with the vicariant patterns found among the New Guinean genera discussed above. The New Guinean representatives of the Prasiini certainly do not form a single monophyletic group (fig. 54; De Boer 1995d), but, as can be inferred from the now available data, belong to at least three different groups: the genus *Arfaka*, the *Lembeja robusta* group, and *Lembeja paradoxa* of the *L. fatiloqua* group. These three groups must have reached New Guinea separately.

The distribution of the genus *Arfaka* is very similar to that of the genus *Rhadinopyga*, and an origin of *Arfaka* on one of the microcontinents that now form the Birds Head, as was inferred for *Rhadinopyga* and *Aedeastria*, must be considered plausible. *Arfaka* has its nearest relations in Sulawesi and on the Lesser Sunda islands.

One of the two Australian species (*L. paradoxa*) has a distribution in Queensland and southern New Guinea very similar to that of *Diceropyga subapicalis* and *Thaumastopsaltria globosa*, but where the latter two species have their nearest relations in eastern New Guinea, notably the Papuan peninsula, *L. paradoxa* apparently belongs to the *L. fatiloqua* group that is otherwise distributed in Borneo, Mindanao, Sulawesi, Sumba and Sumbawa.

The other Australian species (*L. vitticollis*) is restricted to the southeastern corner of the Cape York peninsula, and does have some of its nearest relations in Papua New Guinea (*L. papuensis* and *L. robusta*), but several undescribed species from northern New Guinea, the Birds Head and Obi island are presumably also closely related to *L. vitticollis* and form the *L. robusta* group (De Jong pers. comm). The Sulawesi *Lembeja* species are the nearest relations of this group.

Conclusions

1. – *Dilobopyga*, *Brachylobopyga* and the Prasiini all originate from Sulawesi and presumably from those parts of Sulawesi that are derived from the OMA. Part of the Prasiini, however, might have invaded the OMA parts that originally lay to the east of the Sulawesi fragments.

2. – *Cosmopsaltria* originates from the Sepik Arc fragment of the OMA.

3. – *Diceropyga*, *Gymnotympana*, *Thaumastopsaltria*, and presumably at least the greater part of *Papuapsaltria* originate from the East Papua Composite terrane, although the ancestral area of distribution of *Diceropyga* and *Gymnotympana* probably included parts of northern Maluku and, furthermore, that of *Diceropyga* presumably included the Bismarck Archipelago and parts of the Solomon Islands.

4. – *Rhadinopyga* and, presumably, *Aedeastria* originate from some microcontinental fragments, now forming the Birds Head peninsula.

5. – *Baeturia*, *Scottotympana*, possibly a part of *Papuapsaltria* and possibly *Guineapsaltria* and the greater part of *Mirabilopsaltria* originate from parts of the OMA, now constituting the northern mountain ranges of New Guinea.

6. – *Aceropyga*, the new genus *'T.'*, and *Moana* evolved on the eastern parts of the OMA. The new genus *'T.'* evolved on the Solomon Islands, *Moana* presumably also originates from the Solomon Islands, but possibly in connection with the Bismarck Archipelago, and *Aceropyga* evolved on Fiji.

7. – The Australian genera *Chlorocysta*, *Cystopsaltria*, *Cystosoma*, *Glaucopsaltria*, *Owra*, and *Venustria* present a major problem, since they do not occur on remnants of the former OMA. They presumably reached Australia by dispersal from the OMA and, as will be explained in the next chapter, came most probably from the Sepik Arc terrane.

Discussion

It is curious that *Cosmopsaltria* is the only genus allotted to the Sepik Arc fragment, and that the Chlorocystini (sensu stricto), apart from some species of the *Baeturia nasuta* group and the *B. loriae* group, seem to avoid these terranes, which were the first to collide with the Australian continental plate and must have formed the link between the Sulawesi- and remaining arc fragments of the OMA. On the other hand, the Cosmopsaltriaria do not appear to have any groups originating from northern New Guinea; all genera that are supposed to originate from these parts belong to the Chlorocystini. Furthermore, it is remarkable that none of the genera seem to originate from the Finisterre or Bismarck terranes, the OMA frag-

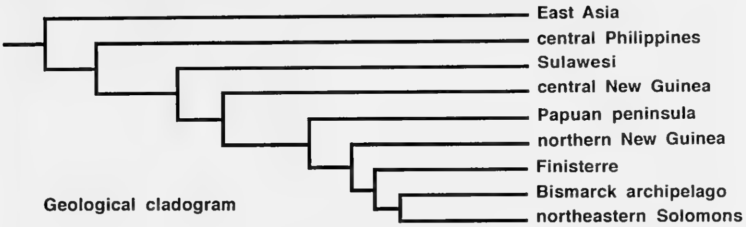


Fig. 50. Geological area cladogram showing the fragmentation sequences in the OMA.

ments that most recently reached New Guinea. Only the genus *Diceropyga* apparently has an 'old' endemic group of species in the Bismarck Archipelago. A remark of Abbot and Silver (1991) that part of the Finisterre terrane was below sea level prior to its collision with New Guinea might indicate an explanation for the absence of a distinct Finisterre group.

Area cladistics

As is stated in the introduction of the previous chapter, it is supposed that the various genera of the Sulawesi, Moluccan, New Guinean, and East-Melanesian cicadas, which belong to the Cosmopsaltriaria and to the Prasiini – Chlorocystini, evolved as a result of vicariance following the fragmentation of an historic island arc, known as the Outer Melanesian Arc (OMA). It is the aim of the present chapter to present the corroborative evidence for this supposition by comparing the phylogenies and biogeographic data of these two groups of cicadas with the palaeogeographic data of the area as discussed in the first chapter.

First, the main vicariant events will be related to geological events by comparing the area cladograms of the two groups with the presupposed fragmentation sequences of the island arcs. This comparison will be accompanied by a discussion of the congruencies and incongruencies between the area cladograms and the palaeogeographical data.

Second, the area relationships between the areas of endemism as indicated by the phylogenies of the cicadas will be discussed. As an interesting result of this discussion it will appear that the biological relationships supply additional data for a palaeogeographic reconstruction of the Outer Melanesian Arc and its connections to adjacent terranes.

Area cladograms

The fragmentation sequences of the OMA, as discussed in chapter 1 are summarised in the 'cladogram-like' graph of fig. 50. The most basal branching in this figure represents the collision between the western part of the OMA and the Asian continent, dated at 40-35 Mya. Subsequent branchings represent fragmentation events of the OMA. The timing of the 3rd, 4th, 5th, and 6th branching (25, 15, 10, and 2 Mya respectively) correspond with the supposed timing of the accretion of respectively the Sepik Arc, the East Papua Composite terrane, the Torricelli and Gauttier terranes, and the Finisterre terrane to New Guinea, though the latter may already have started to accrete 10 Mya. The actual isolation of these respective terranes from other parts of the OMA will have taken place considerably earlier. Areas of a presumed different geological origin like Maluku, the Birds Head, and the East-Melanesian archipelagos are, of course, not included in this cladogram, since they do not form a monophyletic group in geological sense with the other (OMA) terranes.

The genus cladogram of the Cosmopsaltriaria (fig. 51) is taken from Duffels (1993) with the only difference that the southeast Asian genus *Meimuna* Distant is added as a sister group. *Meimuna* is regarded as the

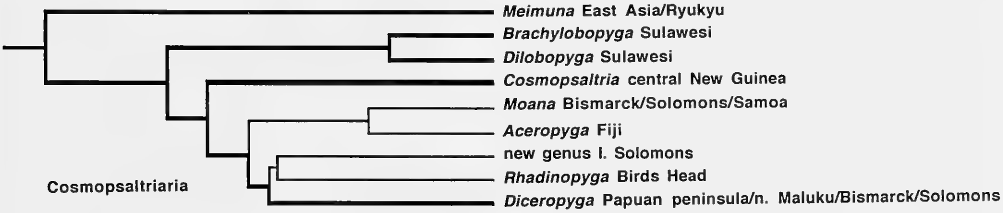

Meimuna East Asia/Ryukyu
Brachylobopyga Sulawesi
Dilobopyga Sulawesi
Cosmopsaltria central New Guinea
Moana Bismarck/Solomons/Samoa
Aceropyga Fiji
new genus I. Solomons
Rhadinopyga Birds Head
Diceropyga Papuan peninsula/n. Maluku/Bismarck/Solomons
Cosmopsaltriaria

Fig. 51. Taxon-area cladogram of the genera of the subtribe Cosmopsaltriaria, with the genus *Meimuna* as sister group. After Duffels (1993). Bold lines correspond with areas in fig. 50; thin lines lead to areas of different geological origin.

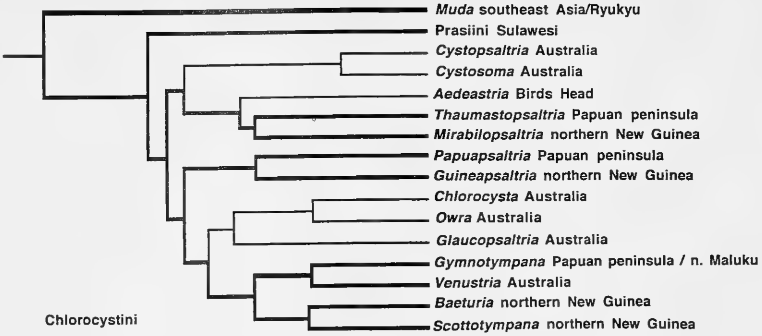

Muda southeast Asia/Ryukyu
Prasiini Sulawesi
Cystopsaltria Australia
Cystosoma Australia
Aedeastria Birds Head
Thaumastopsaltria Papuan peninsula
Mirabilopsaltria northern New Guinea
Papuapsaltria Papuan peninsula
Guineapsaltria northern New Guinea
Chlorocysta Australia
Owra Australia
Glaucopsaltria Australia
Gymnotympana Papuan peninsula / n. Maluku
Venustria Australia
Baeturia northern New Guinea
Scottotympana northern New Guinea
Chlorocystini

Fig. 52. Taxon-area cladogram of the genera of the Chlorocystini sensu stricto, with the oriental Prasiini as sister group, and the genus *Muda* as outgroup. Bold lines correspond with areas in fig. 50; thin lines lead to areas of different geological origin.

most likely sister group of the Cosmopsaltriaria (Duffels pers. comm.).

The phylogeny of the Chlorocystini (sensu stricto) was discussed earlier (De Boer 1995d) and the genus cladogram (fig. 52) is derived from the species cladogram presented in that publication. Phylogenetic analysis of the Chlorocystini left room for alternative positions of the genus *Aedeastria* and the sister genera *Guineapsaltria* – *Papuapsaltria* in the cladogram, which are only slightly less parsimonious (De Boer 1995d). These alternatives are given in fig. 53. Area cladistic implications of the alternatives will be discussed below.

In these cladograms, the most likely areas of origin or source areas discussed in chapter 2 (the geological entities of microcontinental origin or fragments of the oceanic island arc systems) are added to the genus names and treated as areas of endemism for the genera. The resulting figures are 'source-area cladograms' based on the phylogeny and distribution of the Cosmopsaltriaria and of the Chlorocystini – Prasiini.

Comparison of area cladograms

The area cladograms of figs. 51 and 52 both show a striking congruence with the geological cladogram of fig. 50. The bold lines in figs. 51 and 52 show the area relationships that completely match the geological cladogram. The thinner lines show the area relationships that do not match up with the geological cladogram, but one will notice that they all lead to areas of a different geological origin, which are therefore absent in the geological cladogram.

It is remarkable that the area at the base of both area cladograms includes the Ryukyu islands, to the south of Japan. This suggests that the ancestors of the cicadas invaded the OMA in this area through the Bonin and, possibly, Daito arcs and not along a route somewhere near the Philippines or Borneo.

The next branch in both area cladograms leads to Sulawesi (*Brachylobopyga* and *Dilobopyga* are practically endemic to Sulawesi and the Prasiini are definitely most numerous on that island). This branch corresponds with the third branch of fig. 50. Neither the Cosmopsaltriaria or one of its sister groups, nor the Chlorocystini – Prasiini complex or one of its sister groups have representatives on the Philippines (apart from one widely distributed and presumably recently dispersed species of the genus *Lembeja*). That both these groups of cicadas have no 'old' species groups centered on the Philippines could imply either that there has been an island arc connection between the Asian continent and Sulawesi bypassing the central Philippines (the Philippine element of the OMA), or that this Philippine element, which forms the most logical link within the OMA island chain (comp. fig. 55), has been submerged prior to its collision with the western Philippines.

Concerning the subsequent branching, the two area cladograms differ. The Cosmopsaltriaria area cladogram gives a group (*Cosmopsaltria*) centered in central New Guinea, which corresponds perfectly with the fourth branch, the Sepik Arc terrane, in the geological cladogram (fig. 50). The Chlorocystini cladogram, however, is in its most parsimonious solution from here onwards subdivided into three major subgroups (viz., *Aedeastria* to *Mirabilopsaltria*, *Guineapsaltria* – *Papuapsaltria*, and *Chlorocysta* to *Scottotympana*). It is not clear from the geological data what event could have caused the subdivision into these three major subgroups. It suggests, however, that the OMA to the east of its Sulawesi fragments (the Sepik Arc) was not a homogeneous terrane but was divided prior to its accretion to New Guinea and has possibly consisted of several loosely connected arc fragments. At the base of two of these three major subgroups appears a group endemic to Australia. Such a basal group is altogether lacking in the third subgroup, the one consisting of *Guineapsaltria* and *Papuapsaltria*. It is apparently lacking, because the vi-

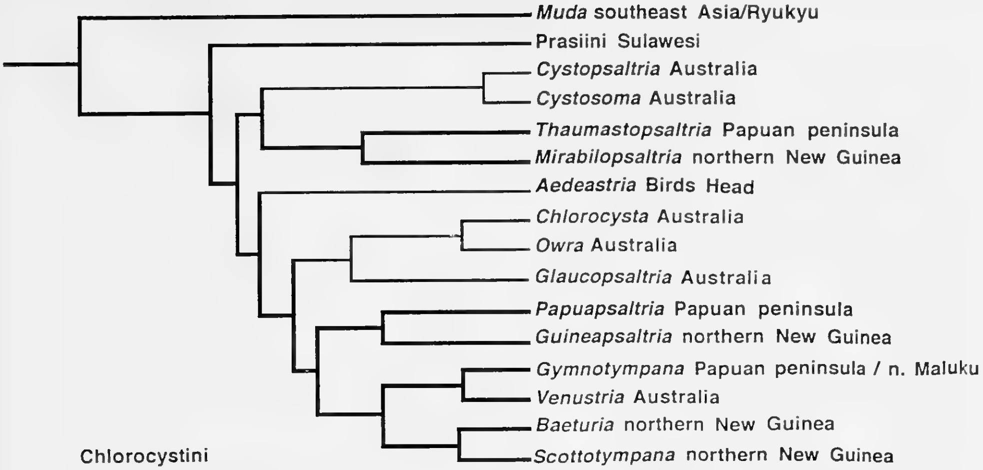

Muda southeast Asia/Ryukyu
Prasiini Sulawesi
Cystopsaltria Australia
Cystosoma Australia
Thaumastopsaltria Papuan peninsula
Mirabilopsaltria northern New Guinea
Aedeastria Birds Head
Chlorocysta Australia
Owra Australia
Glaucopsaltria Australia
Papuapsaltria Papuan peninsula
Guineapsaltria northern New Guinea
Gymnotympana Papuan peninsula / n. Maluku
Venustria Australia
Baeturia northern New Guinea
Scottotympana northern New Guinea
Chlorocystini

Fig. 53. Taxon-area cladogram of the genera of the Chlorocystini sensu stricto with alternative positions for *Guineapsaltria-Papuapsaltria* and *Aedeastria.*

cariance in that subgroup between the Papuan peninsula and northern New Guinea corresponds to the ultimate branching in both other subgroups (*Baeturia – Scottotympana* versus *Gymnotympana – Venustria* and *Thaumastopsaltria* versus *Mirabilopsaltria*) and to the next (the 5th and 6th) branchings in the geological cladogram. On the basis of that geological cladogram and analogue to the Cosmopsaltriaria we would expect to find species groups in central New Guinea (the Sepik Arc fragment of the OMA) at the position where we do find these Australian species groups. This suggests that these species groups dispersed into Australia through the Sepik Arc fragment. This probably occurred after the collision of that fragment with the Australian craton (about 25 Mya) and prior to the subsequent development of the forearc basin, which has long separated the New Guinea orogen from the Australian mainland. The reason for this dispersal and the question why the ancestors of these Australian groups left no descendants in central New Guinea is open to discussion. We must remember, however, that the development of the central mountain ranges was extremely rapid in a geological time scale. The cicadas in the area must have had three options; they could either adapt to the climatic changes inherent to this rapid uplift, or move away, or become extinct. *Cosmopsaltria* obviously adapted, while the ancestors of *Cystosma – Cystopsaltria* and of *Chlorocysta – Glaucopsaltria – Owra* presumably moved away. If so, these ancestors were forced to move southwards to well into Australia in front of the then developing forearc basin. This would also explain why the distribution areas of the Australian genera extend farther southward than the distribution areas of species of the (mainly) New Guinean genera which reached Australia more recently (the Australian representatives of *Diceropyga, Guineapsaltria, Gymnotympana,* and *Thaumastopsaltria*). These were not forced onward by a developing sea. A hypothetical sister group of *Guineapsaltria – Papuapsaltria* might have become extinct. However, the phylogenetic position of *Guineapsaltria* and *Papuapsaltria* is not based on sound synapomorphic characters (see De Boer 1995d) and the alternative phylogenetic reconstruction of fig. 53 (with *Guineapsaltria – Papuapsaltria* as a sister group of *Baeturia, Gymnotympana, Scottotympana,* and *Venustria*) is almost equally parsimonious. In the alternative reconstruction the necessity for a hypothetical and extinct sister group of *Guineapsaltria* and *Papuapsaltria* no longer exists, so this reconstruction is in a biogeographical sense more parsimonious.

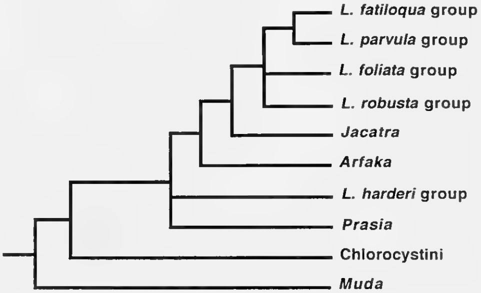
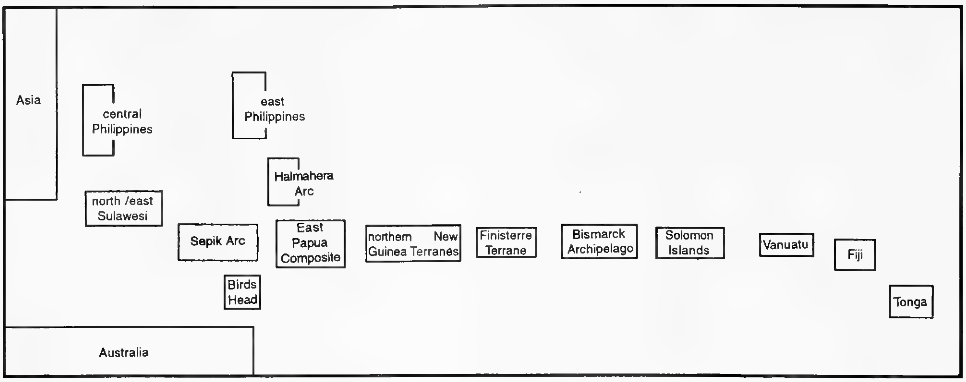
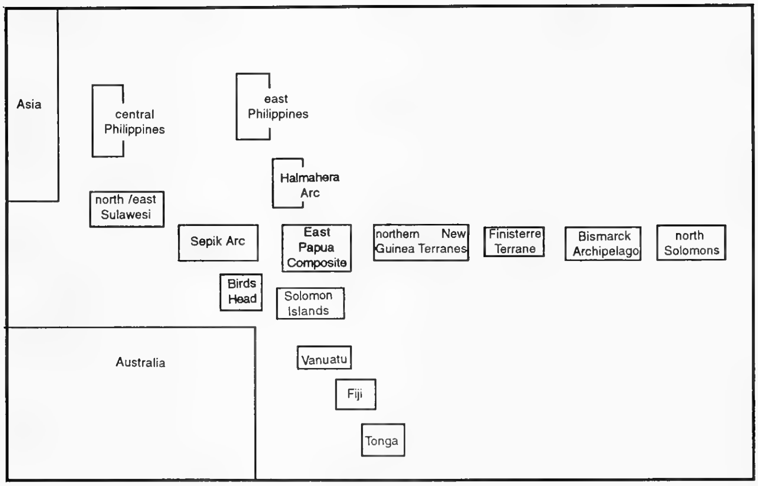


Fig. 54. Taxon cladogram of the genera and species groups of the oriental Prasiini.

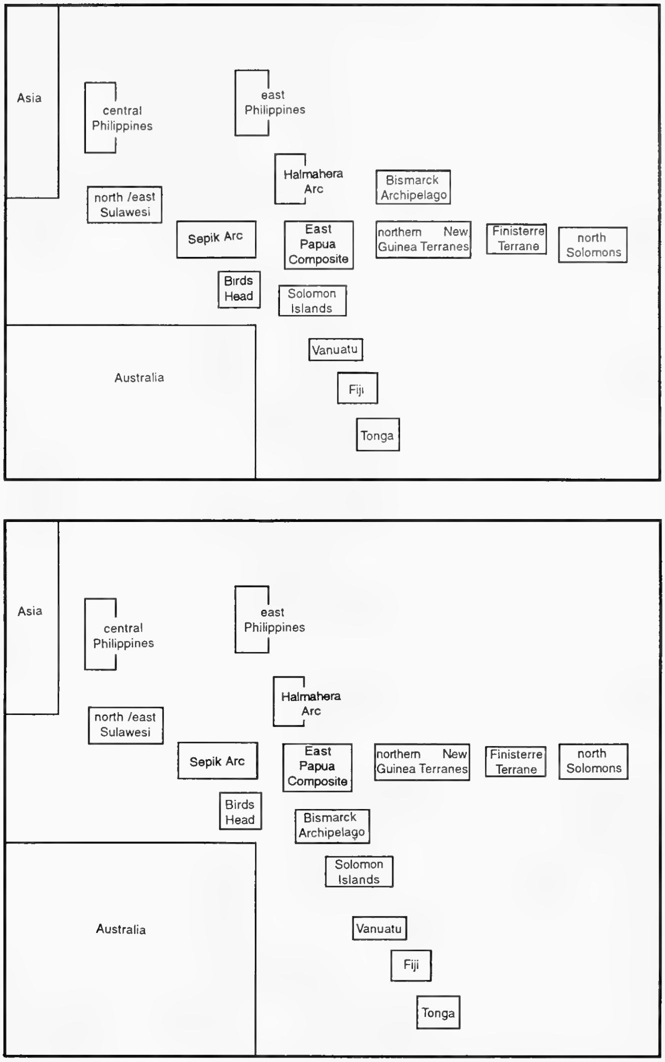




The vicariance between the Papuan peninsula and northern New Guinea is apparent in all three subgroups of the Chlorocystini and represents the separation between the East Papua Composite terrane and the Gauttier, Torricelli, Prince Albert, Mt. Turu, and, possibly, Finisterrre terranes. One of these three subgroups may also indicate a vicariance between the Birds Head (*Aedeastria*) and the Papuan peninsula together with northern New Guinea (*Thaumastopsaltria* and *Mirabilopsaltria*). The evidence for this latter vicariance is rather weak, since the phylogenetic position of *Aedeastria* (see De Boer 1995d), as well as its presumed origin from the Birds Head (see above), are considered very uncertain.

The ensuing branchings in the Cosmopsaltriaria aea cladogram no longer correspond with the branchings in the geological cladogram, since the genera of that subtribe are from here on predominantly distributed in areas of a different geological origin. Only the genus *Diceropyga* occurs in an area that is included in the geological cladogram; its presumed partial origin on the Papuan peninsula nicely corresponds with the next branch in the geological cladogram, which leads to the East Papuan Composite terrane. The area cladogram of the Cosmopsaltriaria indicates a vicariance between the East-Melanesian island chains and a cluster of terranes including the Papuan peninsula, the Birds Head, Solomon Islands, and Bismarck Archipelago. This vicariance suggests a historical connection or proximity between the East Papua Composite terrane and the East-Melanesian islands in bypassing the northern New Guinea and Finisterre terranes. Since these latter terranes are supposed to have been located in the OMA chain between the East Papua Composite terrane and the Solomon Islands (fig. 55a), this fact forms another (biogeographical) indication that the East-Melanesian islands are not a simple continuation of one and the same island arc.

Fig. 55. Schematic reconstructions of the OMA, not related to a certain geological time (the suggested proximities between the various geological entities may have existed in different times). A (top left). reconstruction with a single central Philippines-Tonga arc and an east Philippines-Halmahera arc. B (bottom left). reconstruction based on the most recent geological literature with a central Philippines-north Solomon arc, an east Philippines-Halmahera arc, and a Solomons-Tonga arc. C (top right). reconstruction with an alternative position of the Bismarck Archipelago north of the northern New Guinea terranes. D (bottom right). reconstruction with an alternative position of the Bismarck Archipelago between the East Papua Composite terrane and the Solomon Islands.



The branching between *Aceropyga* and *Moana*, which indicates a vicariance between Fiji and the other East-Melanesian archipelagos, is presumably related to the collision between the Solomon Islands and the Ontong Java plateau, which caused the rotation and isolation of Fiji.

The sister group relationship between *Rhadinopyga* and the new genus *'I.'* indicates a vicariance between the Birds Head microcontinents and the Solomon Islands. The Birds Head and the Solomon Islands together apparently form the sister areas of an area including the Papuan peninsula, Maluku, and the Bismarck Archipelago. The indicated relationship between the Birds Head and the eastern parts of the historic OMA, which are possibly also indicated in the Chlorocystini cladogram (see above the relationships of *Aedeastria*), correspond with the supposed eastern origin of the Birds Head microcontinents (Pigram & Panggabean 1984).

Discussion and palaeogeographic reconstructions

The striking compatibility between the geological cladogram of fig. 50 and the area cladograms of figs. 51 & 52 clearly suggests that fragmentation of the various island arcs played a major role in the vicariant evolution of both our groups of cicadas. However, many minor details in the cicada distribution and phylogeny apparently conflict with the above discussed scenario. Such conflicting data could find their origin in the still insufficient knowledge of the palaeogeographic configurations, or in incorrectnesses in the phylogenetic reconstructions, or could be due to some peculiar and inconceivable long distance dispersal.

The palaeogeographic knowledge of the island arc systems is certainly incomplete. The fragmentation sequences and the order in which the fragments were included in the OMA can roughly be inferred from the order in which these fragments accreted to New Guinea, but it is not clear how large these fragments were when they formed part of the arc, how far they lay apart, or whether these fragments themselves existed as fragments or single blocks. Neither is it known which of the fragments were simultaneously emerged.

The most straightforward schematic reconstruction of the island arc systems, based on the geological literature alone, is the one presented in fig. 55b. This reconstruction shows three distinct island arcs: 1) a central Philippine to Bismarck and northern Solomons arc, 2) an East Philippine – Halmahera arc (both related to the Pacific plate), and 3) an East-Melanesian arc (related to the Australian plate). The terrane sequences in the Philippine to Bismarck and northern Solomons arc correspond from west to east to the fragmentation sequences of the arc (the order in which these terranes are supposed to have become isolated) and, for the New Guinea terranes, to the sequences in which these terranes collided with the Australian continent. In several instances the distributions and phylogenetic relationships of the cicadas suggest area relationships that contradict this reconstruction. In the following sections, these area relationships will be discussed per area of endemism. These relationships often suggest a slightly different or more detailed palaeogeographic reconstruction of the island arcs (see figs 55c, 55d). Recently, Struckmeyer et al. (1993) published some palaeogeographic reconstructions of the New Guinea – Bismarck region for different geologic times. A simplified copy of their Late Eocene reconstruction (that is before the amalgamation of the Sepik Arc) is given in fig. 56. For the moment disregarding the fact that at that time most of the arc terranes are supposed to be submerged, this reconstruction roughly shows the same terrane sequences as the one of fig. 55b. It differs in the position of the Birds Head microcontinents, which lie already west of the Sepik terrane, and the northern New Guinea and Finisterre terranes, which are plotted north of the East Papua Composite terrane. In some instances this reconstruction better fits the biogeographical data, in others it strongly opposes them.

Sulawesi

Of the two monophyletic groups centered on Sulawesi that are supposed to originate from some Sulawesi fragments of the OMA (*Brachylobopyga – Dilobopyga* and the Prasiini) the first (*Brachylobopyga – Dilobopyga*) is almost completely endemic to that island and to some adjacent small islands. The only exception, *D. gemina*, ocurs with two subspecies in Maluku (Buru, Seram, Gorong, Sapurua, and presumably Misool). The occurrence of this species in Maluku must probably be explained by a recent eastward dispersal, since most of these islands only recently emerged (Fortuin & De Smet 1991).

The Prasiini have a much wider distribution. Although this group definitely has most of its species on Sulawesi, the distribution area also includes Java and Sumatra (*Jacatra*), the Lesser Sunda islands (the *Lembeja harderi* group and two species of the *L. fatiloqua* group), Borneo and the Philippines (*L. fatiloqua*), the Birds Head of New Guinea (*Arfaka*), and New Guinea and Queensland (the *L. robusta* group and *L. paradoxa*). The occurrences on Borneo – the Philippines, the Lesser Sunda islands, and, with a little good will, even the occurrence on Java and Sumatra could possibly be explained away by a diffusion or dispersal from Sulawesi. Distributions of widespread species(groups) in the Greater Sunda islands are often explained in connection with the glacial periods of the Pliocene and Pleistocene, during which these islands were connected as a result of lower sea levels. Although Sulawesi remained isolated during the various glacial periods, at times its isolation might have been of a lesser degree and so the glacial periods might have played a role in the dispersal of the Prasiini to Borneo and the Philippines. The supposed basal position of *Jacatra* and the *L. harderi* group in the tentative cladogram of the Prasiini (fig. 54) suggests that the vicariant events that separated these groups happened well before the glacial periods. This does not necessarily mean that their dispersal to Java – Sumatra and the Lesser Sunda islands is not ice age related. The Australian and New Guinean species(groups), however, demand a different explanation. The total absence of Prasiini species from Maluku strongly argues against a recent eastward dispersal and, furthermore, the presence of an endemic genus on the Birds Head, endemic species in Papua New Guinea, and similarities between the distributions of *L. paradoxa*, *Diceropyga subapicalis*, and *Thaumastopsaltria glauca* (in the Papuan peninsula, southern New Guinea and northern Queensland) suggest that these New Guinea distributions are remnants of an older pattern, comparable to the vicariant patterns found for the Cosmopsaltriaria and the Chlorocystini.

If the above outlined theory on the palaeogeography of the Cosmopsaltriaria and the Chlorocystini is in essence correct, and since there is no geological evidence for terrane movements from Sulawesi towards New Guinea (on the contrary, all terranes in the Maluku area move from New Guinea towards Sulawesi), it stands to reason that some ancestral Prasiini species must somehow have entered the OMA terranes that lay east of its Sulawesi fragments. Only then could these Prasiini have gone through a development parallel to that of the Cosmopsaltriaria and the Chlorocystini. This could mean that the apparently monophyletic Prasiini are in fact not monophyletic. In that case part of the Prasiini, notably the New Guinean – Australian species, would have to be the sister group of the Chlorocystini, while the remaining (mainly Sulawesi) species of the Prasiini would be the sister group of these two groups combined. This solution, however, is very unlikely since it would imply that the genus *Arfaka* and the *L. robusta* group are more closely related to each other than to the Sulawesi species of the Prasiini. Although the tentative cladogram of the Prasiini (fig. 54) is not based on a thorough phylogenetic analysis of all characters, a sister group relationship between *Arfaka* and the *L. robusta* group is considered very improbable. Moreover, *L. paradoxa*, a species from Papua New Guinea and Queensland, belongs to the *L. fatiloqua* group and is more closely related to Sulawesi species than to the other New Guinean species of *Lembeja* (De Jong 1987).

Alternatively one could suppose that the Prasiini evolved on some isolated fragments of the OMA that were to end up in Sulawesi, and that at a period in which ongoing speciation had already established several species within the Prasiini, some part of this ancestral distribution area regained contact with the more eastern parts of the OMA. Then one should assume that representatives of several species that have now evolved into the various monophyletic groups simultaneously (re)entered the OMA. The polyphyletic origin of the New Guinean – Australian Prasiini would support such a highly speculative theory, but the question immediately arises why the Cosmopsaltriaria, in casu *Dilobopyga* and *Brachylobopyga,* did not profit by such a renewed route of dispersal.

Pleading against this scenario is the fact that the total number of New Guinean Prasiini is very small compared to that of the New Guinean Chlorocystini and Cosopsaltriaria, and one would have to assume a considerable amount of extinction within the Prasiini, viz., of complete Sepik Arc groups. The New Guinean Prasiini certainly give the impression of a relict distribution.

Maluku and Banda

The cicada fauna of Maluku and the Banda islands is very diverse. Five distinct patterns of distribution can be recognized, each indicating different relationships between (parts of) Maluku and a variety of other areas. It is supposed that most of these patterns are of fairly recent date, since many of the islands only recently emerged (Fortuin & De Smet 1991). Many of the area relationships are therefore presumed to be indicative of various recent dispersal routes into the Moluccas rather than to vicariance events based on palaeogeographical changes.

Two cicada genera with an alleged Papuan peninsula origin, *Diceropyga* and *Gymnotympana,* have a monophyletic group that occurs predominantly in northern Maluku. Only *D. obtecta* occurs on Seram and Buru, but not farther south. A third alledgedly Papuan genus, *Thaumastopsaltria,* might also have a species in northern Maluku (see chapter 2). It is concluded from geological data that northern Maluku moves westward and that the island of Halmahera, or parts of that island (the Halmahera arc), originates from a position far to the east or southeast of its present one. Furthermore, a continuity has been suggested between the Halmahera arc and northern New Guinea. The distribution of cicadas indicates an area relationship between northern Maluku and the Papuan peninsula, which suggests that at least part of northern Maluku, viz. the Halmahera arc, evolved near the East Papua Composite terrane. This need not contradict the geological data, if we suppose that the north New Guinea terranes originate from directly east of the East Papua Composite terrane (fig. 55). Halmahera presumably evolved on a fracture of the Pacific plate, to which possibly also the eastern parts of Mindanao and the islands of Yap and Palau of the Caroline islands are connected. This fracture, which resulted possibly from plate tensions as a result of the Sepik Arc – Australia collision, may have reached the plate boundary somewhere between the East Papua Composite and northern New Guinea fragments of the OMA (see reconstructions of fig. 55). In this respect the biogeographical data strongly oppose the reconstruction of Struckmeyer et al. (1993), where the northern New Guinea and Finisterre terranes are situated between the Halmahrea arc and the East Papua Composite terrane (fig. 56).

Two species of the genus *Baeturia* (*B. exhausta* and *B. macgillavryi*) have a very similar distribution in Maluku, the Banda islands, and Timor. *B. macgillavryi* reaches, with records from Halmahera, Morotai, and Talaud, slightly farther northward than *B. exhausta* (compare figs 38 & 40). It is remarkable that the sister species of both these species (*B. bicolorata* and *B. bloetei* respectively) have a fairly wide distribution in western New Guinea, which apart from one record of *B. bicolorata* from the northwestern Birds Head seems to exclude that peninsula. Furthermore, it is remarkable that in both pairs of species the morphological differences are extremely small, so that in both cases it is not clear whether the material represents two distinct species or not. These facts suggest that *B. exhausta* and *B. macgillavryi* are both fairly recent species, possibly even still in the process of speciation.

A very similar distribution in Maluku and the Banda islands, and also including Timor, was found for *Hamza ciliaris* (Linnaeus) (see Duffels 1991). That species, however, has a much wider distribution in the Philippines and the Caroline islands and has no related species on New Guinea: the relatives of *H. ciliaris* are all found in southeast Asia. Only one other species of the Chlorocystini is recorded from the southern Banda islands. That species, *Papuapsaltria bidigitula*, is fairly widely distributed in western New Guinea and recorded from Wetar island, just to the north of Timor (fig. 45). Since this species is not recorded from any of the islands that lie between Wetar and New Guinea, the record from Wetar is considered doubtful and confirmation is needed before any biogeographical conclusions should be drawn.

All species that occur in the southern Banda region seem to have a fairly wide distribution. This is in contrast with the northern Molucca species, of which several are island endemics. These facts suggest that the southern Banda islands could only be reached by species with good dispersal abilities. Apart from *H. ciliaris*, these species presumably came from New Guinea east of the Birds Head. The north Moluccan fauna of *Diceropyga* and *Gymnotympana*, which is supposed to be older than the two *Baeturia* species discussed here, has not been able to disperse southward into the Banda region. This cannot be explained otherwise than by assuming that they disperse less easily.

Similarities between the distributions of the *Baeturia conviva* and *Cosmopsaltria doryca* groups have been discussed before (Dufffels & De Boer 1990). Both these groups have endemic species in Maluku that show sister group relationships between north and south Maluku. Furthermore, in both these groups the moluccan species have a sister species that is widely distributed in western New Guinea and the Birds Head. The *B. conviva* goup is the sister group of the *B. guttulinervis* group that is endemic to northern New Guinea. The *C. doryca* group is the sister group of all other *Cosmopsaltria* species: the small east and north New Guinean *C. gracilis* group and the mainly central New Guinean *C. mimica* complex. The similarities between the *conviva* and *doryca* groups suggest a similar and contemporal dispersal event from New Guinea through the Birds Head to Maluku. The relative positions of these groups in the cladograms show that the *doryca* group could be much older than the *conviva* group and we must not disregard the possibility therefore that the occurrence of the *doryca* group in Maluku represents an older vicariance pattern between Maluku (the Halmahera arc ?) and arc fragments of New Guinea (the Sepik arc ?).

The distributions of *Aedeastria* and, less clearly of *Rhadinopyga*, also indicate an area relationship between Maluku and western New Guinea plus the Birds Head. *Aedeastria* has three endemic species on northern Maluku, and *Rhadinopyga* has a species that is relatively widely distributed on the Birds Head and also recorded from Bacan. The overall distribution patterns of *Aedeastria* and *Rhadinopyga* are very different from those of the *B. conviva* and *C. doryca* groups, however. Whereas the latter two groups each have a single species widely distributed over the Birds Head and western New Guinea, the former genera each have several endemic species on the Birds Head and/or several of the small nearby islands. For these reasons we may infer that the evolution of *Aedeastria* and *Rhadinopyga* is related to a palaeogeographical isolation of the Birds Head microcontinents. The high rate of speciation on the Birds Head at least suggests that the latter pattern, that of *Aedeastria* and *Rhadinopyga*, is older than that of *Baeturia* and *Cosmopsaltria*. The Moluccan species of *Aedeastria* and *Rhadinopyga* might have dispersed westwards simultaneously with the *B. conviva* and *C. doryca* groups, or at an earlier event, but it is also possible that the distributions of these genera represent an old vicariant pattern related to the westward migration of the Obi – Bacan microcontinent, which shows a geological relationship with the Birds Head microcontinents. The latter explanation demands that this microcontinent had emerged before its westward migration. This might be unlikely, since it contradicts geological data concerning similar microcontinents in the Moluccan area, which were all submerged until recently (see geology chapter).

The distribution of *Dilobopyga gemina* represents yet another pattern in the Moluccan area; it is the only species that is restricted to the central part of the area and has no near relatives in other parts of Maluku or Banda. The species is recorded with two subspecies from Buru, Seram, Gorong, Sapurua, and probably Misool. *D. gemina* indicates a relationship between Maluku and Sulawesi. All its relatives are endemic to Sulawesi. *D. gemina* is supposed to represent a recent dispersal from Sulawesi into the Moluccas, since there are no indications for a palaeogeographic relationship between any part of Maluku and

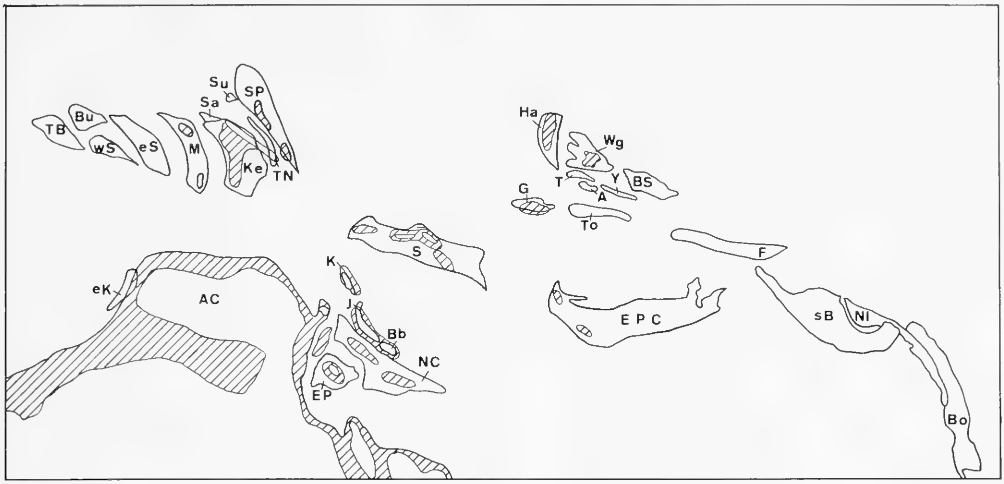


Fig. 56. Palaeogeographic reconstruction of the New Guinea - Bismarck region in Late Eocene. From Struckmeyer et al. (1993). Lettering: A = Arfak, AC = Australian Continent, Bb= Bena Bena, Bo = Bougainville, BS = Biak-Supiori, Bu = Buru, eK = east Kai, EP = Eastern Plateau, EPC = East Papua Composite, eS = east Seram, F = Finisterre, G = Gauttier, Ha = Halmahera, J = Jimmi, K = Kubor block, Ke = Kemum terrane, M = Misool terrane, NC = North Coral Sea, NI = New Ireland, S = Sepik Arc, Sa = Salawati, sB = south Bismarck, SP = Sula Platform, Su =Sulabesi, TB = Tukang Besi-Buton, TN =Tamrau-Netoni, To = Torricelli, T = Tosem, Wg = Waigeu, wS = west Seram, Y = Yapen. Shaded parts supposedly dry land.

Sulawesi, and the greater part of the distribution area of this species only recently emerged.

New Guinea: Birds Head

The Birds Head peninsula of New Guinea has comparatively few endemic species. These species belong to three genera: *Aedeastria*, *Arfaka*, and *Rhadinopyga*. It is curious that all three of these genera are also represented by endemic species on some of the small islands immediately west of the Birds Head. *Arfaka hariola* is endemic to Misool; *Aedeastria waigeuensis*, *R. impar*, and *R. accuminata* are endemic to Waigeu; and *R. recedens* is endemic to Salawati. Apart from the dubious record of *Thaumastopsaltria adipata* from Misool (see above and De Boer 1995a), no other genera have endemic species on any of these three islands. A concentration of species in western New Guinea and endemism on the Birds Head and some of the adjacent islands suggest that the three above mentioned genera evolved on the two microcontinents of Australian origin, which now form the Birds Head. These microcontinents, the Kemum and Misool terranes, originate presumably from somewhere near present day central Papua New Guinea and northern Queensland (Pigram & Panggabean 1984), and they must have travelled westward, somehow finding their way between the Australian continent and some of the advancing OMA fragments (cf. fig. 3, 55). Struckmeyer et al. (1993) solved this problem by placing the Birds Head microcontinents northwest of the Sepik terrane before the Sepik Arc collision (fig. 56), but such a solution strongly contradicts the biological area relationships of the area.

The sister group relationship between *Rhadinopyga* and the new genus *'I.'* indicates a vicariant pattern between the Birds Head and the Solomon Islands. The sister group relationship of these genera together, with *Diceropyga* indicates an area relationship between the Birds Head – Solomon Islands and a cluster of terranes including the Papuan peninsula, the Bismarck Archipelago, northern Maluku, and again the Solomon Islands. These area relationships can of course have existed in different geological times. The presumed sister group relationship between *Aedeastria* and *Thaumastopsaltria* – *Mirabilopsaltria* indicates a very similar vicariant pattern between the Birds Head and the eastern parts of the OMA, in this case with the Papuan peninsula together with northern New Guinea. These patterns can be explained by supposing a historic proximity between the Kemum and/or the Misool terrane and these various terranes as represented in fig. 55b. We must remember, however, that origin and phylogenetic relationships (cf. figs 52 & 53) of *Aedeastria* are very uncertain. The alternative phylogenetic position of *Aedeastria* (fig. 53) would indicate a vicariance between the Birds Head and the same parts of the OMA as discussed above, but then including the Sepik terrane.

On the basis of the palaeogeographic reconstruction given by fig. 55b one would expect that the genus *Arfaka* too has its nearest relatives in such terranes of eastern origin, among which the Papuan peninsula appears to be the common factor. Although the phylogeny of the Prasiini is only partly solved, it is clear that the genus *Arfaka* has its nearest relatives on either Sulawesi (*Prasia*), or the Lesser Sunda islands (the *L. harderi* group), or Java and Sumatra (*Jacatra*) (see fig. 54). Nevertheless, since as discussed in the above section on Sulawesi the New Guinean Prasiini might represent a relict distribution, an extinct sister group of *Arfaka* might well have existed on the Papuan peninsula or there about.

Northern New Guinea

Several species of cicadas are endemic to northern New Guinea, that is to the teranes that according to Pigram & Davies (1987) amalgamated about 10 Mya (e.g., the Gauttier, Torricelli, Mt. Turu, and Prince Albert terranes cf fig. 16). Many of these endemic species belong to the genus *Baeturia*, but several other genera (*Aedeastria*, *Cosmopsaltria*, *Mirabilopsaltria*, *Papuapsaltria*, and *Scottotympana*) are represented by endemic species in these parts. One area in particular, the localities of Araucaria camp, Rattan camp, and Top camp, close to the central mountain ranges in western New Guinea, appear very rich in endemic species. This area presents a major problem, it was visited by Mr L.J. Toxopeus in 1939. He collected the type specimens of no less than 12 species there (De Boer 1995b). Most of these species have never been collected elsewhere. Apart from four species of the genus *Cosmopsaltria*, a genus with presumed Sepik Arc origin, these species apparently are related to northern New Guinea groups. In biogeographical sense the area seems to belong to northern New Guinea therefore, but geologically it might form part of the Rouffaer terrane of the Sepik Arc (cf. fig. 16). The apparently high rate of endemism in this restricted area is presumably partly artificial. The immediately adjacent areas like the Mamberamo valley and the Van Rees mountains are extremely inaccessible and certainly undercollected, and only very few cicada specimens of the inland territories of northwestern New Guinea (i.e., the Gauttier terrane cf. fig. 16) are available.

Many species with an apparent northern New Guinea distribution are not restricted to the above mentioned north New Guinea terranes, but continue into the Finisterre terrane (which includes the Huon peninsula) and, often, to the northwestern corner of the Papuan peninsula. The Huon peninsula in itself is not a notable area of endemism, although there are several species with a distribution area slightly exceeding the size of that peninsula (extending to the northwestern parts of the Papuan peninsula and the eastern parts of northern New Guinea) that should probably be regarded as endemic to Huon. The Huon peninsula forms in geological sense part of the Finisterre terrane, which is supposed to have been connected to the terranes of the Bismarck Archipelago. Although the Bismarck islands also have their endemic species (the *D. obliterans* group and a subgroup of the *B. bloetei* group), these do not have sister species endemic to Huon. There is thus no support in cicada distribution that the Finisterre and Bismarck terranes together are an area of endemism. Most of the species endemic to Huon belong to presumed northern New Guinea groups and the Huon peninsula seems to form an integral part of northern New Guinea. This suggests that at least the beginning of the accretion of the Finisterre terrane might have coincided with the accretion of the other north New Guinea terranes (10 Mya), as was suggested by Pigram & Davies (1987) (fig 17d).

Central New Guinea

The genus *Cosmopsaltria* is the only group of cicadas centred in central New Guinea that presumably originates from the Sepik Arc fragment of the OMA. The *B. nasuta* group, that has several species with a distribution remarkably similar to that of many of the *Cosmopsaltria* species, is supposed to have evolved more recently and not in connection with an isolated Sepik Arc terrane. Two monophyletic groups of Australian genera might have had their origin on the Sepik Arc, but afterwards they must have become extinct on New Guinea (see above and the discussion on Australia below). In the light of a presumed Sepik Arc origin of *Cosmopsaltria*, it is curious that a Moluccan – west New Guinean species group, the *C. doryca* group, is the sister group of all other species of the genus. This could be explained by presuming that the ancestor of the *doryca* group was distributed in an isolated western part of the Sepik terrane and that the occurrence and speciation on Maluku and the Birds Head is of recent date and the result of dispersal. In favour of this supposition is the fact that the *doryca* group (viz., *C. doryca*) does occur in some western parts of central New Guinea that do belong to the Sepik terrane, and that its distribution shows similarities with that of the *B. conviva* group. Since the latter group is considered to be much younger, it means that if the similarities in distribution pattern of these two groups result from the same geological events (the availability of the same dispresal route) the dispersal and speciation of the *doryca* group must be fairly recent. On the other hand, the similarities with the *conviva* group could be pure coincidence, and the distribution of the *doryca* group could indicate a vicariance between parts of northern Maluku and the Sepik Arc terranes.

Less easily explained, is the fact that a second subgroup of *Cosmopsaltria*, the small *gracilis* group with three endemic species in respectively northern New Guinea, the Huon peninsula, and the Papuan peninsula, is the sister group of the mainly central New Guinean '*mimica* complex'. However, in the light of the enormous speciation that took place within the central mountain ranges, this point is regarded as insufficient to reject a Sepik Arc origin for *Cosmopsaltria*. A more detailed knowledge of the palaeogeography might provide a solution, possibly some connections have existed that at present we know nothing of.

It is remarkable that, though most of the *Cosmopsaltria* species occur in the central mountain ranges (14 out of 23), only one is actually endemic to the central mountains, while four are endemic to areas that possibly originate from the Sepik terranes (see above). Many species that occur in the central mountain ranges are distributed all along these ranges from the Wissel lakes in the west to well into the Huon and Papuan peninsulas. The number of co-occurring species in the Papuan peninsula rapidly decreases eastward and, apart from a questionable record of *C. gracilis* from Milne Bay (Duffels 1983), no *Cosmopsaltria* species occur in the easternmost parts of the peninsula. It seems as if many species evolved in and dispersed over the cental mountain ranges and that after the closure of the Aure Trough, that had long separated the Papuan peninsula from other parts of New Guinea, the *Cosmopsaltria* species en masse invaded the montane parts of the peninsula.

The question arises then, why the reverse did not occur, i.e. why the various genera by then present on the Papuan peninsula did not en masse enter and disperse over the central mountain ranges. Several species of *Diceropyga*, *Gymnotympana* and *Thaumastopsaltria* apparently did disperse westward. These genera, however, avoided the central mountain ranges and instead entered the lower northern mountain ranges and the lowlands of southern New Guinea. Only two species of *Gymnotympana* occur in the central mountain ranges, but these are endemic to a very restricted area in the easternmost parts of these ranges.

This phenomenon can possibly be explained as follows. Although *Diceropyga*, *Gymnotympana* and *Thaumastopsaltria* evolved in the partly montane Papuan peninsula, the species of these genera principally remained adapted to lowland. Entering the central mountain ranges just was not an option when northern and southern New Guinea became simultaneously available. In this light, it is remarkable that the two *Gymnotympana* species from the central mountain ranges belong to a subgroup of four species of which the two Papuan peninsula members also have a montane distribution (De Boer 1995a).

The genus *Papuapsaltria* forms a notable exception. This presumably Papuan peninsular, or at least partly Papuan peninsular, genus contains species with a distinctly montane distribution. Most of its species have a limited distribution in the western parts of the Papuan peninsula and in the eastern parts of the central mountains. Just like *Gymnotympana*, the central mountain range species are all endemic to a very restricted area.

It is suggested here that when *Gymnotympana* and *Papuapsaltria* reached the central mountain ranges, the circumstances that enabled species of *Cosmopsaltria* and the *B. nasuta* group to disperse all along these ranges, no longer existed. Whatever these circumstances were is not clear, but presumably the Pliocene – Pleistocene vertical vegetation shifts have played a role. If true, it means that the *B. nasuta* group reached the central mountains before *Gymnotympana* and *Papuapsaltria* could do so, which means before the closure of the Aure Trough (appr. 2 Mya). This again complies with an assumed origin of *Baeturia* on the northern New Guinea terranes, which had accreted to the central New Guinea terranes long before that time (about 10 Mya).

Australia

The species of the Chlorocystini – Prasiini and the Cosmopsaltriaria that occur in Australia can be subdivided into two categories: species that belong to monophyletic groups of Australian genera (*Chlorocysta* – *Glaucopsaltria* – *Owra* and *Cystopsaltria* – *Cystosoma*) and species that belong to genera which also occur in New Guinea (*Diceropyga subapicalis*, *Guineapsaltria flava*, *Gymnotympana rufa*, *G. varicolor*, *Lembeja paradoxa*, *L. vitticollis*, and *Thaumastopsaltria glauca*). The position of the monotypic genus *Venustria* in this subdivision is not clear, since *V. superba* should possibly be included in *Gymnotympana* (De Boer 1995a, d). From comparison of the cladograms it can be deduced for most of these taxa, that the ancestors of the two groups of endemic Australian genera must have reached that continent earlier (possibly following the Sepik Arc collision of 25 Mya) than the various species of the non endemic genera (presumably in the Pliocene – Pleistocene). In this light it is interesting that the Australian species of the genera that have their main distribution in New Guinea are restricted to the Cape York peninsula of Queensland only, while several species of the Australian genera reach much farther southward into New South Wales.

Such differences in size of the distribution area might be explained by difference in time of arrival on Australia. It is considered more likely, however, that the ancestors of *Chlorocysta* – *Glaucopsaltria* – *Owra* and of *Cystopsaltria – Cystosoma* reached Australia before the opening of the foreland basin between the New Guinea orogen and the Australian continent, and then were forced to move farther southward when the basin spread. During the existence of this foreland basin (from 21-3 Mya) large parts of southern New Guinea and northern Australia were submerged. The Australian genera may have migrated northward again when northern Queensland reemerged.

Three of the Australian species that belong to non-Australian genera (*G. rufa, G. varicolor,* and *L. vitticollis*) are endemic to the Cape York peninsula, the others have a wider distribution in southern New Guinea and the Papuan peninsula. It is remarkable that all these species of non-Australian genera either occur on the Papuan peninsula themselves, or belong to genera for which a Papuan peninsula origin was inferred (*Diceropyga, Gymnotympana, Thaumastopsaltria*), or at least have their nearest relatives on the Papuan peninsula. *G. flava,* which belongs to a genus for which a north New Guinea origin was proposed, reaches well into the Papuan peninsula, and has its sister species, *G. flaveola,* in the eastern parts of that peninsula. Even the two *Lembeja* species, which belong to a genus otherwise concentrated in Sulawesi, form no exception. *L. paradoxa,* which has its nearest relations (the *L. fatiloqua* group) on Borneo, the Philippines, Sulawesi, and on some of the Lesser Sunda islands (De Jong 1987), occurs in southern New Guinea and on the Papuan peninsula (De Jong 1982), and *L. vitticollis* belongs to a subgroup of *Lembeja,* which has several species on New Guinea; its nearest relatives (*L. papuensis* and *L. robusta*) are restricted to east Papua New Guinea, including the Papuan peninsula (De Jong pers. comm.). The Australian and New Guinean representatives of the genus *Lembeja* possibly represent a relict distribution (see above) and it cannot be ruled out therefore, that *L. paradoxa* has had extinct relatives on New Guinea and the Papuan peninsula.

It seems that the most recent (Pleistocene) migration route to Australia was only available for species from the Papuan peninsula. Neither *Aedeastria,* with its predominantly west New Guinea distribution, nor *Baeturia,* with its supposedly north New Guinea origin, have reached Australia. Both these genera have been able to invade southern New Guinea since its reemergence (which started about 10 Mya, that is before the Pliocene) and they even reached the Aru islands. For the widely distributed genus *Baeturia* (Maluku – Samoa) the central mountain ranges of New Guinea presumably obstructed a rapid southward migration; the genus might have reached southern New Guinea after the last, Pleistocene, connection with Australia ceased to exist. It is not clear, however, what has prevented *Aedeastria* from reaching Australia.

A distribution in the Cape York peninsula, southern New Guinea and the Papuan peninsula is a fairly common one and the migration route worked two ways. A species of the otherwise endemic Australian cicada genus *Pauropsalta, P. eyrei,* is recorded from Cape York and the Papuan peninsula (Ewart 1989) and two species of the mainly Australian plant genus *Arytera* Blume occur on Cape York and the Papuan peninsula (Turner 1995).

Papuan peninsula

The Papuan peninsula has by far the richest and most diverse cicada fauna of all New Guinean OMA fragments and houses by far the highest number of endemic species. Phylogeny and biogeography of the Papuan cicadas suggest that the Papuan peninsula also has the most complex of area relationships. This biological complexity reflects the geological complexity of the area, which is fourfold:

1) The Papuan peninsula in itself is of composite geological origin, as a part of the East Papua Composite terrane. Prior to the amalgamation of this East Papua Composite terrane, its components formed an archipelago of presumably closely related islands (fig. 20a). The various islands of this archipelago might have had different relationships with the other parts of the OMA.

2) The East Papua Composite terrane presumably took a central position in the OMA, forming a link between the two largest New Guinean arc fragments, the Sepik Arc, and the north New Guinean terranes. The location of the East Papua Composite terrane within the OMA might also have brought this terrane into contact with the westward migrating Halmahera arc and the northward migrating Solomon arc (fig. 55b). The East Papua Composite terrane might at one time have formed the crossroads of several island arc systems.

3) After the collision of the East Papua Composite terrane with the Australian continent, the Papuan peninsula remained separated from other parts of New Guinea by the Aure Trough (fig. 21). The Papuan peninsula is therefore probably the part of New Guinea with the longest history of isolation.

4) The opening of the Woodlark Basin, which is held responsible for the fact that no other terranes accreted in eastern Papua New Guinea, caused a geotectonic whirlpool in which arc fragments curved northward, sliding past the accreted parts of the East Papua Composite terrane. During these processes biological exchange between the various passing terranes might well have been possible.

Four cicada genera (*Diceropyga, Gymnotympana,* *Papuapsaltria*, and *Thaumastopsaltria*) are presumed to have evolved or partly evolved on the Papuan peninsula. The latter three of these genera indicate a sister group relationship of that peninsula with the terranes of northern New Guinea. Since the north New Guinea terranes were, after the East Papua Composite terrane, the next terranes to be accreted to New Guinea, it may be supposed that these terranes lay also the next in order within the OMA island chain immediately to the east of the East Papua Composite terrane (fig. 55).

Monophyletic species groups of *Diceropyga* and *Gymnotympana* show a vicariance between northern Maluku and the Papuan peninsula. (The uncertain locality of *T. adipata* possibly obscures such a vicariance for the genus *Thaumastopsaltria*, see above). This vicariant pattern must presumably be explained by a historical proximity between the Halmahera arc and the East Papua Composite terrane as shown by the reconstructions presented in fig. 55 (see discussion on Maluku).

Diceropyga and its sister group *Rhadinopyga* – new genus '*I.*' show a vicariant pattern between eastern New Guinea (including Maluku, and the Bismarck and Solomon Islands) and the Birds Head plus the Solomon Islands. A somewhat similar pattern seems to be indicated by the presumed sister group relationship between the genus *Aedeastria* with its mainly western New Guinea distribution and *Thaumastopsaltria – Mirabilopsaltria* from the Papuan peninsula and northern New Guinea. These patterns suggest a historical proximity between the Birds Head and a cluster of terranes including the East Papua Composite terrane, northern Maluku, the Bismarck Archipelago and Solomon Islands, as is discussed in the above section on the Birds Head and visualized in figs 55c-d.

The small *Diceropyga obliterans* group (three species), which is endemic to the Bismarck Archipelago, forms the sister group of all other *Diceropyga* species. This suggests an old vicariant pattern rather than a recent dispersal event. Since the occurrence of *Diceropyga* in northern New Guinea is supposed to be due to recent dispersal, and the northern New Guinea *Diceropyga* species certainly do not form the sister group of the *obliterans* group, this pattern indicates a vicariance between the Bismarck Archipelago and an area including the East Papua Composite terrane, the Halmahera Arc, and part of the Solomon Islands. The Bismarck Archipelago is supposed to have formed a continuous arc with the Finisterre terrane of northern New Guinea. The latter accreted most recently to New Guinea, following the accretion of the north New Guinea terranes, and may in theory originate from a position in the OMA east of these north New Guinea terranes (fig. 55a). Such a reconstruction places the Bismarck Archipelago far from the Papuan peninsula, separated from it by the north New Guinea and Finisterre terranes. The *obliterans* group, on the other hand, suggests that there has been a period of some contact between the Bismarck Archipelago and at least part of the East Papua Composite terrane. Although such a contact might have been possible after the north New Guinea terranes had slid past the already accreted Papuan peninsula, the sister group position of the *obliterans* group suggests an older event. Possibly the OMA fragments did not form a perfectly linear constellation, and possibly the Bismarck terrane lay, either with or without the Finisterre terrane, parallel, in the north or the south, to some of the north New Guinea terranes (as schematically drawn in fig. 55c). In this respect the reconstruction of Struckmeyer et al. (1993) might be more accurate. In that reconstruction the north New Guinea and Finisterre terranes lie north of the East Papua Composite terrane (fig. 56). The position of the Finisterre terrane is not clear from a biogeographical point of view. The distribution of cicadas does not indicate a combined Finisterre – Bismarck terrane as area of endemism and the species endemic to Finisterre are related to northern New Guinea groups, rather than to Bismarck groups (see the section on northern New Guinea). The fact that none of the other presumed Papuan genera have an old and endemic group in the Bismarck Archipelago might imply that not all parts of the East Papua Composite terrane have had contact with the Bismarck terrane.

Diceropyga has no less than eight endemic species in the Solomon Islands. These eight species all belong to the *D. subapicalis* group, a group otherwise distributed in New Guinea and centred on the Papuan peninsula, and presumably do not form a monophyletic group (Duffels pers. comm.). This suggests that there have been several invasions from the Papuan peninsula into the Solomon Islands. It is remarkable that most of these invasions apparently did not take place via the Bismarck Archipelago, at present the most logical connection between New Guinea and the Solomon Islands. Only some of these Solomon species might be closely related to *D. gravesteini*, which is distributed in New Guinea and the Bismarck Archipelago. It is not clear whether or not these invasions are related to a historical proximity between the Papuan peninsula and the Solomon Islands.

When the closure of the Aure Trough ended the isolation of the Papuan peninsula, species could migrate into other parts of New Guinea. All four genera with a presumed East Papua Composite terrane origin have species with a comparatively wide distribution along the northern mountain ranges of New Guinea, and some of these distributions include the Bismarck Archipelago. *Diceropyga* and *Thaumasto-*

psaltria have species reaching from the Papuan peninsula to southern New Guinea and northern Queensland, while *Gymnotympana*, which has two endemic species in northern Queensland, is not recorded from southern New Guinea. It is remarkable that all species from northern Queensland that do not belong to endemic Australian genera have their nearest relations in the Papuan peninsula (see the section on Australia). Only two species of *Gymnotympana* and several species of *Papuapsaltria* have invaded the central mountain ranges of New Guinea, but all these species have very restricted areas of distribution in the easternmost parts of the central mountains only.

Melanesian archipelagos

The eastern parts of the OMA system, the East-Melanesian archipelagos from the Solomon Islands to Samoa, form a major problem in the present biogeographic studies. This problem manifests itself in the great many invasion events necessary to explain the present-day cicada fauna of that area. Two groups are distributed throughout these archipelagos: a monophyletic group combining the genera *Aceropyga* and *Moana*, and a part of the *Baeturia bloetei* group. Two other groups occur in the Solomon Islands: eight species of the genus *Diceropyga* – which together apparently do not form a monophyletic group – and the new genus *'I.'* are endemic to this island chain. Since *Aceropyga – Moana* is the sister group of a monophyletic group consisting of *Diceropyga*, the new genus *'I.'*, and *Rhadinopyga*, it is clear that groups of cicadas have reached the Solomon Islands at at least three stages in the evolution of the Cosmopsaltriaria: first the ancestor of *Aceropyga – Moana*, then that of the new genus *'I.'*, and finally (the ancestors of) several *Diceropyga* species. These three groups all show a dispersal or vicariance between the Solomon Islands and eastern New Guinea (the Papuan peninsula), though in the case of *Aceropyga – Moana* the Bismarck Archipelago might be involved as a link between the Solomons and Papua New Guinea. Only the oldest of these three groups (*Aceropyga – Moana*) has been able to spread eastward beyond the Solomon Islands (fig. 49). The occurrence of the *Baeturia* species must be the result of yet another invasion. These species have their nearest relatives on the Bismarck Archipelago and northern New Guinea, but (apart from a questionable record of *B. papuensis*) not on the Papuan peninsula. Although this group is considered much younger than *Aceropyga – Moana* and presumably also younger than the new genus *'I.'*, they also have reached Samoa and Tonga (fig. 38).

The biogeographic complexity of East Melanesia is presumably partly due to the supposed, in chapter 2 discussed, different geological origin of the New Guinean and East-Melanesian arc fragments. If the East-Melanesian archipelagos initially evolved as part of, or in connection with, the Australian plate, the present apparent continuity: New Guinea – Bismarck Archipelago – Solomon Islands must be of a fairly recent date. In case of an 'Australian related' origin, the Solomon – Fiji arc must have moved northward with the Australian plate, while the New Guinean arc fragments moved from east to west on the southern margin of the Pacific plate.

The distribution and phylogeny of *Aceropyga – Moana* seems in agreement with such a dual origin of OMA fragments. *Aceropyga – Moana* forms the sister group of *Diceropyga* – new genus *'I.'* – *Rhadinopyga*. The latter group shows a vicariant pattern between the Papuan peninsula (including the Bismarck Archipelago, Maluku, and Solomon Islands) and the Birds Head – Solomon Islands. Presuming these cicadas came here by dispersal along the OMA, the common ancestor of that group (*Diceropyga* – new genus *'I.'* – *Rhadinopyga*) presumably evolved on the East Papua Composite terrane (Papuan peninsula), which is the first part of the area derived from the OMA they could have reached. The vicariance between *Diceropyga* – new genus *'I.'* – *Rhadinopyga* and *Aceropyga – Moana* is thus essentially a vicariance between the Papuan peninsula and the East-Melanesian arc, and indicates a historical proximity between these terranes. Such a proximity contradicts a 'single arc' theory in which these areas are separated by the northern New Guinea, Finisterre, and Bismarck terranes as in fig. 55a. The common ancestor of *Aceropyga – Moana* could have reached the East-Melanesian arc terranes directly through the East Papua Composite terrane and in bypassing the northern New Guinea, Finisterre and Bismarck terranes. On the other hand the common ancestors of *Aceropyga – Moana* and of *Diceropyga* – new genus *'I.'* – *Rhadinopyga* could have simultaneously reached East Melanesia and the East Papua Composite terrane respectively. Either of these alternatives would be possible in the reconstruction of fig. 55b. The occurrence of *Moana* on the Bismarck Archipelago might be due to a later westward dispersal when the Solomon Islands approached the Bismarck Archipelago. It could also imply that the Bismarck islands are part of the Australian rather than the Pacific arc system, and have always been a northern continuation of the East-Melanesian arc as in the reconstruction of fig. 55d. As discussed in the section on the Papuan peninsula, a position of the Bismarck terranes east of the northern New Guinea and Finisterre terranes (fig. 55a) is also contradicted by the phylogenetic position of the *Diceropyga obliterans* group.

The collision between the Ontong Java plateau and the Solomon arc (9-12.5 Mya) caused a reversal of subduction (see chapter 2) as a result of which the

Solomon arc at present behaves as part of the Pacific plate and consequently moves westward. Moreover, this collision led to fragmentation of the East-Melanesian island arc: Vanuatu rotated (5.5-9 Mya) southward and Fiji became isolated. This fragmentation is presumably responsible for the vicariant pattern between *Aceropyga* and *Moana*.

The *Baeturia bloetei* group has a similarly wide distribution in East Melanesia as *Aceropyga* and *Moana* together, but the former group extends westward to New Guinea and Maluku, and is absent from Fiji. The absence from Fiji has been explained by accepting a younger age for the *bloetei* group. When the *bloetei* group invaded the East-Melanesian archipelagos, Fiji had apparently already rotated away. Such an age difference between these two groups is supported by their relative positions in the cladograms (figs 51 & 52) (which can be compared in a time scale, supposing that *Gymnotympana* and *Diceropyga* are of approximately the same age). Furthermore, the relatively small and few morphological differences between the species of the *bloetei* group also indicate their recent evolution. Since the East-Melanesian species of *Baeturia* have their nearest relatives in northern New Guinea and the Bismarck Archipelago, it is presumed that the *bloetei* group entered East Melanesia when the present-day configuration with the Solomon Islands as a continuation of northern New Guinea and the Bismarck Archipelago already existed. The aforementioned small morphological differences among the *bloetei* group species hamper a phylogenetic reconstruction, and the relationships as indicated by the cladogram presented earlier (De Boer 1995d) are considered very uncertain, especially as far as the position of the three Bismarck species is concerned. Nevertheless, the East-Melanesian species clearly belong to two subgroups, one of which is presumably monophyletic, the other might include the New Guinean, Moluccan, and possibly Bismarck species of the *bloetei* group. These two subgroups have a similar distribution in the Solomon Islands and Vanuatu, but one reaches to Rotuma island and the other to Samoa and Tonga. The distributions of these groups on the Solomon Islands are strikingly similar, both subgroups suggest a subdivision between a northern and southern Solomon arc, which roughly coincides with the subdivision in geological provinces (fig. 25). It is remarkable that such a subdivision does not appear in the older groups like *Moana*, *Diceropyga*, and the new genus *'I.'*

CONCLUSIONS

The almost perfect congruence between the geological cladogram and the source-area cladograms of the Cosmopsaltriaria and the Prasiini – Chlorocystini indicates that fragmentation of the OMA followed by isolation of the fragments, is responsible for the vicariant evolution of these two groups of cicadas. Cicada distributions and relationships sometimes also indicate historic relationships between areas that are at variance with the geological data. These incongruencies may compel us to make some minor modifications and additions to a palaeogeographic reconstruction of the Outer Melanesian Arc systems. Based on the cicada relationships we can make the following observations:

1. – Part of Sulawesi, central New Guinea, the Papuan peninsula, northern New Guinea, and the Finisterre terrane have, in that order, formed a more or less linear island arc. The Sulawesi element in this arc is not widely recognized among geologists.

2. – This island arc was connected to Asia via the Ryukyu Islands. The collision between the OMA and Asia must have occurred in that region. The geological literature is vague about the location of this first collision.

3. – There are no data in cicada distribution suggesting a role of (parts of) the Philippines in this island arc. It is widely accepted among geologists that parts of the central Philippines did form part of the OMA.

4. – Halmahera lay at one time near the East Papua Composite terrane. Geologists widely agree that Halmahera originates from far to the east or southeast of its present position, but no link to eastern New Guinea has ever been suggested.

5. – Cicada biogeography and phylogeny indicates that the Finisterre terrane is an integral part of the northern New Guinea terranes, and not (as indicated in geological literature) related to the Bismarck Archipelago. The Finisterre terrane presumably collided with the Australian continent, or started to collide, at the same time as did the northern New Guinea terranes (10 Mya, as suggested by Pigram & Davies, 1987). Geological literature often places this collision much later (2-4 Mya).

6. – The Bismarck Archipelago presumably always lay near the East Papua Composite terrane and has not been separated from that terrane by the northern New Guinea and Finisterre terranes. The latter is often suggested in geological literature, though a recent palaeogeographic reconstruction of Struckmeyer et al. (1995) complies with this view.

7. – The East-Melanesian archipelagos (the Solomon Islands, Vanuatu, Fiji, and Tonga) form a separate arc system that evolved along the eastern margins of the Australian plate, of which the northern part, the Solomon Islands, lay near the East Papua Composite terrane. The separate evolution of this chain is widely accepted in the geological literature, but no connection to the East Papua Composite terrane has been suggested.

8. – The Bismarck Archipelago may have formed a link between this East-Melanesian arc and the East Papua Composite terrane. Geologists regard the Bismarck Archipelago as an eastern extension of the part of the OMA that derived from the Pacific and suggest a relationship with the Finisterre terrane.

9. – The Birds Head originates from far to the east of its present position and at one time lay near the East Papua Composite terrane and the Solomon Islands. The eastern origin of the Birds Head agrees with the geological data but a proximity between the Birds Head and the East Papua Composite terrane or Solomon Islands has never been suggested in the geological literature.

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References

Abbott, L. D. & E. A. Silver, 1991. Geology of the southern Finisterre range: A case history of modern arc-continent collision. p. 1-7. – In: Proceedings of the P.N.G. Geology, Exploration and Mining Conference. Rabaul Papua New Guinea.

Audley-Charles, M. G., 1987. Dispersal of Gondwanaland: relevance to evolution of the angiosperms. p. 1-25. – In: T. C. Whitmore (ed.), Biogeographical evolution of the Malay Archipelago. Clarendon Press, Oxford.

Boer, A. J. de, 1982. The taxonomy and biogeography of the *nasuta* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Beaufortia 32 (4): 57-78.

Boer, A. J. de, 1986. The taxonomy and biogeography of the *conviva* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Beaufortia 36 (7): 167-182.

Boer, A. J. de, 1989. The taxonomy and biogeography of the *bloetei* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Beaufortia 39 (1): 1-43.

Boer, A. J. de, 1990. *Aedeastria*, a new cicada genus from New Guinea, its phylogeny and biogeography (Homoptera, Tibicinidae), preceded by a discussion on the taxonomy of New Guinean Tibicinidae. – Beaufortia 40 (3): 63-72.

Boer, A. J. de, 1991. *Scottotympana*, a new cicad genus from New Guinea, with the description of three new species, their taxonomy and biogeography (Homoptera, Tibicinidae). – Beaufortia 42 (1): 1-11.

Boer, A. J. de, 1992a. The taxonomy and biogeography of the genus *Thaumastopsaltria* Kirkaldy, 1900 (Homoptera, Tibicinidae). – Beaufortia 43 (3): 17-44

Boer, A. J. de, 1992b. The taxonomy and biogeography of the *viridis* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Bijdragen tot de Dierkunde 61 (3): 163-183.

Boer, A. J. de, 1993a. *Guineapsaltria*, a new genus of the Australian-New Guinean region, with notes on its taxonomy and biogeography (Homoptera, Tibicinidae). – Bijdragen tot de Dierkunde 63 (1): 15-41.

Boer, A. J. de, 1993b. Ten new species of the genus *Aedeastria* De Boer, 1990, with notes on the taxonomy and biogeography (Homoptera, Tibicinidae). – Beaufortia 43 (9):140-167.

Boer, A. J. de, 1994a. The taxonomy and biogeography of the *loriae* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 137: 1-26.

Boer, A. J. de, 1994b. The taxonomy and biogeography of the *guttulinervis* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Bijdragen tot de Dierkunde 64: (2) 87-100.

Boer, A. J. de, 1994c. The taxonomy and biogeography of the *exhausta* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Beaufortia 44 (5): 127-158.

Boer, A. J. de, 1994d. Four species added to the *Baeturia nasuta* group, with notes on taxonomy and biogeography (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 137: 161-172.

Boer, A. J. de, 1995a. The taxonomy, phylogeny and biogeography of the genus *Gymnotympana* Stål, 1861 (Homoptera, Tibicinidae). – Invertebrate Taxonomy, 9 (1): 1-81.

Boer, A. J. de, 1995b. *Mirabilopsaltria*, a new cicad genus from New Guinea, its taxonomy and biogeography (Homoptera, Tibicinidae). – Tropical Zoology, (in press).

Boer, A. J. de, 1995c. The taxonomy and biogeography of the genus *Papuapsaltria* gen. n. (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 138: 1-44.

Boer, A. J. de, 1995d. The phylogeny and taxonomic status of the Chlorocystini (sensu stricto) (Homoptera, Tibicinidae). Bijdragen tot de Dierkunde 65.

Boulard, M., 1981. Sur trois *Toxopeusella* nouvelles des collections du British Museum (Hom. Cicadoidea). – Entomologist's Monthly Magazine 117: 129-138.

Burrett, C., N. Duhig, R. Berry, & R. Varne, 1991. Asian and south-western Pacific continental terranes derived from Gondwana, and their biogeographic significance. – Australian Systematic Botany 4: 13-24.

Chandler, K. J., 1972. The incidence and bionomics of the brown cicada Melampsalta puer (Walk.) in north Queensland cane feelds. – Proceedings of the Queensland Society of Sugar Cane technologists. 39th conf.: 249-255.

Chandler, K.J., 1973. Cicadas damaging sugar cane in Queensland. – Cane growers quarterly bulletin 37 (2): 46-49.

Coffin, M. F. & O. Eldholm, 1993. Large igneous provinces. – Scientific American 269 (4): 26-33.

Cracraft, J., 1988. Deep-history biogeography: retrieving the historical pattern of evolving continental biotas. – Systematic Zoology 37: 221-236.

Daly, M. C., M. A. Cooper, I. Wilson, D. G. Smith & B. G. D. Hooper, 1991. Cenozoic plate tectonics and basin evolution in Indonesia. – Marine and Petroleum Geology (-MPGD) 8 (1): 1-21.

Dietz R.S. & J.C. Holden, 1970. The break-up of Pangea. Scientific American, 223: 30-41.

Dow, D.B., 1977. A geological synthesis of Papua New Guinea. – Bulletin of the bureau of mineral resources Canberra, Geology and Geophysics, Australia 201: 41.

Dubois, J., 1966. Influence de certaines modifications récentes dans la culture de la canne à sucre sur l'évolution des populations de la cigale *Yanga guttulata* Sign. – Agronomie Tropicale Nogent-sur-Marne 21 (6-7): 786-821.

Duffels, J. P., 1977. A revision of the genus *Diceropyga* Stål, 1870 (Homoptera, Cicadidae). – Monografieën nederlandse entomologische Vereniging 8: 1-227.

Duffels, J. P., 1982. *Brachylobopyga decorata* n. gen., n. sp. from Sulawesi, a new taxon of the subtribe Cosmopsaltriaria (Homoptera, Cicadidae). – Entomologische Berichten Amsterdam 42: 156-160.

Duffels, J. P., 1983. Taxonomy, phylogeny and biogeography of the genus *Cosmopsaltria*, with remarks on the historic biogeography of the subtribe Cosmopsaltiaria (Homoptera: Cicadidae). – Pacific Insects Monograph 39: 1-127.

Duffels, J. P., 1985. *Rhadinopyga* n. gen. from the 'Vogelkop' of New Guinea and adjacent islands, a new genus of the subtribe Cosmopsaltriaria (Homoptera, Cicadoidea: Cicadidae). – Bijdragen tot de Dierkunde 55 (2): 275-279.

Duffels, J. P., 1986. Biogeography of Indopacific Cicadoidea, a tentative recognition of areas of endemism. – Cladistics 2 (4): 318-336.

Duffels, J. P., 1988a. The Cicadas of Fiji Samoa and Tonga Islands, their taxonomy and biogeography (Homoptera, Cicadoidea). – Entomonograph 10: 1-108.

Duffels, J. P., 1988b. Biogeography of the cicadas of the island of Bacan, Maluku, Indonesia, with description of *Diceropyga bacanensis* n. sp. (Homoptera, Cicadidae). – Tijdschrift voor Entomologie 131: 7-12.

Duffels, J. P., 1988c. *Cosmopsaltria halmaherae* n. sp. endemic to Halmahera, Maluku, Indonesia (Homoptera, Cicadidae). – Bijdragen tot de Dierkunde 58: 20-24.

Duffels, J. P., 1988d. *Cosmopsaltria kaiensis* n. sp., a new cicada from the Kai Islands, Indonesia (Homoptera: Cicadidae). – Entomologische Berichten Amsterdam 48:187-190.

Duffels, J. P., 1989. The Sulawesi genus *Brachylobopyga* (Homoptera: Cicadidae). – Tijdschrift voor Entomologie 132, 123-127.

Duffels, J. P., 1990. Biogeography of Sulawesi cicadas (Homoptera: Cicadoidea). *In*: W.J. Knight & J.D. Holloway (Eds) Insects and the Rain Forrest of South East Asia (Wallacea). (Royal Entomological Society, London).

Duffels, J. P., 1991 The eye-catching cicada *Hamza ciliaris* (Linnaeus, 1758) comb. n. in Indonesia and the Pacific: taxonomic status, synonymy, and distribution (Homoptera, Cicadoidea). – Bijdragen tot de Dierkunde 61 (2) 119-130

Duffels, J. P., 1993. The systematic position of *Moana expansa* (Homoptera, Cicadidae), with reference to sound organs and the higher classification of the superfamily Cicadoidea. – Journal of Natural History 27: 1223-1237.

Duffels, J. P. & A. J. de Boer, 1990. Areas of endemism and composite areas in East Malesia. – In: P. Baas, C. Kalkman & R. Geesink (eds.), The plant diversity of East Malesia: Proceedings of the Flora Malesiana symposium commemorating Professor Dr. C. G. G. J. van Steenis, Leiden, August 1989: 249-272 (Kluwer Academic Publishers, Dordrecht).

Duffels, J. P. & H. J. G. van Mastrigt, 1991. Recognition of cicadas (Homoptera, Cicadidae) by the Ekagi people of Irian Jaya (Indonesia), with a description of a new species of Cosmopsaltria. – Journal of Natural History 25: 173-182.

Ewart, A., 1988. Geological history of the Fiji - Tonga - Samoan region of the S.W. Pacific and some paleogeographic and biogeographic implications. *In*: J. P. Duffels, 1988: The Cicadas of Fiji Samoa and Tonga Islands, their taxonomy and biogeography (Homoptera, Cicadoidea). – Entomonograph 10: 15-23.

Ewart, A., 1989. Revisionary notes on the genus *Pauropsalta* Goding and Froggatt (Homoptera: Cicadidae) with special reference to Queensland. – Memoirs of the Queensland Museum 27 (2): 289-375.

Fortuin, A. R., M. E. M. De Smet, S. Hadiwasastra, L. J. Van Marle, S. R. Troelstra, & S. Tjokrosapoetro, 1990. Late Cenzoic sedimentary and tectonic history of south Buton, Indonesia. – Journal of Southeast Asian Earth Sciences 4 (2): 107-124.

Fortuin, A. R. & M. E. M. De Smet, 1991. Rates and magnitudes of late Cenozoic vertical movements in the Indonesian Banda Arc and the distinction of eustatic effects. – Special Publications of the International Association of Sedimentology 12: 79-89.

Giddings, J. W., W. Sunata & C. J. Pigram, 1993. Reinterpretation of palaeomagnetic results from the Bird's Head, Irian Jaya: new constraints on the drift history of the Kemum Terrane. – Exploration Geophysics 24: 283-290.

Gill, J. & M. Gorton, 1973. A proposed geological and geophysical history of eastern Melanesia. p. 543-566. *In*: P. J. Coleman (ed.) The Western Pacific; island arcs, marginal seas, geochemistry. (Univ. of Western Australia Press, Perth).

Green, D. & D. J. Cullen, 1973.The tectonic evolution of the Fiji region. p. 127-145. *In*: P.J. Coleman (ed.) The Western Pacific; island arcs, marginal seas, geochemistry. (Univ. of Western Australia Press, Perth).

Hackman, B. D., 1973. The Solomon islands fractured arc. p. 179-191. *In*: P.J. Coleman (ed.) The Western Pacific; island arcs, marginal seas, geochemistry. (Univ. of Western Australia Press, Perth).

Hall, R. & G. J. Nichols, 1990. Terrane amalgamation in the Philippine sea margin. – Tectonophysics 181: 207-222.

Hamilton, W.B., 1979. Tectonics of the Indonesian region. – United States Geological Survey profesional Papers 1078: i-ix, 1-345.

Hamilton, W.B., 1986. Convergent-plate tectonics viewed from the Indonesian region. p. 655-698. In: Sengor, A.M.C. (ed.). Tectonic of the Tethyan Region: Proceedings of the NATO Advanced Study Institute on Tectonic Evolution of the Tethyan Region. The Faculty of mines, Istabul Technical Unversity, Istabul, Turkey, 23 sep-2oct 1985(6?). NATO ASI series; series C:

Mathematical and Physical sciences-Vol. 259. (Kluwer Acadmic Publishers. Dordrecht).

Hartono, H. M. S., 1990. Late Cenozoic tectonic development of the southeast Asian continental margin in the Banda sea area. – Tectonophysics 181: 267-276.

Hennig, W., 1950. Grundzüge einer Theorie der phylogenetischen Systematik. (Deutscher Zentralverlag, Berlin).

Hennig, W., 1966. Phylogenetic systematics. (University of Illinois Press, Urbana).

Holloway, J. D., 1979. A survey of the Lepidoptera, biogeography and ecology of New Caledonia. – Series Entomologica 15: i-xii, 1-588.

Holloway, J. D., 1987. Lepidoptera patterns involving Sulawesi: What do they indicate of past geography. p. 103-118. T.C. Whitmore (ed.) *In*: Biogeographical evolution of the Malay archipelago. (Clarendon Press, Oxford).

Honza, E., 1991. The Tertiary arc chain in the western Pacific. – Tectonophysics 187: 285-303.

Humphries, C. J. & L. R. Parenti, 1986. Cladistic biogeography. (Clarendon Press, Oxford).

Hutchison, C. S., 1989. The paleo-Tethyan realm and Indonesian orogenic system of southeast Asia. p. 585-643. In: Sengor, A.M.C. (ed.). Tectonic Evolution of the Tethyan Region: Proceedings of the NATO Advanced Study Institute on Tectonic Evolution of the Tethyan Region. The Faculty of mines, Istabul Technical Unversity, Istabul, Turkey, 23 sep-2oct 1985(6?). NATO ASI series; series C: Mathematical and Physical sciences-Vol. 259. (Kluwer Acadmic Publishers. Dordrecht).

Itô, Y. & M. Nagamine, 1974a. Distribution of infestations of a sugar cane cicada, *Mogannia iwasakii* Matsumura (Hemiptera, Cicadidae) in Okinawa Island with discussion on the cause of the outbreak. – Japanese society of applied entomology and Zoology 9: 58-64.

Itô, Y. & M. Nagamine, 1974b. Population dynamics of a sugar cane cicada, *Mogannia iwasakii* Matsumura in Okinawa Island. – Proceedings XV Congres International Society of Sugar Cane Technologists. Durban, 1: 468-474.

Jong, M. R. de, 1982. The Australian species of the genus *Lembeja* Distant, 1892 (Homoptera, Tibicinidae). – Bijdragen tot de Dierkunde 52 (2): 175-185.

Jong, M. R. de, 1985. Taxonomy and biogeography of Oriental Prasiini 1: The genus Prasia Stål, 1863 (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 128: 165-191.

Jong, M. R. de, 1986. Taxonomy and biogeography of Oriental Prasiini 2: The *foliata* group of the genus *Lembeja* Distant, 1892 (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 129: 141-180.

Jong, M. R. de, 1987. Taxonomy and biogeography of Oriental Prasiini 3: The *fatiloqua* and *parvula* groups of the genus *Lembeja* Distant, 1892 (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 130: 177-209.

Jong, M. R. de & J. P. Duffels, 1981. The identity, distribution and synonymy of *Lembeja papuensis* Distant, 1897 (Homoptera, Tibicinidae). – Bulletin zoologisch Museum Universiteit van Amsterdam, 8 (7): 53-62.

Katili, J. A., 1989. Review of past and present geotectonic concepts of eastern Indonesia. Proc. Snellius II Symp., – Netherlands Journal of Sea Research 24: 103-129.

Kitching, I. J., R. I. Vane-Wright & P. R. Ackery, 1987. The cladistics of *Ideas* (Lepidoptera, Danaidae). – Cladistics 3:14-34.

Kuniata, L.S. & H. Nagaraja, 1992. Biology of *Baeturia papuensis* De Boer (Homoptera, Tibicinidae) on sugarcane in Papua New Guinea. – Science in New Guinea18 (2): 65-72.

Lee, C.S. & R. McCabe, 1986. The Banda-Celebes-Sulu basin: a trapped piece of Cretaceous-Eocene oceanic crust? – Nature 322: 51-54.

Mallick, D.I.J., 1973. Some petrological and structural variations in the New Hebrides, p. 193-211. *In*: P. J. Coleman (ed.) The Western Pacific; island arcs, marginal seas, geochemistry. (Univ. of Western Australia Press, Perth).

Monsarrat, A., 1966. Premières observations sur *Yanga guttulata* Sign. Homoptère Cicadidae, ravageur de la canne à sucre dans le nord-ouest de Madagascar. – Bulletin de Madagascar. Tananarive 237: 165-168.

Moore, G. F. & E. A. Silver, 1982. Collision processes in the northern Molucca sea. The tectonic and geologic evolution of southeast Asian seas and islands, part 2. – Geophysical Monograph series 27: 360-372.

Moulds, M.S., 1990. Australian cicadas: 1-217. (New South Wales University Press, Kensington).

Nagamine, M & R. Teruya, 1976. Life history of *Mogannia iwasakii* Matsumura. – Bulletin Okinawa Agricultural experiment Station 2: 15-26.

Nelson, G. & N. Platnick, 1981. Systematics and biogeography. Cladistics and vicariance. (Columbia University Press, New York).

Nichols, G., Hall, R., Milsom, J., Masson, D., Parson, L., Sikumbang, N., Dwiyanto, B. & H. Kallagher, 1990. The southern termination of the Philippine trench. – Tectonophysics 183: 289-303.

Nishimura, S. & S. Suparka, 1990. Tectonics of east Indonesia. – Tectonophysics 181: 257-266.

Nur, A. & Z. Ben-Avraham, 1977. Lost Pacifica continent. – Nature 270: 41-43.

Nur, A. & Z. Ben-Avraham, 1981. Lost Pacifica continent: a mobilistic speculation. p. 341-358. *In*: Gareth Nelson & Donn E. Rosen (eds) Vicariance biogeography, a critique. (Colombia University Press, New York).

Packham, G. H., 1973. A speculative phanerozoic history of the south-west Pacific. p. 369-388. *In*: P.J. Coleman (ed.) The Western Pacific; island arcs, marginal seas, geochemistry. (Univ. of Western Australia Press, Perth).

Pigram, C. J., & P. J. Davies, 1987. Terranes and the accretion history of the New Guinea orogen. – B.M.R. Journal of Australian Geology & Geophysics 10: 193-212.

Pigram, C. J., Davies, P. J., Feary, D. A. & P. A. Symonds, 1989. Tectonic controls on carbonate platform evolution in southern Papua New Guinea: passive margin to foreland basin. – Geology 17: 199-202.

Pigram, C.J. & H. Panggabean, 1984. Rifting of the northern margin of the Australian continent and the origin of some microcontinents in eastern Indonesia. – Tectonophysics 107: 331-353.

Pigram, C .J., Surono & J. B. Supandjono, 1985. Origin of the Sula platform, eastern Indonesia. – Geology 13: 146-148.

Pigram, C. J. & P. A. Symonds, 1991. A review of the timing of the major tectonic events in the New Guinea orogen. – Journal of S.E. Asian Earth Sciences 6: 307-318.

Platnick, N. I. & G. Nelson, 1978. A method of analysis for historical biogeography. – Systematic Zoology 27: 1-15.

Rangin, G., L. Jolivet & M. Pubellier, 1990a. A simple model for the tectonic evolution of the southeast Asia and Indonesia region for the past 43 m. y. – Bulletin de la Société géologique de France, (8), 6 (6): 889-905.

Rangin, G., Pubellier, M., Azema, J., Briais, A., Chotin, P., Fontaine, H., Huchon, P., Jolivet, L., Maury, R., Muller, C., Rampnoux, J.-P., Stephan, J.-F., Tournon, J., Cottereau, N., Dercourt, J. & L. E. Ricou, 1990b. The quest for Tethys in the western Pacific. 8 paleogeodynamic maps for Cenozoic time. – Bulletin de la Société géologique de France (8), 6 (6): 907-913.

Rosen, D.E., 1978. Vicariant patterns and historical explanation in biogeography. – Systematic Zoology 27: 159-188.

Sclater, P.L. 1858. On the general distribution of the members of the class Aves. – Journal of the Proceedings of the Linnean Society of London, Zoology 2: 130-145.

Schuh, R.T. and G.M. Stonedahl, 1986. Historical biogeography in the Indo-Pacific: a cladistic approach. – Cladistics 2: 337-355.

Silver, E. A. & Smith, R.B., 1983. Comparison of terrane accretion in modern southeast Asia and the Mesozoic north American Cordillera. – Geology 11: 198-202.

Silver, E. A., J. B. Gill, D. Schwartz, H. Prasetyo & R.A. Duncan, 1985. Evidence for a submerged and displaced continental borderland, north Banda sea, Indonesia. – Geology 13: 687-691.

Silver, E. A., L. D. Abbott, K. S. Kirchoff-Stein, D. L. Reed, & B. Bernstein-Tailor, 1991. Collision propagation in Papua New Guinea and the Solomon Sea. – Tectonics 10: 863-874.

Simpson, G. G., 1977. Too many lines; the limits of the Oriental and Australian zoogeographic regions. – Proceedings of the American Philosophical Society 121: 107-120.

Smet, M. E. M. de, 1989. A geometrically consistent plate-tectonic model for eastern Indonesian. – Netherlands Journal of Sea Research 24 (2/3): 173-183.

Smet, M. E. M. de, A. R. Fortuin, S. R. Troelstra, L. J. Van Marle, M. Karmini, S. Tjokrosapoetro & S. Hadiwasastra, 1990. Detection of collision-related vertical movements in the Outer Banda Arc (Timor, Indonesia), using micropaleontological data. – Journal of Southeast Asian Earth Sciences 4: 337-356.

Smith, A. G., & J. C. Briden, 1977. Mesozoic and Cenozoic paleocontinental maps. (Cambridge University Press, Cambridge).

Smith, R. B. & E. A. Silver, 1991. Geology of a Miocene collision complex, Buton, eastern Indonesia. – Geological society of America Bulletin 103: 660-678.

Struckmeyer, H. I. M., M. Young, & C. J. Pigram, 1993. Mesozoic to Cainozoic plate tectonic and palaeogeographic evolution of the New Guinea region. p. 261-290. *In* G.J & Z. Carman (Eds) Petroleum exploration and development in Papua New Guinea: proceedings of the second PNG petroleum convention, Port Moresby, 31st May-2nd June 1993.

Turner, H., 1995. Cladistic and biogeographic analyses of *Arytera* Blume and *Mischarytera* gen. nov. (Sapindaceae). – Blumea special suplement 9: 1-230.

Veevers, J.J., 1991. Phanerozoic Australia in the changing configuration of proto-Pangea through Gondwanaland and Pangea in the present dispersed continents. – Australian Systematic Botany 4:1-11.

Wallace, A.R., 1863. On the physical geography of the Malay Archipelago. – Journal of the Royal Geographical Society 33: 217-234.

Wallace, A.R, 1876. The geographical distribution of animals. (McMillan, London).

Wallace, A.R, 1910. The world of life. (Chapman & Hall, London).

Welzen, P.C. van, 1990. *Guioa* Cav. (Sapindaceae): Taxonomy, phylogeny, and historical biogeography. (Rijksherbarium/Hortus Botanicus, Leiden).

Wegener, A., 1912. Die Entstehung der Kontinente. – Petermanns Mitteilungen, pp.185-195, 253-256, 305-309.

Wiley, E.O., 1988. Parsimony analysis and vicariance biogeography. – Systematic Zoology 37: 271-290.

Wilson, G., 1969. Cicadas as pest of sugar cane in Queensland. – Proceedings of the Queensland Society of Sugar Cane Technologists 34: 141-143.

Wilson, G., B. E. Hitchcock & R. B. Moller, 1963. Entomological investigations. 63rd Annual report of the director to the Hon. the minister for agriculture and forestry, Bureau of Sugar Experiment Station, Brisbane, Queensland: 59 63-64.

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GLOSSARY

Accretion – Process in which a landmass merges after collision to another landmass.

Craton – Structure of precambrian rock, unaffected by orogenesis. Here the crust of the northern margin of the Australian plate.

Fault – Fracture along which two parts of tectonic plates slide past each other.

Hot spot – Weak spot in the earth's crust through which magma occasionally wells up.

Lithology – General characteristics of sediments.

Microcontinent – Part of a continent that has become detached by rifting.

Orogenesis – Mountain building.

Rifting – Process in which continental plates are split by newly formed sea floor.

Sea floor spreading – Process of growth of an oceanic plate caused by upwelling of magma along a mid oceanic ridge.

Subduction – Proces in which one of two colliding tectonic plates dips under the other.

Terrane – Geotectonic unit of which the geological properties differ from adjacent terranes.

Trench – Deep sea area marking the place of Subduction.

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THE PHYLOGENY OF THE *TIPULA* (*LUNATIPULA*) *BULLATA* AND *FALCATA* SPECIES GROUPS (DIPTERA: TIPULIDAE)

Jong, H. de, 1995. The phylogeny of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups (Diptera: Tipulidae). – Tijdschrift voor Entomologie 138: 245-267, figs. 1-76, tabs. 1, 2, appendices A, B. [ISSN 0040-7496]. Published 15 November 1995.

A phylogenetic analysis of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups (Diptera: Tipulidae) is presented, based on the examination of 36 morphological characters of the adults of the currently recognized 20 species within these groups. The distribution of the species of both groups is briefly outlined. *T.* (*L.*) *cirrata* is described as new, based on material originating from south-east Spain.

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Key words. – Diptera, Tipulidae, *Lunatipula*, *bullata* group, *falcata* group, phylogeny, distribution.

The phylogeny of the species of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups is discussed as part of a research project on the historical biogeography of the western Mediterranean. Both *bullata* and *falcata* groups primarily contain western Mediterranean endemics and thus could provide clues for a better understanding of the historical biogeography of the area.

Dividing the huge genus *Tipula* Linnaeus into smaller units, Riedel (1913) was the first to distinguish a group Falcatae within the traditionally recognized Tipulae Subunicolores. The Falcatae sensu Riedel were composed of the species *bullata* Loew, *onusta* Riedel, *magnicauda* Strobl, *selenitica* Meigen, and *falcata* Riedel, five species characterized by the presence of a sickle-shaped posterior part of the inner gonostylus ['App. interm. (pars secunda) sichelförmig'; Riedel 1913: 11]. Edwards (1931) erected the subgenus *Lunatipula* within the genus *Tipula* to contain 'most of the European and North American species with unicolorous or subunicolorous wings'. Thus Riedel's Falcatae, together with other species of *Tipula*, were transferred to the subgenus *Lunatipula*.

On account of the presence of erect setae on the basal half of male sternite 8, Mannheims & Theowald (1959: 31) distinguished a *bullata* group that, besides *bullata* and *onusta*, accommodated the then newly described *bezzii*, *buchholzi*, and *subonusta*. Savchenko (1964) referred to this same unit as the *onusta* group. In his standard work on the western Palaearctic Tipulidae, Mannheims (1963-1968) proposed an array of species groups within *Lunatipula*. Mannheims arranged the members of the Falcatae sensu Riedel into two species groups, viz. the *bullata* and *falcata* groups. The *bullata* group still contained the five species originally included in this unit (Mannheims 1967, 1968). According to Mannheims (1963, 1967), the *falcata* group is characterized by the presence of a well-developed and mostly long and posteriorly produced posterior part of the inner gonostylus, a definition which reflects Riedel's concept of the Falcatae. The *falcata* group sensu Mannheims (1967) contained 15 species of which *handschini* Mannheims, *trifasciculata* Strobl, and *zangherii* Lackschewitz, by the structure of the posterior part of the inner gonostylus, do not conform to Mannheims' definition of the group. Other character states, however, indicate a close relationship of these three species with the remaining members of the *falcata* group.

Theowald & Oosterbroek (1990) referred to Savchenko (1964) to notify the transfer of three Balkan species from the *falcata* group sensu Mannheims to the *fascingulata* species group of *Lunatipula*. Actually, Savchenko removed the Balkan inhabiting *pannonia* Loew and *jordansi* Mannheims (both as subspecies of *pannonia*) together with the Italian *zangherii* from the *falcata* group sensu Mannheims to the *fasciculata* (= *fascingulata*) group. Savchenko placed the third Balkan species of Mannheims' *falcata* group, viz. *bifasciculata* Loew, in a miscellaneous group together with most of the other species of the *falcata* group sensu Mannheims. Considering their different morphology, the removal of *bifasciculata*, *pannonia pannonia*, and *pannonia jordansi* from the *falcata*

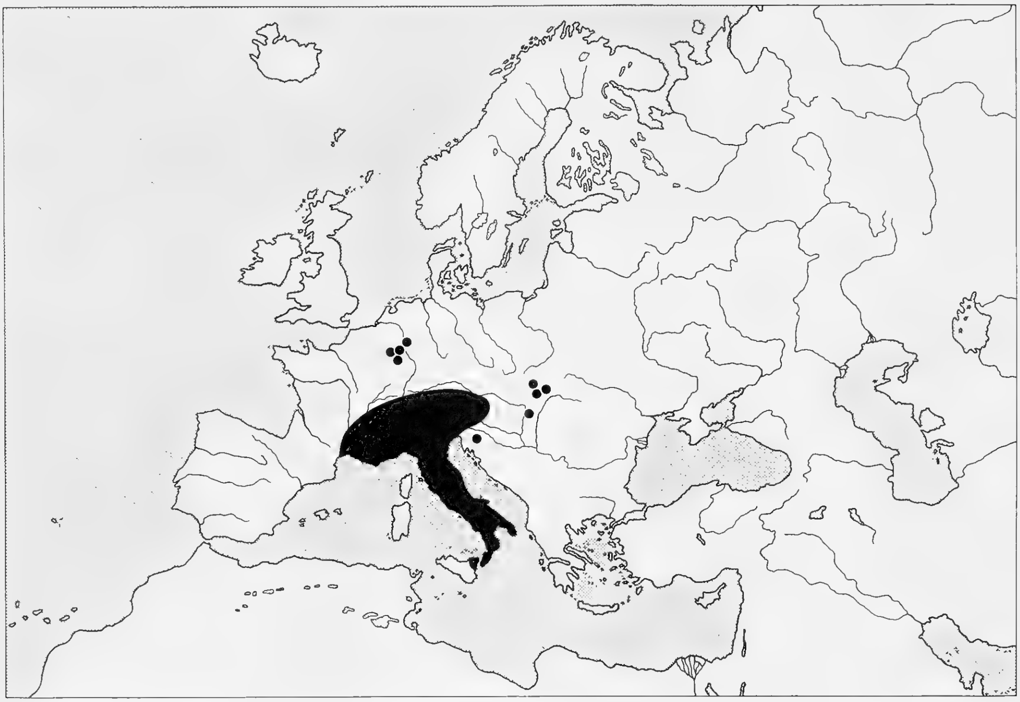


Fig. 1. Distribution of the *Tipula* (*Lunatipula*) *bullata* species group.

group as such is fully justified. However, as the *fascingulata* group in its present-day concept is overtly non-monophyletic, their inclusion in that group does not contribute to our understanding of the systematics of *Lunatipula*. The species *zangherii* definitely belongs to the *falcata* group and is treated as such below.

More recently, the species *eyndhoveni* (Theowald 1972) and *parallela* (Theischinger 1977) were added to the *falcata* group. In Appendix A, a species of the *falcata* group originating from south-east Spain is described for the first time. Table 1 lists the species of the *bullata* and *falcata* groups as recognized here. Phylogenetic analysis of the species of the *bullata* and *falcata* groups shows that both groups most probably represent monophyletic units.

As noted above, the *bullata* and *falcata* groups have a primarily western Mediterranean distribution, and most of their species are endemic to the region. Three species, viz. *bullata*, *longidens*, and *magnicauda*, are more widely distributed and occur in central Europe as well. The distribution of the *bullata* group is given in fig. 1, that of the *falcata* group in fig. 2. More detailed maps with the ranges of the individual species of the groups will be published in a forthcoming paper on the historical biogeography of the western Mediterranean. A summary of the distribution of the species dealt with in this paper is given below. A synopsis of the distribution of all Palaearctic species of the Tipulidae can be found in Oosterbroek & Theowald (1992).

MATERIAL, METHODS AND TERMINOLOGY

Material of all species of the *bullata* and *falcata* groups, with the exception of *jativensis*, was examined (table 1). Most specimens studied are deposited in the collection of the Institute for Systematics and Population Biology (Zoological Museum), Amsterdam (ZMAN). The material consisted largely of pinned specimens, supplemented by a few alcohol preserved specimens. Additional material was borrowed from the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany. The present depository of the holotype of *jativensis*, the only recorded specimen of this species, is unknown. Mannheims (1967) studied the at that time well-preserved specimen ('das wohlerhaltene Holotypus') from Strobl's collection and (erroneously) recorded it for both the collections at Graz and at Admont. Dr Karl Adlbauer (Graz) and Dr Elisabeth Krasser (Admont) kindly informed me that the holotype is not present in the collections under their care.

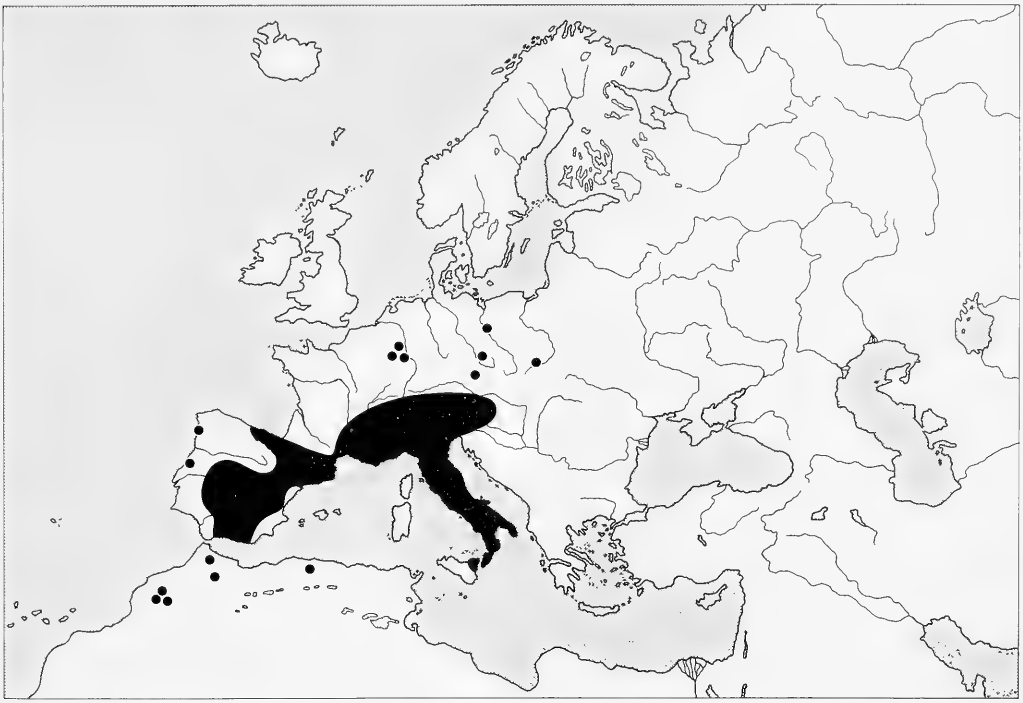


Fig. 2. Distribution of the *Tipula* (*Lunatipula*) *falcata* species group.

Preparations of the male and female terminalia were made by removing these parts and clearing them in a nearly boiling 10% KOH solution for about five minutes. After rinsing with water and 70% alcohol, the terminalia were transferred to glycerol. Examination of the specimens and their terminalia was carried out with a Wild stereo microscope, using a magnification of up to 100 ×. Drawings were made with the aid of a drawing tube attached to the microscope. Illustrations of the genital structures were made from macerated specimens. For permanent storage, the terminalia were transferred to a microvial containing some glycerol. The microvial was pinned with the relevant specimen.

The parsimony programs Hennig86, version 1.5 (Farris 1988) and PAUP, version 3.1 (Swofford 1993) were used to analyze the phylogeny. More information on the procedures followed is given in 'Discussion of adopted phylogeny'.

The terms for the structures of the Tipulidae as used in this paper are generally in accord with those employed by McAlpine (1981), with a few additions for particular features of *Lunatipula.* The term fragmentum for the structure lateral of the aedeagal guide is adopted from Rees & Ferris (1939) and Frommer (1963). Mannheims (1951 et seqq.) designated the

Table 1. The species of the *Tipula* (*Lunatipula*) *bullata* and *falcata* species groups as recognized in this paper. + : examined; – : not examined; u : unknown.

	♂	♀
***bullata* group**		
bezzii Mannheims & Theowald, 1959	+	+
buchholzi Mannheims & Theowald, 1959	+	+
bullata Loew, 1873	+	+
onusta Riedel, 1913	+	+
subonusta Mannheims & Theowald, 1959	+	+
***falcata* group**		
cirrata sp.n.	+	+
eyndhoveni Theowald, 1972	+	+
falcata Riedel, 1913	+	+
handschini Mannheims, 1967	+	u
jativensis Strobl, 1909	–	u
longidens Strobl, 1909	+	+
magnicauda Strobl, 1895	+	+
parallela Theischinger, 1977	+	+
selenaria Mannheims, 1967	+	u
selenitica Meigen, 1818	+	+
subfalcata Mannheims, 1967	+	+
subselenitica Theowald, 1957	+	+
trifasciculata Strobl, 1900	+	+
zangherii Lackschewitz, 1932	+	+
zarcoi Mannheims, 1967	+	+

same structure A9s (appendage of sternite 9). The substructures of the hypogynial valve of the female are termed according to Tjeder (1958). The terminology as adopted here is explained in figs. 4-9, 38, 58, 59, 61, 63. A recent overview of the morphology of the terminalia of Tipulidae was given by Tangelder (1985) to which paper the reader is referred for more information.

BIOLOGY

As is typical of the majority of species of the subgenus *Lunatipula*, the members of the *bullata* and *falcata* groups are adapted to relatively warm and dry environmental conditions. Species were recorded from cedar forests (*eyndhoveni*, Theowald 1972), dry oak groves (*falcata*, *handschini*, *longidens*, Dufour 1986), and dry fir woods (*magnicauda*, Dufour 1986). Mannheims (1967) supposed that *bullata* is associated with beech woods, but, although this preference to beech woods was confirmed, *bullata* can be common also in alder brakes and fir woods (Dufour 1986). Recorded altitudes usually range from about 275 m to 2000 m, with an extreme of 2800 m recorded for *selenaria* near Oukaimeden in the High Atlas of Morocco (material in ZMAN). In general, the species of the *bullata* and *falcata* groups are strong fliers and hard to catch in the field.

The species *subselenitica* is the only member of the *falcata* group of which one of the immature stages, viz. the pupa, is known. The pupa of this species, originating from humus in a cleft in the face of a limestone cliff, was described and illustrated by Theowald (1957, 1967).

SYSTEMATIC POSITION

The Palaearctic species of *Lunatipula* have been assigned to an array of species groups by Mannheims (1963, 1965a, 1966, 1967, 1968) and Savchenko (1964). In a similar way, Alexander (e.g., 1942, 1966, 1967) arranged the Nearctic species of the subgenus into smaller units. In the course of time, some of the more conspicuous species groups of *Lunatipula* were raised to subgenera of *Tipula*, viz. the *bistilata* group to *Lindnerina* (Mannheims 1965b, Mannheims & Pechlaner 1963), the *impudica* group to *Eremotipula* (Alexander 1965), the *californica* and *streptocera* groups to *Hesperotipula* (Alexander 1946, 1947), the *macrolabis* group to *Labiotipula* (Alexander 1965), and the *triplex* group to *Triplicitipula* (Alexander 1965). It is nevertheless clear that some of the above subgenera are more closely related to species groups that still remain within *Lunatipula* rather than to other subgenera of *Tipula*. (This situation can be illustrated for instance by the

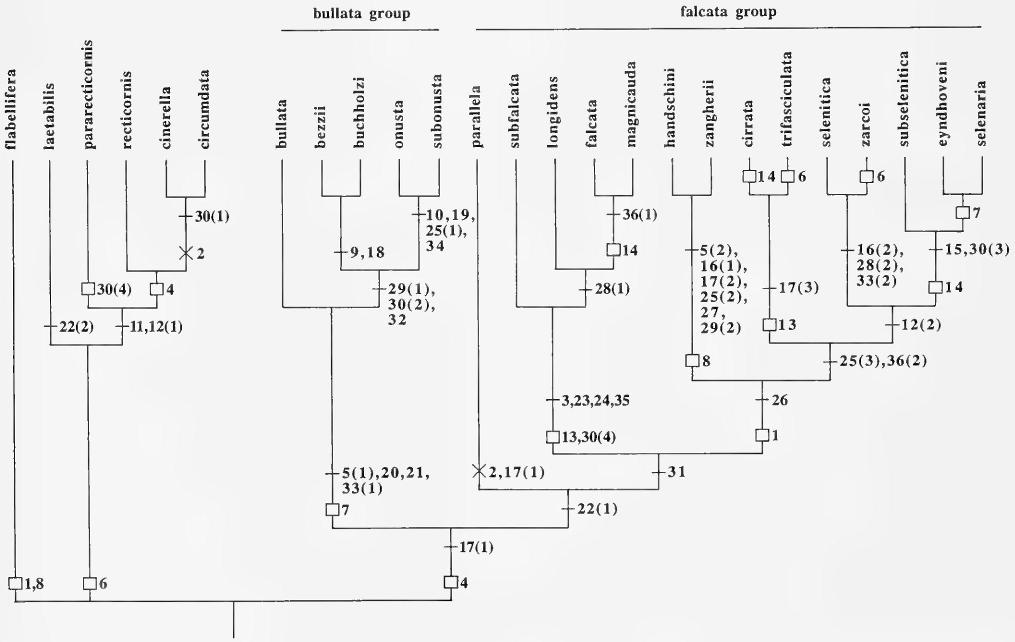


Fig. 3. Preferred tree of two equally parsimonious trees for *Tipula* (*Lunatipula*) *cinerella*, *circumdata*, *flabellifera*, *laetabilis*, *pararecticornis*, *recticornis*, and the species of the *T.* (*L.*) *bullata* and *falcata* species groups. Length 63, consistency index 80, retention index 92. –: synapomorphy; ☐ : homoplasy; ×: reversal.

subgenus *Labiotipula* and the *laetabilis* group of *Lunatipula* which, judging from the structure of the aedeagal guide and the intersegmental membrane of male sternites 8 and 9, are closely related). Another complicating factor in solving the higher level phylogeny of *Lunatipula* and its allies is the apparent non-monophyletic character of some of the included subgenera and species groups. A phylogenetic analysis of *Lunatipula* and its allies should start at the species level and should include not only the species of the subgenera listed above, but also those of the subgenera *Beringotipula* Savchenko, *Eumicrotipula* Alexander, *Odonatisca* Savchenko, *Pectinotipula* Alexander, *Pterelachisus* Rondani, *Ramatipula* Alexander, *Serratipula* Alexander, *Setitipula* Alexander, and *Vestiplex* Bezzi. This will indeed be a formidable task as these taxa together contain about 1200 species, i.e., more than a fourth of the total number of described species of the Tipulidae.

A first attempt to explore the phylogenetic relationships between larger groups of Palaearctic species of *Lunatipula* was published in Theowald & Oosterbroek (1990). They recognized a group Falcatae, which contained the *bullata*, *helvola*, and *falcata* groups, as the most primitive unit within *Lunatipula*. Although the majority of species currently attributed to the (non-monophyletic) *helvola* group are probably more closely related to species at present assigned to the (non-monophyletic) *fascingulata* group, I agree with Theowald & Oosterbroek that the *bullata* and *falcata* groups probably represent two of the more plesiomorphous species groups within *Lunatipula*. This conjecture can be inferred from the form of the aedeagal guide and its appendages, and from the condition of the intersegmental membrane of sternites 8 and 9 in the male. The aedeagal guide in the species of the *bullata* and *falcata* groups is a relatively simple, upright structure with at most a single posteromedial and two paired posterolateral appendages (see 'Character discussion', below). This type of aedeagal guide probably is primitive compared to the aedeagal guide of the majority of species of *Lunatipula*, which usually show additional lateral and midventral modifications. Within *Lunatipula*, a relatively simple aedeagal guide is found also in the species of the *laetabilis*, *livida*, *recticornis*, and *zimini* groups.

In the *bullata* and *falcata* groups, the intersegmental membrane between male sternites 8 and 9 is provided with two or three setal brushes of which the setae are directly implanted in the membrane (see 'Character discussion', below). The intersegmental membrane of sternites 8 and 9 carries a single medial or a pair of mediolateral setal brushes in the species of the *laetabilis*, *livida*, *recticornis*, and *zimini* groups. At present, these groups together contain about 85 species. For comparative purposes, six of these, viz. *laetabilis* Zetterstedt (*laetabilis* group), *cinerella* Pierre and *circumdata* Siebke (*livida* group), *pararecticornis* Savchenko & Theischinger and *recticornis* Schummel (*recticornis* group), and *flabellifera* Savchenko (*zimini* group) were studied and included in the phylogenetic analysis of the present paper.

Character discussion

This section presents a survey of the characters used in the phylogenetic analysis of the *bullata* and *falcata* groups. The character states recognized are briefly outlined, accompanied by their respective codes, after which a more detailed discussion follows. The data are summarized in the character state matrix of table 2, where the six supplementary species of the *laetabilis*, *livida*, *recticornis*, and *zimini* groups are listed first, followed by the species of the *bullata* and *falcata* groups in alphabetical order. As the male holotype of *jativensis*, the single known specimen of this species, was not available for study, *jativensis* is not included in the following discussion. The probable phylogenetic position of *jativensis* is indicated in the 'Discussion of adopted phylogeny', below. A list of recognized autapomorphies of the species of the *bullata* and *falcata* groups is given in Appendix B.

Head

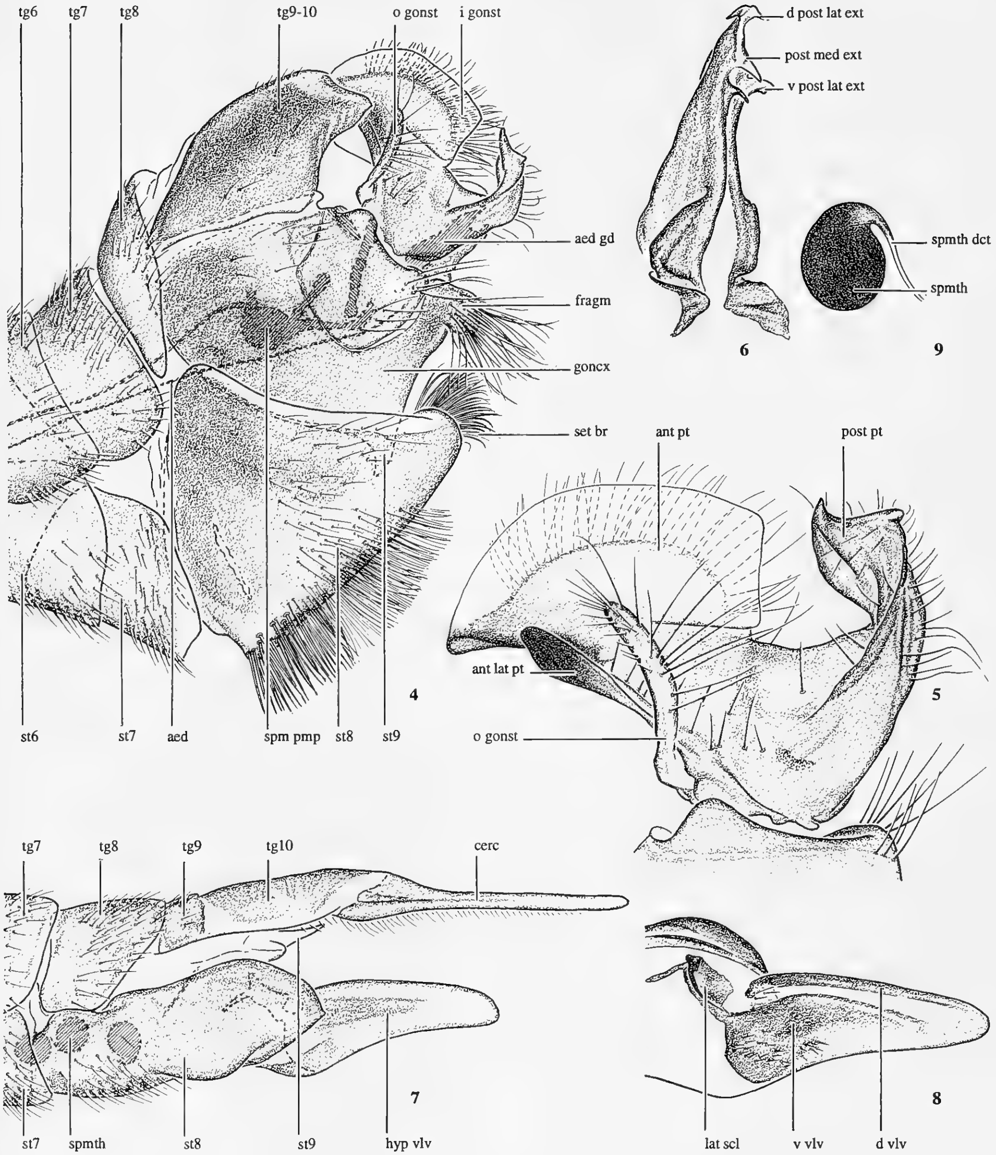
1. – Nasus: (0) present, long; (1) short or absent.

The presence of a well-developed nasus is a common feature in the Tipulidae and most probably represents a plesiomorphy within the family (fig. 10, arrow). Among the species studied, *flabellifera* and a number of species of the *falcata* group are distinguished by the presence of a very short nasus or the total absence of this structure (fig. 11). The species of the *falcata* group showing this character state are *cirrata*, *eyndhoveni*, *handschini*, *selenaria*, *selenitica*, *subselenitica*, *trifasciculata*, *zangherii*, and *zarcoi*.

Male terminalia

2. – Aedeagal guide, apical part, pair of dorsal posterolateral extensions: (0) absent; (1) present.

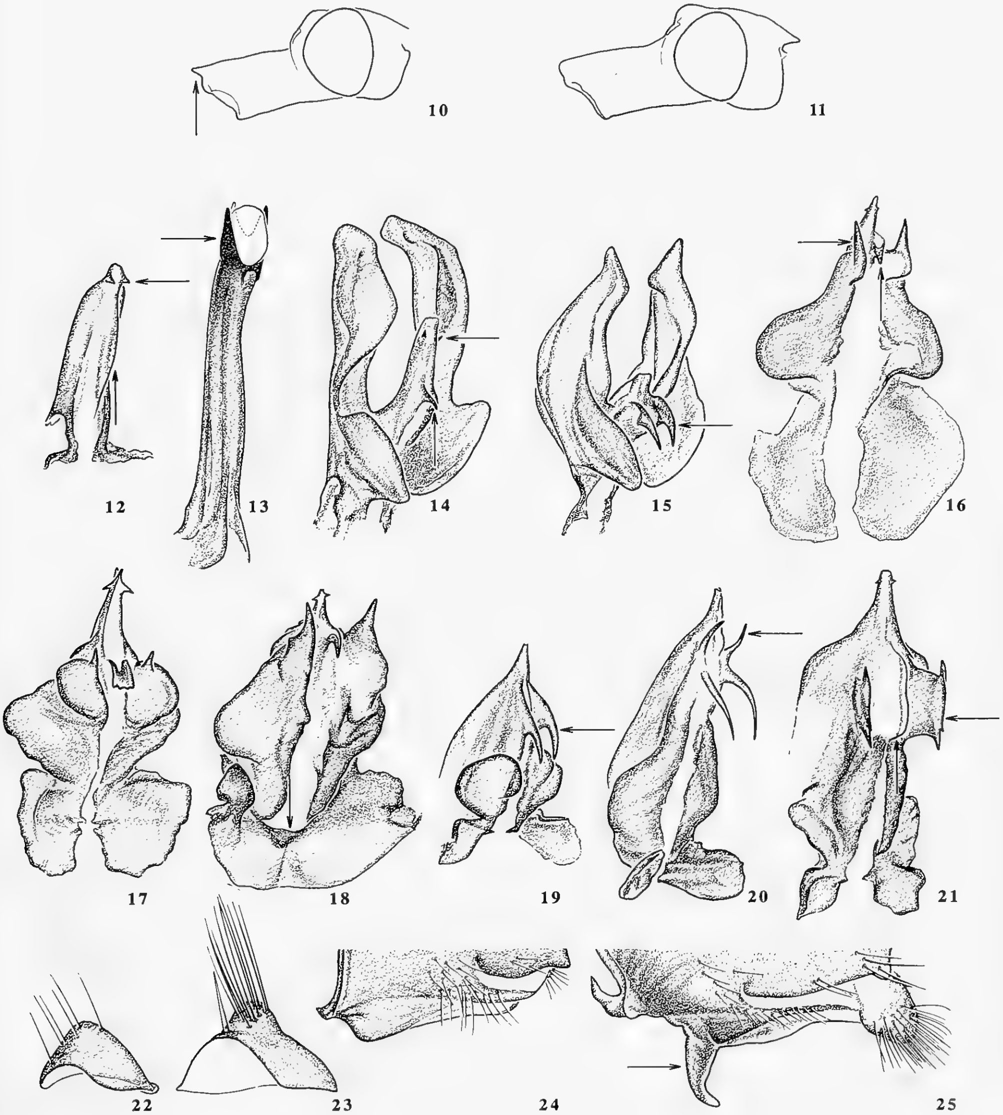
The aedeagal guide shows a wide variety of forms throughout *Lunatipula* and its allies. In the future, detailed study of this structure will doubtlessly lead to a better understanding of the actual higher level phylogenetic relationships within this group. Formerly, Theischinger (1977-1987) made extensive use of the shape of the aedeagal guide to classify his newly described species. Simova-Tosic & Vukovic (1983) underlined the importance of this structure for the establishment of supra-specific relationships within *Lunatipula*. Theowald & Oosterbroek (1990) presented a cladogram depicting the inferred phylogenetic relationships of six main groups of Palaearctic



Figs. 4-9. – 4, 5, 7-9, *Tipula* (*Lunatipula*) *bullata*; 6, *T.* (*L.*) *eyndhoveni*; 4, male terminalia, lateral view; 5, left inner and outer gonostyli, lateral view; 6, aedeagal guide, posterolateral view; 7, female terminalia, lateral view; 8, right hypogynial valve, medial view; 9, spermatheca, lateral view.
Abbreviations: aed: aedeagus; aed gd: aedeagal guide; ant pt: anterior part of inner gonostylus; ant lat pt: anterolateral part of inner gonostylus; cerc: cercus; d post lat ext: dorsal posterolateral extension; d vlv: dorsal valve of hypogynial valve; fragm: fragmentum; goncx: gonocoxite; hyp vlv: hypogynial valve; i gonst: inner gonostylus; lat scl: lateral sclerotization; o gonst: outer gonostylus; post med ext: posteromedial extension; post pt: posterior part of inner gonostylus; set br: setal brush; spm pmp: sperm pump; spmth: spermatheca; spmth dct: spermathecal duct; st6 etc.: sternite 6 etc.; sut x: suture x; tg6 etc.: tergite 6 etc.; v post lat ext: ventral posterolateral extension; v vlv: ventral valve of hypogynial valve.

Lunatipula that was partly based on the structure of the aedeagal guide.

With the exception of *parallela* (fig. 19), all species of the *bullata* and *falcata* groups are distinguished by the presence of a pair of dorsal posterolateral extensions at the extreme tip of the aedeagal guide (figs. 6, 16-18, 20, 21, 74). Structures that can be interpreted as dorsal posterolateral extensions are present also in *flabellifera* (fig. 12, horizontal arrow), *pararecticornis*, and *recticornis* (fig. 14, horizontal arrow). In *laetabilis*, the apex of the aedeagal guide terminates in a pair of dorsally directed, laterally placed, and heavily scle-



Figs. 10-25. – 10, 11, contours male head, antennae and mouthparts omitted; 10, *Tipula* (*Lunatipula*) *subfalcata*; 11, *T.* (*L.*) *handschini*; 12-21, aedeagal guide and appendages, posterolateral view; 12, *T.* (*L.*) *flabellifera*; 13, *T.* (*L.*) *laetabilis*; 14, *T.* (*L.*) *recticornis*; 15, *T.* (*L.*) *circumdata*; 16, *T.* (*L.*) *bullata*; 17, *T.* (*L.*) *bezzii*; 18, *T.* (*L.*) *onusta*; 19, *T.* (*L.*) *parallela*; 20, *T.* (*L.*) *subfalcata*; 21, *T.* (*L.*) *handschini*; 22, 23, left fragmentum, dorsal view; 22, *T.* (*L.*) *trifasciculata*; 23, *T.* (*L.*) *selenitica*; 24, 25, ventral parts of sternite 9 and gonocoxite, lateral view; 24, *T.* (*L.*) *parallela*; 25, *T.* (*L.*) *subfalcata*.

rotized triangles that enclose a medial membranous area (fig. 13, arrow). It remains to be studied whether these triangles in *laetabilis* represent the homologues of the dorsal posterolateral extensions of the species of the *bullata* and *falcata* groups.

3. – Aedeagal guide, apical part, pair of dorsal posterolateral extensions: (0) short; (1) slender and rather long, dorsally directed.

The dorsal posterolateral extensions are short in the majority of species studied (figs. 6, 12, 14, 16-18, 21, 74). The species *falcata*, *longidens*, *magnicauda*, and *subfalcata* differ from this by the presence of a pair of slender and elongate, dorsally directed posterolateral extensions at the tip of the aedeagal guide (fig. 20, arrow).

4. – Aedeagal guide, apical part, pair of ventral posterolateral extensions: (0) absent; (1) present.

With the exception of *flabellifera*, *laetabilis*, and *pararecticornis*, all species studied have a pair of ventral posterolateral extensions to the aedeagal guide (figs. 6, 14, vertical arrow, 15, arrow, 16, horizontal arrow, 17, 18, 19, arrow, 20, 21, horizontal arrow, 74). The actual shape of the extensions varies among these species (see next character).

5. – Aedeagal guide, apical part, pair of ventral posterolateral extensions: (0) ventrally curved, slender; (1) dorsally directed, slender; (2) blade-like, with serrate posterior margin.

The ventral posterior extensions of the aedeagal guide are slender and downward curved structures in the majority of species studied (figs. 6, 14, 15, 19, 20, 74). The species *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta* are characterized by the presence of a pair of laterally placed, dorsally directed slender extensions that are probably homologous with the ventral posterolateral extensions of the other species (figs. 16, horizontal arrow, 17, 18). The extensions terminate in an acute point in *bezzii*, *bullata*, *onusta*, and *subonusta*, in *buchholzi* their tip is rounded off.

The species *handschini* and *zangherii* are distinguished by the presence of a dorsoventrally extended and mediolaterally compressed pair of ventral posterolateral extensions (fig. 21, horizontal arrow). The posterior margins of the extensions carry a number of spinous projections, three in *handschini* and four or five in *zangherii*.

6. – Aedeagal guide, apical part, posteromedial area: (0) flat or tumid; (1) posteriorly projecting.

The posteromedial surface of the shaft of the aedeagal guide is flat to tumid in *cinerella*, *circumdata*, *laetabilis*, *pararecticornis*, *recticornis*, *trifasciculata*, and *zarcoi*. In the remainder of species studied it partly projects posteriorly. The actual condition of the projection differs among the species concerned (see next characters).

7. – Aedeagal guide, apical part, posteromedial projection: (0) a dorsoventrally extended, laterally compressed carina; (1) elongate and slender.

The species *bezzii*, *buchholzi*, *bullata*, *eyndhoveni*, *onusta*, *selenaria*, and *subonusta* are distinguished by the presence of a slender and elongate posteromedial projection (figs. 6, 16, vertical arrow, 17, 18). The posteromedial projection is present as a laterally compressed, dorsoventrally extended carina in the other species that have this part of the aedeagal guide posteriorly produced.

8. – Aedeagal guide, apical part, posteromedial carina: (0) membranous; (1) sclerotized.

The posteromedial carina of the aedeagal guide is sclerotized in *flabellifera* (fig. 12, vertical arrow), *handschini* (fig. 21, vertical arrow), and *zangherii*. In the other species with a posteromedial carina, this structure is membranous.

9. – Aedeagal guide, apical part, posteromedial slender projection: (0) about as high as broad; (1) dorsoventrally compressed.

The posteromedial slender projection of the aedeagal guide is dorsoventrally compressed in *bezzii* (fig. 17) and *buchholzi*. In the other species with a slender posteromedial projection, this structure is about as high as broad (figs. 6, 16, 18).

10. – Aedeagal guide, base: (0) ventromedially separate; (1) ventromedially fused.

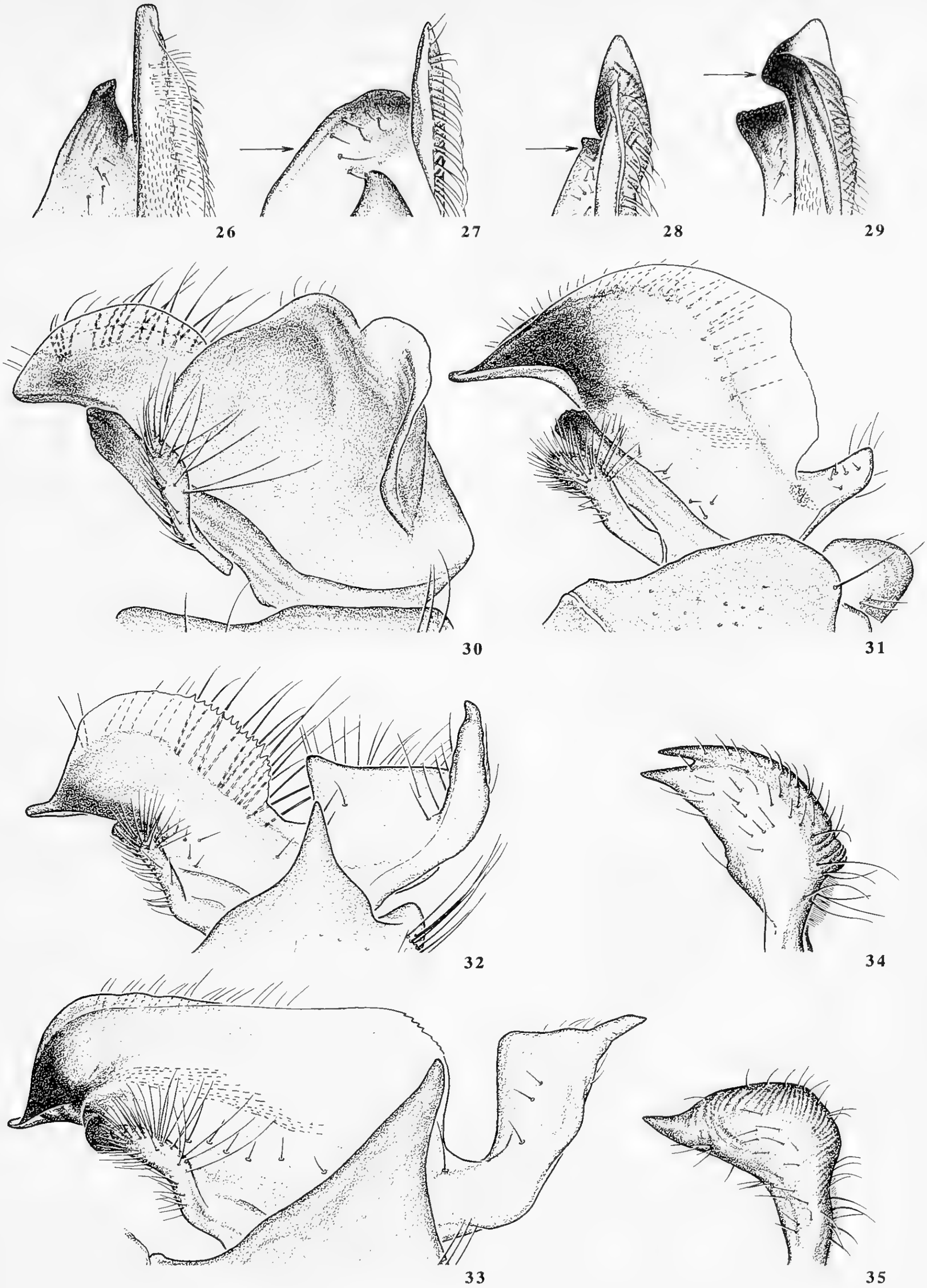
The base of the aedeagal guide consists of a pair of – usually well-separated – posteroventral extensions in the majority of species studied (figs. 6, 12-17, 19-21, 74). As a special feature, the base of the aedeagal guide forms a broad sclerotized bridge in *onusta* and *subonusta* (fig. 18, arrow).

11. – Aedeagal guide, large two-lobed and compressed gonapophysis: (0) absent; (1) present.

Among the species studied, *cinerella*, *circumdata* (fig. 15), *pararecticornis*, and *recticornis* (fig. 14) are characterized by the presence of a pair of large two-lobed and mediolaterally compressed gonapophyses that flank the aedeagal guide. Similar structures are present in all species of the *Lunatipula livida* and *recticornis* species groups, and in the species of the subgenera *Eumicrotipula* and *Pectinotipula*.

12. – Fragmentum: (0) variously shaped; (1) ventrally produced into slender extension; (2) cone-shaped, constricted near midheight.

The fragmentum shows a wide range of shapes



Figs. 26-35. – 26-29, anterior apices of anterior and anterolateral parts of left inner gonostylus, dorsal view; 26, *Tipula* (*Lunatipula*) *bullata*; 27, *T.* (*L.*) *handschini*; 28, *T.* (*L.*) *selenitica*; 29, *T.* (*L.*) *subselenitica*; 30-33, left inner gonostylus lateral view; 30, *T.* (*L.*) *handschini*; 31, *T.* (*L.*) *trifasciculata*; 32, *T.* (*L.*) *selenitica*; 33, *T.* (*L.*) *subselenitica*; 34, 35, apex of posterior part, posterior view; 34, *T.* (*L.*) *bullata*; 35, *T.* (*L.*) *bezzii.*

throughout *Lunatipula*. It can be low or elongate, ventrally, posteriorly or dorsally directed, with its apex pointing posteriorly or medially. Its tip can be adorned with a pencil of long or short setae, or it can be covered with spinous points. Among the species studied, a slender and ventrally produced fragmentum was studied in *cinerella*, *circumdata*, *pararecticornis*, and *recticornis*. The majority of species of the *bullata* and *falcata* groups are distinguished by a relatively low or evenly conically shaped broad-based fragmentum (figs. 22, 71). The species *eyndhoveni*, *selenaria*, *selenitica*, *subselenitica*, and *zarcoi* differ from this by the presence of a cone-shaped fragmentum that is distinctly narrowed in its apical half (fig. 23).

13. – Gonocoxite, midventral area: (0) tumescent; (1) with long conical projection.

The midventral area in between the gonocoxites is membranous and evenly curved without further modifications in the majority of species studied (fig. 24). The species *cirrata*, *falcata*, *longidens*, *magnicauda*, *subfalcata*, *trifasciculata*, and the unexamined *jativensis* are distinguished by the presence of a long and conical extension in the anterior part of the midventral membrane. The projection is anteriorly and laterally sclerotized in *falcata*, *longidens*, *magnicauda*, and *subfalcata* (fig. 25, arrow), in *cirrata* and *trifasciculata* (and probably also in *jativensis*) it is entirely membranous (fig. 69).

14. – Inner gonostylus, anterior part: (0) short, at most about 1.5 times as long as high; (1) elongate, about 2 times as long as high.

The anterior part of the inner gonostylus of the majority of species studied is a rather short structure that can be up to about 1.5 times as long as high (figs. 5, 30-32). The species *cirrata*, *eyndhoveni*, *falcata*, *magnicauda*, *selenaria*, and *subselenitica* have a long anterior part that is about 2 times as long as high (figs. 33, 70).

15. – Inner gonostylus, anterior part, apex (dorsal view): (0) relatively long and gradually narrowing towards tip; (1) short and broad.

The anterior part of the inner gonostylus in the majority of species studied is mediolaterally compressed and slender when seen in dorsal view (fig. 26-28), whereas it is short and plump in *eyndhoveni*, *selenaria*, and *subselenitica* (fig. 29, arrow).

16. – Inner gonostylus, anterolateral part (dorsal view): (0) relatively narrow, lateral margin moderately convex to concave; (1) broad, lateral margin strongly diverging from anterior part; (2) lateral margin with sharp emargination.

When seen in dorsal view, the anterolateral part of the inner gonostylus appears as a relatively narrow structure with a moderately convex to concave lateral margin in most species studied (figs. 26, 29). The species *handschini* and *zangherii* are distinguished by the presence of a broad anterolateral part of which the lateral margin diverges strongly from the anterior part (fig. 27, arrow). In *selenitica* and *zarcoi* there is a rather sharp emargination near the anterior apex of the anterolateral part (fig. 28, arrow).

17. – Inner gonostylus, posterior part: (0) a well-developed blade; (1) an elongate structure with laterally produced tip; (2) huge, shell-like; (3) small.

The posterior part of the inner gonostylus is a well-developed blade-like structure in the majority of species of *Lunatipula*. Among the species studied, this situation is present in *cinerella*, *circumdata*, *flabellifera*, *laetabilis*, *parallela*, *pararecticornis*, and *recticornis*. The posterior part is present as an elongate structure with a laterally produced, and in most cases slender, tip in *bezzii*, *buchholzi*, *bullata* (fig. 5), *eyndhoveni*, *falcata*, *longidens*, *magnicauda*, *onusta*, *selenaria*, *selenitica* (fig. 32), *subfalcata*, *subonusta*, *subselenitica* (fig. 33), and *zarcoi*. In *handschini* and *zangherii* the posterior part consists of a large and laterally concave shell-like structure (fig. 30). A very small posterior part is present in *cirrata* (fig. 70) and *trifasciculata* (fig. 31).

18. – Inner gonostylus, posterior part, surface: (0) even; (1) with closely placed parallel grooves.

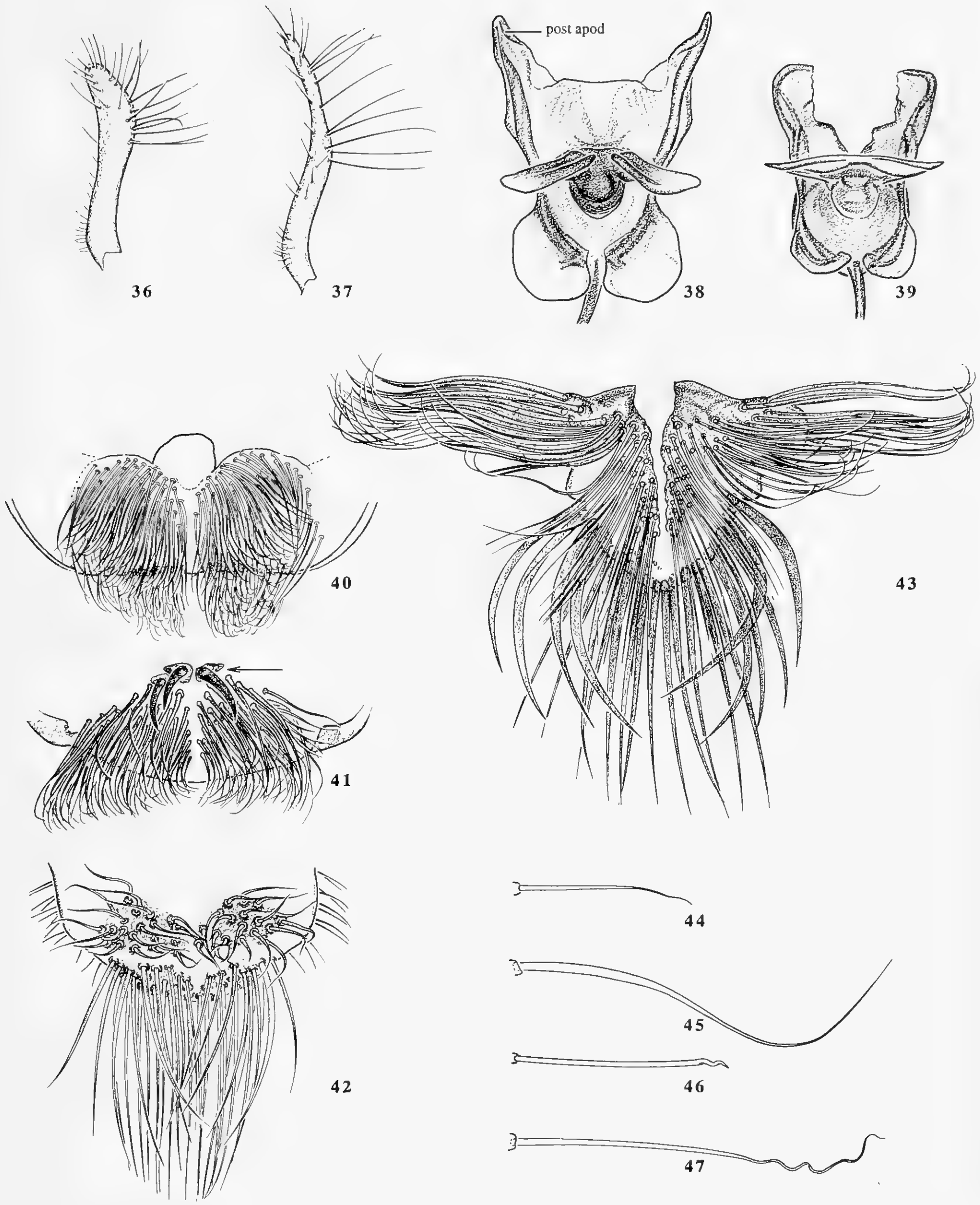
The surface of the posterior part of the inner gonostylus is even in most species studied (fig. 34). Both *bezzii* and *buchholzi* are distinguished by the textured posterodorsal surface of the conically elongate posterior part which shows a large number of closely placed parallel grooves (fig. 35).

19. – Outer gonostylus: (0) widening in apical part, usually short and broad; (1) narrowing in apical part, remarkably slender.

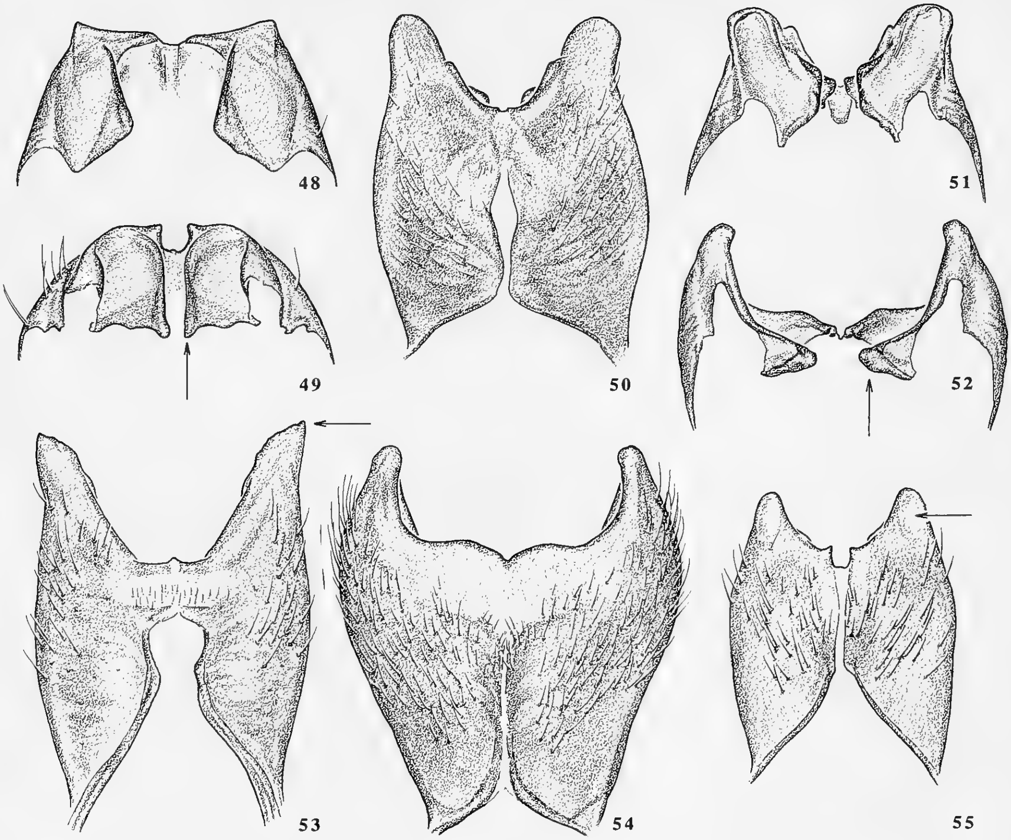
The shape of the outer gonostylus varies considerably within *Lunatipula*, but the structure is usually rather short and broadens in its apical part (fig. 36). Most species studied conform to this state, with the exception of *laetabilis*, *onusta*, and *subonusta*. In *laetabilis* the outer gonostylus is relatively slender, but widens in the apical portion. In *onusta* and *subonusta* it is elongate and very slender, and narrows towards its tip (fig. 37).

20. – Sperm pump, posterior apodemes: (0) separate up to lumen of sperm pump; (1) basally connected by sclerotized plate.

The species of the *bullata* group, viz. *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta*, differ from the other species studied by the presence of a sclerotized connection between the bases of the posterior apo-



Figs. 36-47. – 36, 37, left outer gonostylus, lateral view; 36, *Tipula* (*Lunatipula*) *bezzii*; 37, *T.* (*L.*) *onusta*; 38, 39, sperm pump, dorsal view; 38, *T.* (*L.*) *bullata*; 39, *T.* (*L.*) *parallela*; 40-43, setal brushes on intersegmental membrane sternite 8 and 9, posterior view; 40, *T.* (*L.*) *bezzii*; 41, *T.* (*L.*) *onusta*; 42, *T.* (*L.*) *parallela*; 43, *T.* (*L.*) *subfalcata*; 44-47, representative seta from dorsolateral setal brush; 44, *T.* (*L.*) *parallela*; 45, *T.* (*L.*) *subfalcata*; 46, *T.* (*L.*) *handschini*; 47, *T.* (*L.*) *cirrata*. Abbreviation: post apod: posterior apodeme.



Figs. 48-55. – 48, 49, 51, 52, posterior portion of male tergite 9-10, ventral view; 50, 53-55, male tergite 9-10, dorsal view; 48, *Tipula* (*Lunatipula*) *bullata*; 49, *T.* (*L.*) *bezzii*; 50, 51, *T.* (*L.*) *subfalcata*; 53, *T.* (*L.*) *longidens*; 52, 54, *T.* (*L.*) *handschini*; 55, *T.* (*L.*) *selenitica*.

demes (fig. 38). The posterior apodemes are separate structures up to the body of the sperm pump in the other species examined (fig. 39).

21. – Sternite 8: (0) covered with scattered decumbent setae; (1) anterior part with concentration of erect long setae.

Sternite 8 in the Tipulidae is usually covered with scattered decumbent setae, a character state found also in the majority of species of *Lunatipula* and doubtlessly representing a plesiomorphy (fig. 69). The species *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta* differ from the remainder of species examined by the presence of a concentration of long and erect setae on the anterior half or more of sternite 8 (fig. 4). The erect setae are confined to the ventromedial part of the sternite. Most setae are slender, but in *bullata* (fig. 4), and to a much lesser extent in *bezzii* and *subonusta*, the setae implanted near the anterior margin of the sternite are stronger than the others.

22. – Sternites 8 & 9, intersegmental membrane, setal brushes: (0) one (paired) brush; (1) three brushes; (2) four brushes.

The intersegmental membrane in between sternites 8 and 9 is generally adorned with one or more setal brushes in the species of *Lunatipula*. Among the species studied, a single medial brush or one pair of medial brushes is present in *cinerella*, *circumdata*, *flabellifera*, *pararecticornis*, *recticornis*, *bezzii*, *buchholzi*, *bullata*, *onusta*, and *subonusta* (figs. 40, 41). The species *laetabilis* is characterized by the presence of four setal brushes arranged in two pairs. All other species studied are distinguished by the presence of three setal brushes on the intersegmental membrane, consisting of a pair of dorsal brushes and a single ventromedial one (figs. 42, 43, 73; see next two characters).

23. – Sternites 8 & 9, intersegmental membrane, setal brushes, area of insertion: (0) oval shaped, laterally extended; (1) dorsal brushes ventrally extended, elongate.

The area of insertion of the setal brushes on the intersegmental membrane of sternites 8 & 9 is wider than long and more or less oval in shape in the majority of species studied (figs. 40-42, 73). In *falcata, longidens, magnicauda,* and *subfalcata* the dorsal brushes are ventrally extended. The ventrally orientated extensions provide the brushes a V-shaped appearance when seen in posterior view (fig. 43).

24. – Sternites 8 & 9, intersegmental membrane, setal brushes, area of insertion: (0) oval shaped, laterally extended; (1) ventromedial brush strongly protruding, margin semi-circular.

As noted above, the area of insertion of the setal brushes on the intersegmental membrane of sternites 8 & 9 is oval shaped in most of the examined species. A different condition occurs in *falcata, longidens, magnicauda,* and *subfalcata.* In these species, the setae of the ventromedial brush are arranged in a semi-circular formation and the brush protrudes as a tongue-like extension (fig. 43).

25. – Sternites 8 & 9, intersegmental membrane, setal brushes, condition of setae: (0) slightly curved and slender; (1) thorn-like (in part); (2) short and stout (in part); (3) strong (in part).

The setae of the setal brushes on the intersegmental membrane of sternites 8 & 9 are generally slightly curved and slender in the majority of species studied (figs. 44, 45). The species *onusta* and *subonusta* differ from the other examined species by the presence of one or two pairs of thorn-like setae in the dorsal part of the setal brushes (fig. 41, arrow). The setae of the dorsal setal brushes are remarkably short and stout in *handschini* and *zangherii* (fig. 46). The species *cirrata, eyndhoveni, selenaria, selenitica, subselenitica, trifasciculata,* and *zarcoi* are distinguished by the presence of two to four strong lateral setae that are about two times as thick as the remainder of setae in the ventromedial brush (fig. 73).

26. – Sternites 8 & 9, intersegmental membrane, setal brushes, condition of setae: (0) slightly curved; (1) frizzled at tip (in part).

The setae of the setal brushes on the intersegmental membrane between sternites 8 and 9 are usually slightly curved in the majority of species examined (figs. 44, 45). However, the setae of the dorsal brushes are frizzled at their tips in *cirrata, eyndhoveni, handschini, selenaria, selenitica, subselenitica, trifasciculata, zangherii,* and *zarcoi* (figs. 46, 47). The extent to which the apices of the setae are curled is less in both *handschini* and *zangherii* compared with the other species involved. According to the illustrations given by Mannheims (1967), the unexamined *jativensis* also has frizzled setae in the dorsal brushes.

27. – Tergite 9-10: (0) lateral margins evenly curved, tergite of equal width throughout (dorsal view); (1) tergite widening towards posterior margin.

Seen in dorsal view, tergite 9-10 appears to be more or less parallel-sided in the majority of species examined. The lateral margins are slightly curved, with the widest portion of the tergite lying at about midlength (figs. 50, 53, 55, 72). The species *handschini* and *zangherii* deviate from this norm by having tergite 9-10 distinctly widening towards the posterior margin (fig. 54).

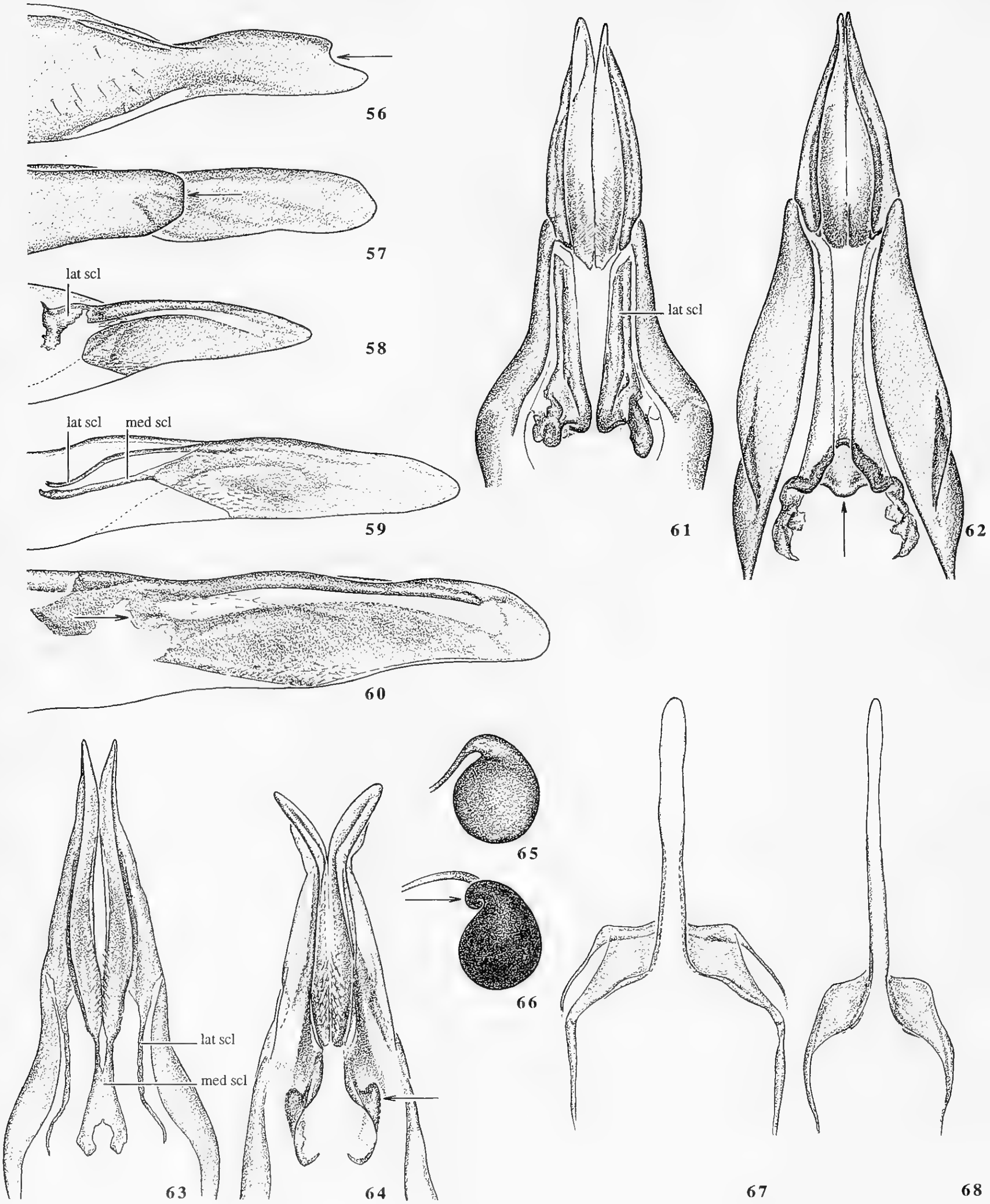
28. – Tergite 9-10, posterolateral extensions: (0) tip rounded (dorsal view), dorsal surface convex; (1) elongate, tip laterally angular; (2) dorsal surface concave.

Among the species studied, the posterolateral extensions of tergite 9-10 vary considerably in shape, but mostly they are relatively short and more or less rounded (figs. 48-52, 54, 55). The species *falcata, longidens,* and *magnicauda* differ from the remainder of examined species by the long and laterally acutely pointed posterolateral extensions of tergite 9-10 (dorsal view, fig. 53, arrow).

The dorsal surface of the posterolateral extensions of tergite 9-10 is convex in the majority of examined species. Two species of the *falcata* group, viz. *selenitica* and *zarcoi,* are distinguished by a concave dorsal surface of the extensions. The concave area covers the extreme tip of the extensions in *selenitica* (fig. 55, arrow), in *zarcoi* it extends further anteriorly.

29. – Tergite 9-10, ventral sclerotizations: (0) medially wide apart, relatively long; (1) medially approximate, anteromedial corner produced; (2) short, medially projecting.

In most species examined, the ventral sclerotizations near the posterior margin of tergite 9-10 consist of a pair of widely separate and well-developed plates of which the medial margins run more or less parallel for some distance (figs. 48, 51). The species *bezzii, buchholzi, onusta,* and *subonusta* are distinguished by the close approximation of the ventral sclerotizations. The anteromedial corners of the ventral sclerotizations are anteriorly produced in these four species (fig. 49, arrow). The species *handschini* and *zangherii* differ from the other species studied by the short and medially directed ventral sclerotizations (fig. 52, arrow).



Figs. 56-68. – 56, 57, sternite 8 and left hypogynial valve, lateral view; 56, *Tipula* (*Lunatipula*) *circumdata*; 57, *T.* (*L.*) *bezzii*; 58-60, right hypogynial valve, medial view; 58, *T.* (*L.*) *parallela*; 59, *T.* (*L.*) *subfalcata*; 60, *T.* (*L.*) *subselenitica*; 61-64, sternite 8 and hypogynial valves, dorsal view; 61, *T.* (*L.*) *bezzii*; 62, *T.* (*L.*) *onusta*; 63, *T.* (*L.*) *subfalcata*; 64, *T.* (*L.*) *selenitica*; 65, 66, spermatheca and base spermathecal duct; 65, *T.* (*L.*) *parallela*; 66, *T.* (*L.*) *subfalcata*; 67, 68, female sternite 9, ventral view; 67, *T.* (*L.*) *longidens*; 68, *T.* (*L.*) *falcata*.
Abbreviations: lat scl: lateral sclerotization; med scl: medial sclerotization.

Female terminalia

30. – Hypogynial valves: (0) well-developed, tapering towards rounded tip (lateral view), dorsal and ventral valves separate; (1) tip emarginate; (2) short, almost parallel sided; (3) dorsal and ventral valves anteriorly connected; (4) dorsal and ventral valves entirely fused.

Most species of *Lunatipula* have well-developed hypogynial valves in the female, a situation doubtlessly representing the plesiomorphous condition within the subgenus. The hypogynial valves in this state are usually tapering towards a more or less rounded tip (figs. 57-60, 75). Among the species studied, both *cinerella* and *circumdata* are distinguished by the emarginate tip of the hypogynial valves, a condition that probably represents a synapomorphy for the species of the *livida* group (fig. 56, arrow). The species *bezzii, buchholzi, onusta,* and *subonusta* differ from the other species studied by their short and almost parallel-sided hypogynial valves (fig. 57). The species *eyndhoveni* and *subselenitica* are unique among the examined species in having a sclerotized connection at the base of the dorsal and ventral valves (fig. 60, arrow). The female of *selenaria* remains unknown, but may also show the latter condition. Complete fusion of the dorsal and ventral valves is found in *falcata, longidens, magnicauda,* and *subfalcata* (fig. 59).

31. – Spermatheca, base of spermathecal duct: (0) evenly curved; (1) making a loop.

The spermathecal duct gradually curves away from the spermatheca in the greater majority of the Tipulidae, a condition found also in the majority of species examined (fig. 65). A different condition is found in *cirrata, eyndhoveni, falcata, longidens, magnicauda, selenitica, subfalcata, subselenitica, trifasciculata, zangherii,* and *zarcoi,* where the base of the spermathecal duct shows a clockwise or counterclockwise rotation (fig. 66, arrow). The direction of the rotation of the spermathecal duct can vary intraspecifically. The females of *handschini, jativensis,* and *selenaria* remain unknown, but may also show a twisted base of the spermathecal duct.

32. – Sternite 8, lateroposterior apex: (0) tapering and usually gradually merging with hypogynial valve; (1) broad, truncate.

Lateroposteriorly, sternite 8 tapers and gradually merges with the hypogynial valve or terminates in an acute point that is separate from the hypogynial valve in the majority of species examined (figs. 7, 56, 75). In *bezzii, buchholzi, onusta,* and *subonusta* the lateroposterior end of sternite 8 is broad and truncate (fig. 57, arrow).

33. – Sternite 8, lateral sclerotization: (0) fused with dorsal valve of hypogynial valve, unmodified; (1) separate from dorsal valve; (2) with cavity.

Within *Lunatipula,* the dorsal valves of the hypogynial valves are often extended into a sclerotization that lies lateral within sternite 8. In most species examined, the dorsal valves are connected with these lateral sclerotizations (fig. 58). The species *bezzii, buchholzi, bullata, onusta,* and *subonusta* are distinguished by the presence of a membranous gap in between the base of the dorsal valve and the accompanying anterior sclerotization. In *bullata* the sclerotization is short and fused with the anterodorsal part of the ventral valve (fig. 8), in the four other species the sclerotization is elongate and lies entirely free from the hypogynial valves (figs. 61, 62). The lateral sclerotization is relatively flat in most of the examined species, but *selenitica* and *zarcoi* show a posteriorly directed cavity in this structure (fig. 64, arrow).

34. – Sternite 8, lateral sclerotizations: (0) separate; (1) anteriorly fused.

The lateral sclerotizations at the base of the hypogynial valves are separate in most of the examined species (figs. 61, 63, 64). Both *onusta* and *subonusta* differ from the remainder of species studied by the presence of a sclerotized bridge that connects the anterior tips of the lateral sclerotizations (fig. 62, arrow).

35. – Sternite 8, medial sclerotization: (0) absent; (1) present.

In the majority of females examined, sternite 8 contains at most a pair of lateral sclerotizations (figs. 61, 62, 64). A unique feature is found in *falcata, longidens, magnicauda,* and *subfalcata,* where an elongate medial sclerotization stretches anteriorly from its attachment to the anterior margin of the ventral valves (figs. 59, 63).

36. – Sternite 9, posterior extension: (0) relatively short, at most 1.5 times width of sternite 9, about as high as broad; (1) about two times as long as width of sternite 9; (2) dorsoventrally compressed, broad.

The females of *falcata* and *magnicauda* are distinguished among the species examined by the elongate posterior extension of sternite 9. In these two species the posterior extension is about two times as long as the width of sternite 9 (fig. 68), whereas it usually is much shorter in the other species (figs. 67, 76). A few species of the *falcata* group are distinguished by the presence of a disk-like dorsoventrally compressed and broad posterior extension of sternite 9. The species concerned are *cirrata, eyndhoveni, selenitica, subselenitica, trifasciculata,* and *zarcoi.* The extension is extremely broad and terminates in an emarginate apex in *cirrata* (fig. 76). In the other species with a broad and flat posterior extension, the structure is less broad and terminates in an acute tip. Note that the female of *selenaria* is unknown, but probably also shows the latter character state.

Discussion of adopted phylogeny

The character state matrix given in table 2 was analyzed with the parsimony programs Hennig86 and PAUP. In table 2, unknown characters are coded '?' and inapplicable characters '-' for matters of reference only. Platnick et al. (1991) discussed the potentially different treatment of such missing entries by Hennig86 and PAUP. Maddison (1993) discussed the consequences of coding inapplicable characters as missing data. In the analysis presented here, multistate characters were treated unordered and all characters were, by default, given equal weight. The matrix was run under the ie*; (implicit enumeration) option of Hennig86 and the branch-and-bound algorithm of PAUP. Both methods guarantee to find all optimal trees (Farris 1988; Swofford 1993).

Using Hennig86, the first six species in the matrix, viz. *cinerella, circumdata, flabellifera, laetabilis, pararecticornis,* and *recticornis,* were selected as the outgroup before the program was run (Hennig86 does not allow the outgroup to be empty; Farris 1988). A methodologically more sound procedure was followed with PAUP, where the complete matrix was used to construct unrooted trees that were afterwards rooted by outgroup rooting (see Nixon & Carpenter 1993 for a recent discussion on the proper use of outgroups). Outgroup rooting of the unrooted trees under PAUP was done in the default fashion, i.e., with the outgroup taxa forming a basal polytomy with the ingroup (Swofford 1993). In this case, the first six species of the data matrix were a posteriori assigned to the outgroup.

Both methods resulted in two equally most parsimonious trees with length 63, consistency index 80 (Hennig86) or 0.810 (PAUP), and retention index 92 (Hennig86) or 0.922 (PAUP). The preferred resulting cladogram is given in fig. 3 and differs from the other equally parsimonious solution by the position of *parallela.* Whereas *parallela* is the sister species of the clade *subfalcata* to *selenaria* in fig. 3, it is the sister species of the clade *bullata* to *selenaria* in the alternative solution. The reasons for preferring the cladogram of fig. 3 will be given below. The results of the phyloge-

Table 2. Character state matrix for *Tipula* (*Lunatipula*) *cinerella, circumdata, flabellifera, laetabilis, pararecticornis, recticornis,* and the species of the *T.* (*L.*) *bullata* and *falcata* species groups. ?: unknown or not interpretable; –: inapplicable.

Character		10		20		30		36
cinerella	00–10	0–––0	11000	00000	00000	00001	00000	0
circumdata	00–10	0–––0	11000	00000	00000	00001	00000	0
flabellifera	1100–	101–0	00000	00000	00000	0000?	?????	?
laetabilis	0?–0–	0–––0	00000	00000	02000	00000	00000	0
pararecticornis	0100–	0–––0	11000	00000	00000	00004	00000	0
recticornis	01010	0–––0	11000	00000	00000	0000?	?????	?
bezzii	01011	11–10	00000	01101	10000	00012	01100	0
buchholzi	01011	11–10	00000	01101	10000	00012	01100	0
bullata	01011	11–00	00000	01001	10000	00000	00100	0
cirrata	11010	100–0	00110	03000	01003	10000	10000	2
eyndhoveni	11010	11–00	02011	01000	01003	10003	10000	2
falcata	01110	100–0	00110	01000	01110	00104	10001	1
handschini	11012	101–0	00000	12000	01002	1102?	?????	?
longidens	01110	100–0	00100	01000	01110	00104	10001	0
magnicauda	01110	100–0	00110	01000	01110	00104	10001	1
onusta	01011	11–01	00000	01011	10001	00012	01110	0
parallela	00–10	100–0	00000	00000	01000	00000	00000	0
selenaria	11010	11–00	02011	01000	01003	1000?	?????	?
selenitica	11010	100–0	02000	21000	01003	10200	10200	2
subfalcata	01110	100–0	00100	01000	01110	00004	10001	0
subonusta	01011	11–01	00000	01011	10001	00012	01110	0
subselenitica	11010	100–0	02011	01000	01003	10003	10000	2
trifasciculata	11010	0–––0	00100	03000	01003	10000	10000	2
zangherii	11012	101–0	00000	12000	01002	11020	10000	0
zarcoi	11010	0–––0	02000	21000	01003	10200	10200	2

netic analysis will be discussed with reference to fig. 3.

A trichotomy uniting *flabellifera*, the clade *laetabilis* to *circumdata*, and the clade *bullata* to *selenaria*, is found at the base of fig. 3. The clade *laetabilis* to *circumdata* is supported by the absence of a posteromedial projection on the aedeagal guide only (character 6). This character state occurs also in *trifasciculata* and *zarcoi*. Future study of the phylogeny of *Lunatipula* must settle the question whether this character state actually represents an apomorphy at this level of analysis. The examined species of the *recticornis* and *livida* groups (*pararecticornis* and *recticornis*, and *cinerella* and *circumdata*, respectively) together form a monophyletic group supported by the presence of the two-lobed and compressed gonapophyses (character 11) and the shape of the fragmentum (character 12). Both species of the *recticornis* group, however, do not constitute a monophyletic unit. Considering the fact that Savchenko & Theischinger (1978) in their revision of the *recticornis* group did not distinguish any character state that can be considered a synapomorphy for all species of the group, the monophyly of the *recticornis* group seems to be questionable. Both *cinerella* and *circumdata* are united on account of the absence of the dorsal posterolateral extensions of the aedeagal guide (character 2) and the presence of the emarginate apex of the hypogynial valve (character 30). The latter character state is found in all species of the *livida* group.

Fig. 3 depicts the *bullata* and *falcata* groups as two monophyletic units. The *bullata* group is substantiated by four synapomorphies and one homoplasy, the *falcata* group by one synapomorphy. The *bullata* group as distinguished here is identical to the original concept of this group as recognized by Mannheims & Theowald (1959). Within the *bullata* group, *bullata* appears to be the sister species of the remaining four species, which in their turn can be separated into two species pairs. Mannheims & Theowald appreciated the close relationship of *bezzii* and *buchholzi* on the one hand and, as was expressed by the name giving, that of *onusta* and *subonusta* on the other. As can be inferred from the descriptions of the species given by Mannheims and Theowald, the postulated relationship of *bezzii* and *buchholzi* was primarily inspired by the form of the elongate and single pointed posterior part of the inner gonostylus, that of *onusta* and *subonusta* by the shape of the posterior margin of male tergite 9-10 and the extension of the setal area on male sternite 8. Although these character states are not employed in the present paper, the results as regards the hypothesized phylogenetic relationships of the species are the same.

The clade *parallela* to *selenaria* represents the *falcata* group in the sense of the present paper. Mostly because of the structure of the aedeagal guide, Theischinger (1977) tentatively assigned *parallela* to the *falcata* group with the annotation that the posterior part of the inner gonostylus and posterior margin of tergite 9-10 isolate *parallela* so much that no other species can be regarded as truly closely related. This opinion is reflected in the phylogenetic position of *parallela* in the cladogram adopted here. In the alternative equally parsimonious solution of the phylogenetic analysis, *parallela* is the sister species of the *bullata* and *falcata* groups combined. In the latter case, the presence of a moderately developed posterior part of the inner gonostylus in *parallela* (character 17) is considered primitive and the presence of three setal brushes on the intersegmental membrane of sternites 8 and 9 (character 22) is treated as a homoplasy. Instead of this, I prefer to interpret the presence of a moderately developed posterior part of the inner gonostylus in *parallela* as the result of reduction, as, under reference to fig. 3, must be postulated also to account for the small posterior part in *cirrata* and *trifasciculata*. In the preferred alternative, the three setal brushes on the intersegmental membrane indicate the phylogenetic affinity of *parallela* with the other members of the *falcata* group.

The remainder of species of the *falcata* group consists of two monophyletic groups, the clades *subfalcata* to *magnicauda* and *handschini* to *selenaria*. The first group was recognized by Mannheims (1967) on account of the presence of the extension on the midventral area of the gonocoxites (character 13) and the structure of the posterior part of the inner gonostylus (character 17). The latter character is employed here at a different level in the analysis. Mannheims (1967) did not unequivocally ventilate his views on the interspecific phylogenetic relationships of *falcata*, *longidens*, *magnicauda*, and *subfalcata*. On account of the shape of the posterior margin of male tergite 9-10 (character 28), the length of the anterior part of the inner gonostylus (character 14), and the length of the posterior extension of female sternite 9 (character 36), the relationships as depicted in fig. 3 are postulated.

The clade *handschini* to *selenaria* contains species that are characterized by the absence of a nasus (character 1) and the presence on the intersegmental membrane of male sternites 8 and 9 of setae with a frizzled tip in the dorsal setal brushes (character 26).

The first lineage within the clade *handschini* to *selenaria* leads to the species pair *handschini* and *zangherii*, a monophyletic group which was already isolated as a subgroup within the *falcata* group by Mannheims (1967). Both species are distinguished here from the remainder of the *falcata* group by six synapomorphies and a single homoplasy concerning the aedeagal guide (characters 5, 8), the inner gonostylus (characters 16, 17), the shape of setae in the setal brushes (character

25), and male tergite 9-10 (characters 27, 29).

The sister group of the pair *handschini* and *zangherii*, the clade *cirrata* to *selenaria*, is substantiated by two synapomorphies, one concerning the presence of strong lateral setae in the ventral setal brush on the intersegmental membrane of male sternites 8 and 9 (character 25), the other pertaining to the compressed posterior extension of female sternite 9 (character 36).

Within the clade *cirrata* to *selenaria*, the first lineage contains *cirrata* and *trifasciculata* which are considered sister species on account of the presence of a small posterior part of the inner gonostylus (character 17). Both species also share the presence of a cone-shaped extension on the midventral area of the gonocoxites (character 13), a feature encountered also in the members of the clade *subfalcata* to *magnicauda* and in the unexamined *jativensis* (see below for the presumed phylogenetic position of this species).

Mannheims (1967) grouped the then known species of the clade *selenitica* to *selenaria*, together with *jativensis*, in a subgroup of the *falcata* group. Mannheims supposed that there are close relationships between *jativensis*, *selenitica*, and *zarcoi* and between *selenaria* and *subselenitica*. The phylogenetic analysis presented here substantiates the supposed relationship of *selenitica* and *zarcoi*, which are combined here on account of the sharply emarginate anterolateral part of the inner gonostylus (character 16), the dorsally concave posterior extensions of male tergite 9-10 (character 28), and the presence of a concavity in the lateral sclerotization of female sternite 8 (character 33). The species *selenaria* and *subselenitica* also appear to be closely related, which can be substantiated by the shape of the anterior apex of the anterior part of the inner gonostylus (character 15), the length of the anterior part of the inner gonostylus (character 14), and possibly by the partly fused dorsal and ventral valves in the female (character 30; the female of *selenaria* is not known). The later described *eyndhoveni* probably is the actual sister species of *selenaria*, as can be inferred from the presence of the elongate membranous extension in between the dorsal and ventral posterolateral extensions of the aedeagal guide (character 7). Theowald (1972) introduced *eyndhoveni* under reference to *selenaria*.

Although no material was examined of *jativensis*, information provided by Mannheims (1967) helps to allocate the probable phylogenetic position of this species, which is known from the male holotype only. According to Mannheims, *jativensis* has no nasus (character 1), it has the fragmentum evenly rounded (character 12), it has a membranous extension on the ventromedial area in between the gonocoxites (character 13), while the setae in the dorsal brush of the intersegmental membrane of sternites 8 and 9 are frizzled at their tips (character 26). This combination of character states suggests a sister group relationship of *jativensis* and the species pair *cirrata* and *trifasciculata*, thus contradicting Mannheims' view (1967) that *jativensis* is more closely related to species now contained in the clade *selenitica* to *selenaria*.

DISTRIBUTION

This section provides a brief account on the distribution of the species of the *bullata* and *falcata* groups. As noted above, more detailed information on the distribution of these species will be given in a forthcoming paper on the historical biogeography of the western Mediterranean. The sequence of taxa in the summary below follows that of fig. 3.

The *bullata* group is primarily distributed in Italy (fig. 2). The most widespread species of this group is *bullata*, which is known from the secondary mountain-chains in central Europe. It has been found in the eastern Ardennes and neighbouring Eifel, south-eastern France, the Alps and adjacent mountainous areas. It seems to be absent though from the Pyrenees, Apennines and Carpathians. Martinovsky (1987) reported *bullata* for the first time from Slovakia.

The species *bezzii* seems to be restricted to lower areas as it occurs along the coast of southern France and in the valley of the Po in northern Italy. The single known Swiss specimen of *bezzii* was captured at an altitude of 340 meters (Dufour 1986). The species *buchholzi* is endemic to Italy, where it has been recorded from the Apennines in the north to Calabria in the south. About the same range is shown by *onusta*, which is also known from Croatia (Simova-Tosic & Vukovic 1981). The species *subonusta* is endemic to Sicily.

The *falcata* group is more widespread than the *bullata* group (fig. 2). As far as available records show, *parallela* seems to be distributed over the entire Iberian Peninsula. The range of *subfalcata* extends over central and southern Spain and the Rif mountains of northern Morocco. The species *longidens* has a wider range, with the centre of distribution lying in central and northern Spain. It is also known from a few localities in central France, western Switzerland, south-eastern Belgium and eastern Germany. The distribution area of *falcata* ranges from the southern border of Switzerland southward to Calabria and the eastern tip of Sicily. Its sister species *magnicauda* is distributed in the Ardennes in Belgium, the Eifel in Germany, and the Alps. Martinovsky (1987) recorded *magnicauda* for the first time from Bohemia in the present-day Czech Republic and also reported the first find of this species for Poland (Martinovsky in litt.).

The species pair *handschini* and *zangherii* is primarily distributed over Italy, with *handschini* occurring in the Alps and southern Italy, and *zangherii* in northern and central Italy. A single male of *handschini* has been recorded from south-west Switzerland by Dufour (1986).

The newly described *cirrata* is known from south-east Spain, its sister species *trifasciculata* is distributed in central and southern Spain. The species *selenitica* is known from Portugal, north-west Spain, the Pyrenees, and south-eastern France. Pierre (1924) claimed that *selenitica* also occurred in the environment of Paris, France. The presumed sister species of *selenitica*, *zarcoi*, is endemic to Spain, where it has been recorded from several provinces in the central and southern part of the country. Another endemic Spanish species with about the same range as *zarcoi* is *subselenitica*. The two remaining species of the *falcata* group are endemics to north-west Africa, viz. *eyndhoveni*, which is known from the type locality in northern Algeria only, and *selenaria*, which occurs in the High and Middle Atlas of Morocco. As far as presently known, there are no species of the *bullata* and *falcata* groups recorded from Corsica or Sardinia.

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REFERENCES

Alexander, C. P., 1942. See Alexander 1966.

Alexander, C. P., 1946. Records and descriptions of North American crane-flies (Diptera) part VI. Tipuloidea of Arizona, New Mexico and trans-Pecos Texas, I. – The American Midland Naturalist 35: 484-531.

Alexander, C. P., 1947. Undescribed species of crane-flies from the western United States and Canada (Dipt.: Tipulidae). Part VII. – Entomological News 58: 61-67.

Alexander, C. P., 1965. New subgenera and species of crane-flies from California (Diptera: Tipulidae). – Pacific Insects 7: 333-386.

Alexander, C. P., 1966. Family Tipulidae. – In: Crampton, G. C. et al. (eds.) Guide to the insects of Connecticut. Part VI. The Diptera or true flies of Connecticut. First fascicle. Bulletin of the Connecticut State Geological and Natural History Survey 64: 196-486b. (Reprint of Alexander 1942).

Alexander, C. P., 1967. The crane flies of California. – Bulletin of the California Insect Survey 8: 1-269.

Dufour, C., 1986. Les Tipulidae de Suisse (Diptera, Nematocera). – Documenta Faunistica Helvetiae 2: 1-187, + 1-149.

Edwards, F. W., 1931. Some suggestions on the classification of the genus *Tipula* (Diptera, Tipulidae). – Annals and Magazine of Natural History (10) 8: 73-82.

Farris, J. S., 1988. Hennig86, version 1.5 + reference. – Port Jefferson Station, New York.

Frommer, S. I., 1963. Gross morphological studies of the reproductive system in representative North American crane flies (Diptera: Tipulidae). – Kansas University Science Bulletin 44: 535-626, pls. I-XX.

McAlpine, J. F., 1981. Morphology and terminology - adults. – In: McAlpine, J. F. et al. (eds.) Manual of Nearctic Diptera. Volume 1. Research Branch, Agriculture Canada, Monograph 27: 9-63.

Maddison, W. P., 1993. Missing data and missing characters in phylogenetic analysis. – Systematic Biology 42: 576-581.

Mannheims, B., 1951. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 167: 1-64, pls. I-VII.

Mannheims, B., 1963. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 238: 137-176.

Mannheims, B., 1965a. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 256: 177-212.

Mannheims, B., 1965b. Enumeratio Tipulidarum Fenniae. – Lounais-Hämeen Luonto 20: 1-3.

Mannheims, B., 1966. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 267: 213-256.

Mannheims, B., 1967. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 270: 257-288.

Mannheims, B., 1968. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 275: 289-320.

Mannheims, B. & E. Pechlaner, 1963. Die Tipuliden Nordtirols (Dipt.). – Stuttgarter Beiträge zur Naturkunde 102: 1-29.

Mannheims, B. & B. Theowald, 1959. Die Tipuliden Italiens (Dipt., Tipulidae). – Memorie della Società Entomologica Italiana 38: 15-54.

Martinovsky, J., 1987. Tipulidae. – Acta Entomologica Musei Nationalis Pragae 18: 11-14.

Nixon, K. C. & J. M. Carpenter, 1993. On outgroups. – Cladistics 9: 413-426.

Oosterbroek, P. & B. Theowald, 1992. Family Tipulidae. – Catalogue of Palaearctic Diptera 1: 56-178.

Pierre, C., 1924. Diptères: Tipulidae. – Fauna de France 8: 1-159.

Platnick, N. I., C. E. Griswold & J. A. Coddington, 1991. On missing entries in cladistic analysis. – Cladistics 7: 337-343.

Rees, B. E. & G. F. Ferris, 1939. The morphology of *Tipula reesi* Alexander (Diptera: Tipulidae). – Microentomology 4: 143-178.

Riedel, M. P., 1913. Die paläarktischen Arten der Dipteren-(Nematocera polyneura-) Gattung *Tipula* L. (Dipt.). – Abhandlungen des Vereins für Naturwissenschaftliche Erforschung der Niederrheins- (Bezirksgruppe des deutschen Lehrervereins für Naturkunde.) I. Band 1913: 1-

122, pls. I-III.

Savchenko, E. N., 1964. Crane flies (Fam. Tipulidae), subfam. Tipulinae: genus *Tipula* L. (part 2). – Fauna SSSR (N.S. 89) Two-winged insects II (4): 1-502. (In Russian).

Savchenko, E. N. (as Savtshenko) & G. Theischinger, 1978. Die Arten der *Tipula* (*Lunatipula*) *recticornis*-Gruppe (Diptera, Tipulidae). – Bulletin Zoologisch Museum, Universiteit van Amsterdam 6: 117-128.

Simova-Tosic, D. & M. Vukovic, 1981. The results of crane flies (Diptera, Tipulidae) studies in Yugoslavia. – Acta Entomologica Jugoslavica 17: 113-119.

Simova-Tosic, D. & M. Vukovic, 1983. The significance of the male genitalia for identification of the crane flies species (Tipulidae, Diptera). – Acta Entomologica Jugoslavica 19: 27-32. (In Serbo-Croatian, English summary).

Swofford, D. L., 1993. PAUP, Phylogenetic Analysis Using Parsimony, version 3.1. – Illinois Natural History Survey, Champaign, Illinois.

Tangelder, I. R. M., 1985. Phylogeny of the *Nephrotoma dorsalis* species-group (Diptera, Tipulidae), mainly based on genital characters. –Beaufortia 35: 135-174.

Theischinger, G., 1977. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Paläearktis (Diptera, Tipulidae, *Tipula* Linnaeus). – Beaufortia 26: 1-38.

Theischinger, G., 1979a. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). I. Fortsetzung. – Beaufortia 28: 121-150.

Theischinger, G., 1979b. Über *Lunatipula* aus Afghanistan (Diptera, Tipulidae, *Tipula* Linnaeus). – Bulletin Zoologisch Museum, Universiteit van Amsterdam 6: 145-150.

Theischinger, G., 1979c. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). II. Fortsetzung. – Beaufortia 29: 275-308.

Theischinger, G., 1980. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). III. Fortsetzung. – Beaufortia 30: 17-29.

Theischinger, G., 1982. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). IV. Fortsetzung. – Beaufortia 32: 79-96.

Theischinger, G., 1987. Neue Taxa von *Lunatipula* Edwards aus der mediterranen Subregion der Palaearktis (Diptera, Tipulidae, *Tipula* Linnaeus). V. Fortsetzung. – Beaufortia 37: 99-120.

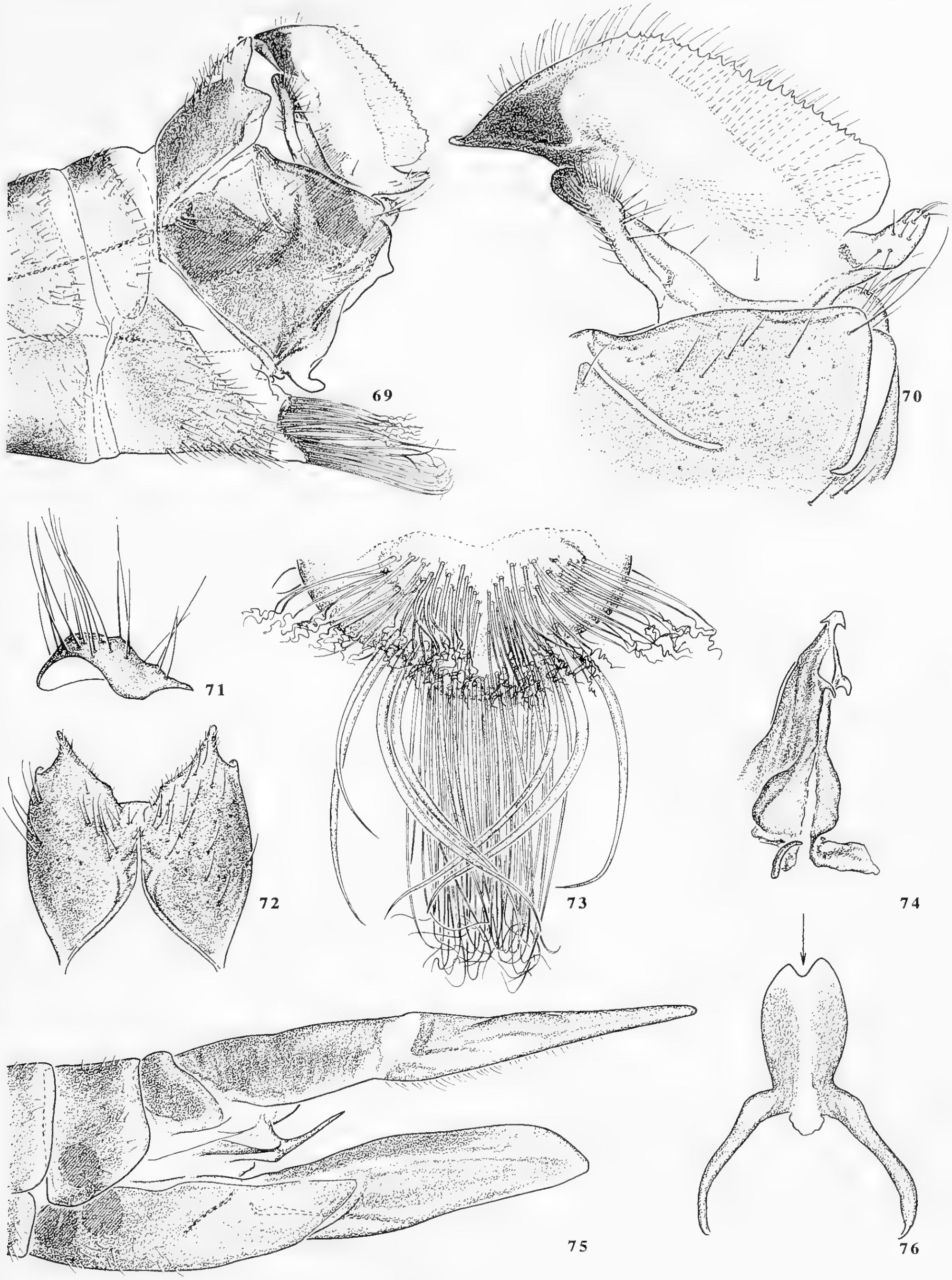
Theowald, B., 1957. Die Entwicklungsstadien der Tipuliden (Diptera, Nematocera), insbesondere der west-palaearktischen Arten. – Tijdschrift voor Entomologie 100: 195-308.

Theowald, B., 1967. Familie Tipulidae. (Diptera, Nematocera). Larven und Puppen. – Bestimmungsbücher zur Bodenfauna Europas 7: 1-100.

Theowald, B., 1972. Die Tipuliden Algeriens (Diptera, Tipulidae). – Entomologische Berichten 32: 3-5.

Theowald, B. & P. Oosterbroek, 1990. Zur Zoogeographie der westpaläarktischen Tipuliden. IX. Die Tipuliden des Vorderen Orients. – Tijdschrift voor Entomologie 133: 85-95.

Tjeder, B., 1958. A synopsis of the Swedish Tipulidae, I. Subfam. Limoniinae: tribe Limoniini. – Opuscula Entomologica 23: 133-169.



Figs. 69-76, *Tipula* (*Lunatipula*) *cirrata* sp.n.; 69, male terminalia, lateral view; 70, left inner and outer gonostyli, lateral view; 71, left fragmentum, dorsal view; 72, tergite 9-10, dorsal view; 73, setal brushes on intersegmental membrane sternites 8 and 9, posterior view; 74, aedeagal guide and appendages, posterolateral view; 75, female terminalia, lateral view; 76, female sternite 9, ventral view.

Appendix A

Tipula (*Lunatipula*) *cirrata* sp.n.
(figs. 69-76)

Type material. – Holotype ♂: Spain, Jaén, Sierra de Cazorla, Rio Guadalquivir, 900 m, 22.IV.1994, P. Oosterbroek & C. Hartveld (ZMAN). – Paratypes: 2♂, same data as holotype; 3♂, 1♀, Spain, Jaén, Sierra de Cazorla, Rio Aguamula, 700 m, 23.IV.1994, P. Oosterbroek & C. Hartveld (ZMAN).

Description

Body length 15.5-17 mm (♂), 20 mm (♀); wing length 15.5-18 mm (♂), 15.5 mm (♀); antennal length 4.2-4.8 mm (♂), 2.8 mm (♀).

Colour. – Ground colour light brown, head and thorax extensively brownish-grey pruinose. Anterior part of rostrum and vertex dorsally with dark brown median vitta. Antenna with scape and pedicel light brown, dorsolaterally brownish-grey pruinose, first flagellomere basally light brown becoming darker towards tip, remainder of flagellum dark brown. Palpus brown, dorsally and apically darker. Pronotum with dark brown medial vitta. Prescutum with two pairs of broad dark brown stripes, medial pair separated by broad lighter stripe. Scutellum and metatergite with dark brown medial vitta indicated. Wing veins dark brown, pterostigma dark brown, distinct. Membrane darkish coloured, except for yellowish subcostal cell and anterior margin of cubital cell, pale area in front of pterostigma reaching base of cell m3. Haltere with light brown stem, knob largely dark brown. Coxae greyish pruinose, pruinosity less dense on posterior pairs of legs. Trochanters and base of femora light brown, femora becoming dark brown towards apex. Tibiae brown, becoming darker towards tips, remainder of legs dark brown. Abdomen light brown, with broad dark brown continuous medial stripe on tergites 1 to 7 and less distinct dark brown sublateral stripe on tergites 2 to 6, tergite 8 light brown, accompanying sternite and following segments of abdomen darker brown.

Head. – Rostrum about as long as remainder of head, nasus absent. Eyes dorsally and ventrally separated by about 2.5 times diameter of scape. Antenna with five verticils in whorl at base of flagellomeres, the two medial ones short, the dorsally and laterally placed ones longer, longest verticils slightly longer than length of flagellomere.

Thorax. – Wing fully developed in both sexes, squama with about ten distinct macrotrichia. Tarsal claws with medial tooth in male, toothless in female.

Male terminalia (figs. 69-74). – Sternite 8 at posterior margin in intersegmental membrane with single ventral and pair of dorsal setal brushes. Setae of brushes about as long as greatest length of sternite 8, those of dorsal brushes curled at tip. Medial setae of ventral brush wavy at tip, ventral brush laterally with two setae about twice the diameter of the remainder of setae (fig. 73). Tergite 9-10 and gonocoxites separated by membranous zone (fig. 69). Tergite 9-10 (fig. 72) broad and short, with narrow medial membranous area. Anterior margin of tergite 9-10 V-shaped, posterior margin widely U-shaped, posterolateral extensions narrow in dorsal view. Posterodorsal part of gonocoxite incompletely separated from the remainder of gonocoxite by sutures, this part of gonocoxite not produced (fig. 70). Fragmentum a broad sclerotized low lobe set with scattered long golden yellow setae (fig. 71). Midventral area in between gonocoxites membranous, lateral margins diverging posteriorly, anteriorly carrying membranous conical extension (fig. 69). Sp2 small, squarish, moderately sclerotized. Foramen of gonostyli medially very weakly sclerotized to membranous. Sp1 small, V-shaped, separate from sp2. Outer gonostylus (fig. 70) short and slender, slightly broader at apex. Inner gonostylus (fig. 70) with large anterior part provided with serrate dorsal crest, posterior part short, lateral carrying a few setae. Inner gonostylus medially provided with sensory area at base of posterior part. Proctiger entirely membranous. Aedeagal guide (fig. 74) a compact sclerotized structure, at tip with dorsal and ventral pair of posterolateral extensions. Sperm pump with anterior and posterior apodemes short, compressor apodeme dorsally deeply emarginate, lumen well-developed, body strongly convex. Aedeagus long, slender, tubular throughout, anteriorly reaching abdominal segment 1.

Female terminalia (figs. 75, 76). – Cercus in lateral view with almost straight margins, tapering to tip. Sternite 8 dorsolaterally near base of hypogynial valve ending in acute angle. Hypogynial valve strong, pointed at lower posterior corner (fig. 75). Sternite 9 with broad and dorsoventrally compressed posterior extension (fig. 76). Three spermathecae, oblong oval, spermathecal duct rotated at base.

Etymology. – The name *cirrata*, an adjective in the nominative singular, refers to the presence of frizzled setae in the brushes on the intersegmental membrane of male sternites 8 and 9. Cirratus (Latin) means with curly hairs.

Remarks. – As the above given phylogenetic analysis shows, *cirrata* is closely related to *trifasciculata*. Differences are found in the shape of the inner gonostylus, which in *trifasciculata* has a shorter and dorsally rounded anterior part (fig. 31) compared to that of *cirrata* (fig. 70), in the structure of the posterior margin of male tergite 9-10, which in *trifasciculata* has shorter posterior extensions, in the shape of the fragmentum, which is higher in *trifasciculata* (fig. 22; cf. fig. 71), in the length of the female cerci, which are shorter in *trifasciculata*, and in the tip of the posterior extension of female sternite 9, which is acute in *trifasciculata* and emarginate in *cirrata* (fig. 76).

APPENDIX B

Autapomorphies of the species of the *Tipula* (*Lunatipula*) *bullata* and *falcata* groups

BOOK REVIEWS

Gábor Ronkay & László Ronkay, 1994. Noctuidae Europaeae. Volume 6. Cuculliinae I. – Entomological Press, Sorø. 282 pp, 10 colour-plates, 218 figs., many maps. [ISBN 87-89430-03-4]. Price DKK 680 excl postage; subscribers to the series receive 10% discount. Distributed by Apollo Books, Kirkeby Sand 19, DK-5771-Stenstrup, Denmark. Fax +4562263780.

Volume 6 is the third volume appearing in this 12 volume series. It is also the first one not written by Michael Fibiger, editor and organizer of the series (see also review of vol. 2 in this journal, vol 136, p. 82). The book shows the same set-up as previous volumes, each species described with taxonomic notes, diagnosis, bionomics and distribution, colour plates of adults and maps of the distribution. The text is bilingual, english and french, printed alongside. The only criticism could be that this inevitably makes the books somewhat more expensive.

This volume deals with the large genus *Cucullia* and two genera recently separated from it by the same authors. It covers 60 species, including one new and several subspecies, also one new, and many new combinations and synonyms. A novelty is the inclusion of colour plates of the larvae, which are in this group of noctuids more important because adults of many species can only be obtained by breeding the larvae. The plates show the same high quality as in the previous volumes. The drawings of the genitalia (the first shown in the series) are very detailed, based on pencil and/or ink drawings. Especially the detailed drawings of the everted vesica and cornuti will be helpful for the identification of the many similar species.

The book is well prepared, and well printed. The brothers Ronkay are to be congratulated with this wonderful volume, a worthy counterpart to the previous volumes.

[E. J. van Nieukerken]

Rimantas Puplesis, 1994. The Nepticulidae of Eastern Europe and Asia, Western, Central and Eastern Parts. – Backhuys Publishers, Leiden. 291 pp, 840 figs on unnumbered pages.[ISBN 90-73348-29-3]. Price NLG 210.– (US $ 140), excl. postrage. Can be ordered form Universal Book Services, PO Box 321, NL-2300 AH Leiden, fax +31-71-5171856.

Nepticulidae are amongst the smallest Lepidoptera (ca 2-12 mm wingspan), with leafmining larvae. They are especially known for their characteristic feeding patterns, mostly gallery mines in leaves. The book deals with 221 palaearctic species. The title is somewhat misleading: the area covered is the territory of the former Soviet Union, but it is understandable that the author prefers his more neutral description. So in spite of the title, it does not treat species from Japan (about 30 known) or China (only one species known at present) nor from any other part of Asia south of the former Soviet Union.

The book starts with an introduction on methods, adult morphology, phylogeny and classification, a key to the genera and a checklist. For all species a diagnosis is given and a description of male, female, genitalia plus short notes on biology and distribution. The black and white drawings of adults, genitalia and leafmines are brought together at the end of the book, in the systematic order. Most drawings are new, some are copied from previous publications by the author and a few are redrawn from other sources.

It is to be regretted that the publisher has not spend more attention to the composition of the plates. Several rough sketches could better be more reduced in printing, and the lettering is very coarse. A major point of criticism is the complete lack of figure captions on the plates themselves: they are all brought together before the plates. This is very impracticle when one tries to identify specimens. In my own copy I have glued photocopies of the captions on the plates: something one would not expect doing in a book with this price.

One could wonder whether it is the right time to publish a book on a fauna, yet so scanty known. More than half of the species have been described by the author between 1984 and 1994, a few in this book, and many more new species and new data on biology are expected to be found in the recent future. On the other hand I think that the author should be praised to bring together all this material, which mostly was only described in Russian in separate journals. It is the first time that a group of Microlepidoptera of this area is treated in English from the start: previous books were translations from Russian. The details of the genitalia could in many drawings be improved, and hopefully in a new edition the aedeagus will be drawn separately so that its details are better seen. Also hopefully more details of biology will become known: many species are now only known from a few light trapped adults.

The black and white landscape photographs, made from colour-slides, give a good impression of the very different habitats in the area covered. It is a pity that it has not been possible to reproduce them in colour.

In short: a very useful account of a hitherto almost unknown fauna and a good starting point for future research of the Palaearctic Nepticulidae. An initiative to be followed for other insect groups.

[E. J. van Nieukerken]

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THE PHYLOGENY OF THE SUBGENUS *TIPULA* (*MEDIOTIPULA*) (DIPTERA: TIPULIDAE)

Jong, H. de, 1995. The phylogeny of the subgenus *Tipula* (*Mediotipula*) (Diptera: Tipulidae). – Tijdschrift voor Entomologie 138: 269-282, figs. 1-48, tabs. 1, 2, appendices A, B. [ISSN 0040-7496]. Published 15 November 1995.

The phylogeny of the species of the subgenus *Tipula* (*Mediotipula* Pierre) (Diptera: Tipulidae) is discussed, based on the examination of 24 morphological characters of the adults of the currently recognized 11 species. The synonymy of *aragoniensis* Theowald under *cataloniensis* Theowald is established. A short discussion on the distribution of the species is given.

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Key words. – Diptera, Tipulidae, *Mediotipula*, phylogeny, distribution.

This paper presents an analysis of the phylogeny of the species of the subgenus *Tipula* (*Mediotipula* Pierre, 1924) as part of a research project dealing with the historical biogeography of the western Mediterranean. About half of the species of *Mediotipula* are confined to the western Mediterranean and could provide clues for a better understanding of the historical biogeography of the area.

Pierre (1924) introduced *Mediotipula* as a genus to accommodate his new species *fulvogrisea* from northern Algeria. As recorded by Theowald (1978), the study of type material of *fulvogrisea* enabled Mannheims to recognize this species as a member of the *Tipula stigmatella* species group sensu Lackschewitz (1934). Correspondence on these findings with Mannheims led Theowald (1957) to use the name *Mediotipula* for the species of the *stigmatella* group. In the text of Theowald's 1957 paper, *Mediotipula* was used in the subgeneric sense, while Theowald's table 2, which presented a proposal for a new classification of the western Palaearctic Tipulidae, listed *Mediotipula* as a genus. Following Savchenko (1961), *Mediotipula* is usually considered a subgenus of *Tipula* Linnaeus. Savchenko, dealing with five species of *Mediotipula*, distinguished two species groups within the subgenus. A revision of *Mediotipula* was provided by Theowald (1978), who recognized a total of 12 species divided over four species groups. The arrangements of both authors will be commented upon in the 'Discussion of adopted phylogeny', below. In Appendix A of the present paper, the synonymy of *aragoniensis* Theowald under *cataloniensis* Theowald is established, thus reducing the number of valid species to 11. A list of the species of *Mediotipula* as recognized in this paper is given in table 1.

Mediotipula has a strictly western Palaearctic distribution, with about half of the species being confined to the western Mediterranean. The general distribution of *Mediotipula* is given in fig. 1. More detailed maps with the ranges of individual species will be provided in a forthcoming paper on the historical biogeography of the western Mediterranean. A short discussion on the distribution of the species of *Mediotipula* is given at the end of the present paper. A synopsis of their distribution can also be found in Oosterbroek & Theowald (1992).

Material, methods and terminology

With the exception of the female of *fulvogrisea*, material of both sexes of all species of *Mediotipula* was examined. The majority of specimens studied originate from the collection of the Institute for Systematics and Population Biology (Zoological Mu-

Table 1. The species of *Tipula* (*Mediotipula*) as recognized in this paper. +: examined; -: not examined.

	♂	♀
anatoliensis Theowald, 1978	+	+
brolemanni Pierre, 1922	+	+
cataloniensis Theowald, 1978	+	+
caucasiensis Theowald, 1978	+	+
fulvogrisea Pierre, 1924	+	–
galiciensis Theowald, 1978	+	+
mikiana Bergroth, 1888	+	+
nitidicollis Strobl, 1909	+	+
sarajevensis Strobl, 1898	+	+
siebkei Zetterstedt, 1852	+	+
stigmatella Schummel, 1833	+	+

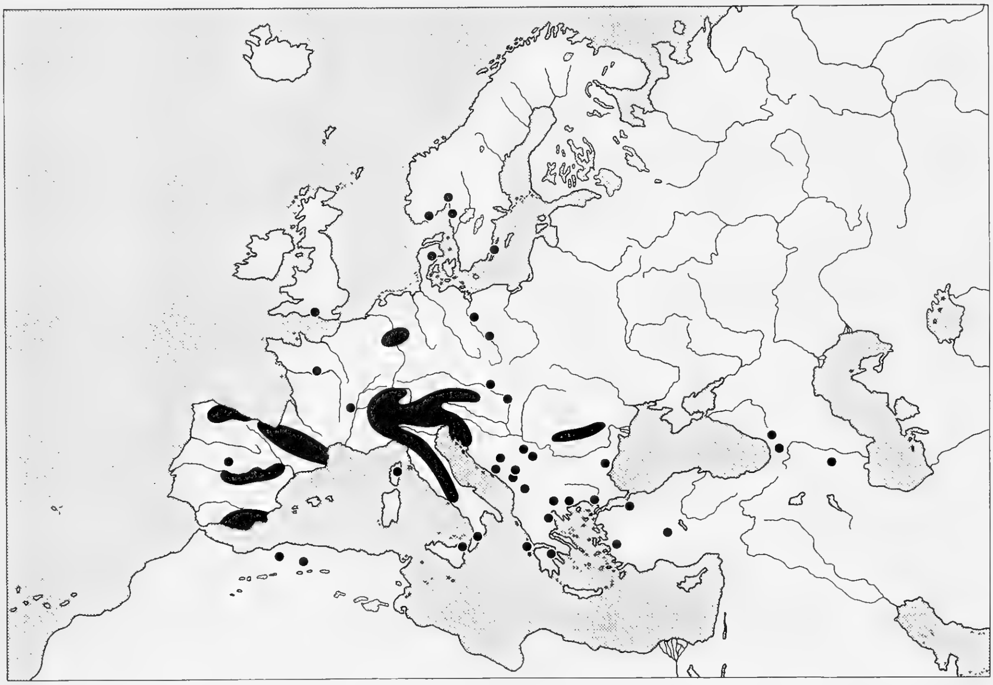


Fig. 1. Distribution of *Tipula* (*Mediotipula*).

seum), Amsterdam (ZMAN). This material consisted of dry pinned and alcohol preserved specimens. A male paratype and the female paratype of *caucasiensis* were borrowed from the Zoological Institute of the Academy of Sciences, St. Petersburg, the female paratype of *anatoliensis* was borrowed from the Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, and some material of *cataloniensis* was borrowed from the Musée d'Histoire Naturelle, Neuchâtel.

Only two female specimens of *fulvogrisea* are mentioned in the literature (Theowald 1978), viz., Pierre's female paratype in the Paris Muséum and another female in the collection in Vienna. Both specimens, however, are in a very bad condition and without terminalia (Matile in litt. and Contreras-Lichtenberg in litt., respectively). I did not examine the remaining parts of these females.

Preparations of the male and female terminalia were made by removing these parts and clearing them in a nearly boiling 10% KOH solution for about five minutes. After rinsing with water and 70% alcohol, the terminalia were transferred to glycerol. Examination of the specimens and their terminalia was carried out with a Wild stereo microscope, using a magnification of up to 100 ×. Drawings were made with the aid of a drawing tube attached to the microscope. Illustrations of the genital structures were made from macerated specimens. For permanent storage, the terminalia were transferred to a microvial containing some glycerol. The microvial was pinned with the relevant specimen.

The parsimony programs Hennig86, version 1.5 (Farris 1988) and PAUP, version 3.1 (Swofford 1993) were used to analyze the phylogeny. More information on the procedures followed is given in 'Discussion of adopted phylogeny'.

The terms for the structures of *Mediotipula* as used in this paper are generally in accord with those employed by McAlpine (1981), with a few additions for particular features of Tipulidae. The terminology as adopted here is explained in figs. 3-6, 8. A recent overview of the morphology of the terminalia of Tipulidae was given by Tangelder (1985) to which paper I refer the reader for more information.

BIOLOGY

The most comprehensive information on the biology of adult *Mediotipula* – and of other adult Tipulidae occurring in the region – can be found in Dufour's 1986 monograph on the Tipulidae of

Switzerland. Three of the four Swiss species of *Mediotipula*, viz., *sarajevensis*, *siebkei*, and *stigmatella*, are usually found at the colline and montane levels. The species *mikiana* occurs primarily at the subalpine level. The occasional occurrence of *mikiana* at lower levels either suggests altitudinal movements or the availability of favourable habitats even at these lower altitudes. Adults of *mikiana* can be found at higher levels in moors on slopes and along the banks of rivers. The greater majority of localities of *mikiana* in Switzerland are situated in crystalline domains, and none on lime. Therefore, Dufour supposed that the geological substrate plays a determinant role in the occurrence of *mikiana*. The species is absent from the calcareous Alps of northern Tirol (cf. Mannheims & Pechlaner 1963), while its absence from the Carpathians is possibly related to the essentially sedimentary nature of the pertaining rock formations. The species *sarajevensis* is associated with open woods and hedges exposed to the sun, most often in steep terrains. It is seldom found in uniform plains and dark woods. The few Swiss localities known of the relatively rare *siebkei* suggest a habitat of deciduous woods (*Quercus*, *Castanea*). The species *stigmatella* was found in Switzerland at two localities only, both very steep woods on thin and gravelly soil, one an oak grove, the other an *Ostrya* grove in the so-called *Querco-ostryetum* zone. Dufour supposed that the distribution of *stigmatella* in Switzerland is determined by the rarity of suitable habitats. Both sexes of the Swiss species of *Mediotipula* were captured in light traps. The non-Swiss species of *Mediotipula* are also found at colline to montane levels, with recorded altitudes ranging for *anatoliensis* from 430-1000 m, for *brolemanni* from 1000-1450 m, for *cataloniensis* from 1035-2000 m, for *galiciensis* from 200-700 m, and for *nitidicollis* from 350-900 m. The type couple of the Algerian *fulvogrisea* was captured on a wall in Mascara (Pierre 1924). Mascara lies at an altitude of about 600 m. The flight of the species of *Mediotipula* is swift and straight.

Theowald (1957, 1967) described and illustrated

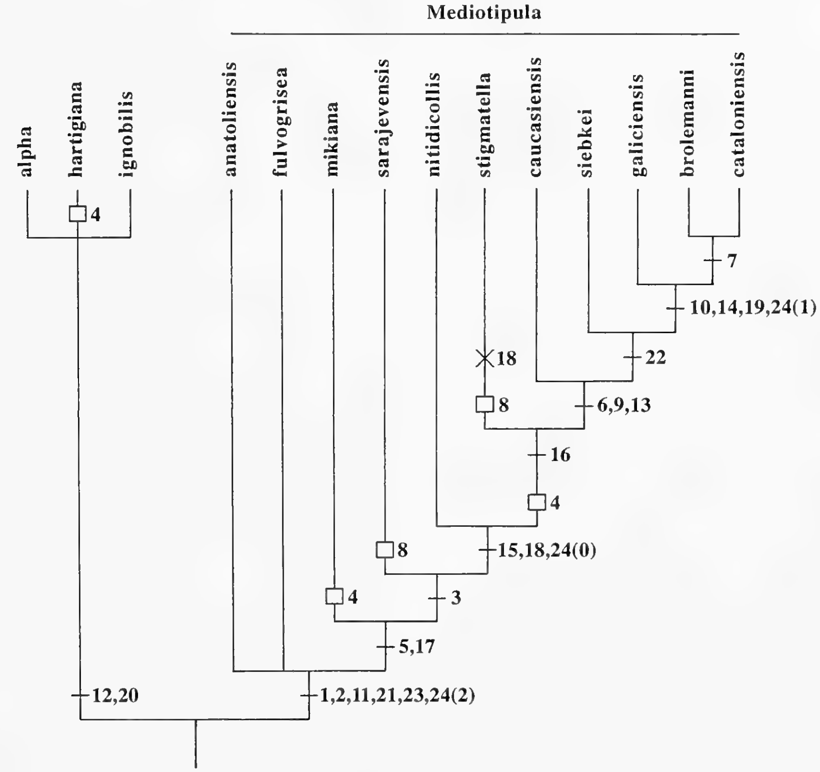


Fig. 2. Cladogram of *Tipula* (*Savtshenkia*) *alpha*, *hartigiana*, and *ignobilis*, and the species of *Tipula* (*Mediotipula*). Length 30, consistency index 0.83, retention index 0.93. See 'Discussion of adopted phylogeny' for further details. –: synapomorphy; □: homoplasy; ×: reversal.

the larvae and pupae of *mikiana* (as *stigmatella*), *sarajevensis*, and (1967) *stigmatella* (as *bidens* Bergroth). The larva and pupa of *stigmatella* were also treated in detail by Savchenko (1966a, 1966b; as *bidens*). Höchstetter (1963) described and illustrated the larva of *mikiana* (as *stigmatella*). The information provided by Höchstetter, Savchenko and Theowald suggests that the habitats of the larvae and pupae of *Mediotipula* species are restricted to moss cushions. Whereas Theowald recorded both stages of the species he dealt with from very moist moss on rocks in and along brooks, Savchenko characterized *stigmatella* as an obligate briobiont and xerophil, occurring under dry moss, especially *Brachythecium velutinum* (Hedwig). Höchstetter knew the larva of *mikiana* from dry moss in woods only.

Certain authors (e.g., Collin 1954; Stubbs 1992) referred to the occurrence of larvae of *siebkei* in rotting wood of alder (*Populus tremula* Linnaeus). This report goes back to Zetterstedt's description of *siebkei* (1852; 'Larva in Populo tremula capta, secundum *Siebkè*'), but, as it has not been confirmed since, this reference should be considered with reserve.

SYSTEMATIC POSITION

On account of the long and apparently non-verticillate antennae in the male of *fulvogrisea*, Pierre (1924, 1926) placed *Mediotipula* in his first group of the tribus Tipulini. Besides *Mediotipula*, this group contained *Habromastix* Skuse, *Idiotipula* Alexander, *Leptotipula* Alexander, *Longurio* Loew, *Macromastix* Osten Sacken, *Phymatopsis* Skuse, and *Xenotipula* Alexander. According to Pierre, the presence of 12 antennal segments in *Mediotipula* should indicate a close relationship with *Leptotipula*. However, distinct verticils among the long pubescence on the flagellomeres and a minuscule thirteenth apical antennal segment are actually present in the male of *fulvogrisea*. Both character states indicate a relationship with the more derived Tipulidae as are presently arranged in the genus *Tipula* and its near relatives. The structures of the male and female terminalia also show that there is no direct phylogenetic relationship between *Mediotipula* and the other taxa of Pierre's first group of Tipulini. With the exception of *Idiotipula*, the remaining taxa of this group are at present considered subgenera of *Leptotarsus* Guérin (cf. Hutson 1980, Oosterbroek 1989). *Leptotarsus* contains about 300 described species and has a primarily southern hemisphere distribution. The current systematics of *Leptotarsus* and its close relatives, which belong to the phylogenetically more primitive Tipulidae, are unsatisfactory and in need of a cladistic revision. At present, the monotypic South African *Idiotipula* is considered a genus. It is doubtless closely related to *Leptotarsus*.

According to Theowald (1957: 300), *Mediotipula* takes a rather isolated phylogenetic position among the western Palaearctic Tipulidae. Theowald considered the presence of a tooth-like protuberance at the end of the pupal hypogynial sheaths in *Mediotipula* and the subgenus *Tipula* (*Savtshenkia* Alexander) (i.e., the '*Tipula rufina*-Komplex' in Theowald 1957) a convergence. However, on account of the same character state, Savchenko (1966a, 1979, 1983) postulated a sister group relationship between *Mediotipula* and *Savtshenkia*. Theowald (1978) and De Jong (1994) accepted this tentative arrangement as a working hypothesis. Three species of *Savtshenkia*,

Table 2. Character state matrix of *Tipula* (*Savtshenkia*) *alpha*, *hartigiana*, and *ignobilis*, and the species of *T.* (*Mediotipula*).

Character		1 0		2 0	2 4
alpha	00000	0000-	01000	00–01	0000
hartigiana	00010	0000-	01000	00–01	0000
ignobilis	00000	0000-	01000	00–01	0000
anatoliensis	11000	0000-	10000	00–00	1012
brolemanni	11111	11011	10111	11110	1111
cataloniensis	11111	11011	10111	11110	1111
caucasiensis	11111	10010	10101	11100	1010
fulvogrisea	11000	0000-	10000	00–??	?? ??
galiciensis	11111	10011	10111	11110	1111
mikiana	11011	0000-	10000	01000	1012
nitidicollis	11101	0000-	10001	01100	1010
sarajevensis	11101	0010-	10000	01000	1012
siebkei	11111	10010	10101	11100	1110
stigmatella	11111	0010-	10001	11000	1010

viz., *alpha* De Jong, *hartigiana* Theowald, Dufour & Oosterbroek, and *ignobilis* Loew, are included in the phylogenetic analysis of *Mediotipula* given below. The phylogeny of the species of *Savtshenkia* was examined by De Jong (1994).

CHARACTER DISCUSSION

This section provides a discussion of the characters employed in the phylogenetic analysis of the species of *Mediotipula.* The character states recognized are briefly outlined, accompanied by their respective codes, after which a more detailed discussion follows. Table 2 gives the data set for the three supplementary *Savtshenkia* species, which are listed first, and the species of *Mediotipula.* The resultant cladogram (fig. 2) is discussed in the next section. Autapomorphies recognized for the species of *Mediotipula* are listed in Appendix B.

Wing

1. – Discal cell: (0) relatively large; (1) small.

All species of *Mediotipula* are distinguished by the presence of a small discal cell that is about 1.5 times as long as wide (fig. 6). Usually, the discal cell is much larger in the Tipulidae and has a length-width ratio of about 2 or more. The latter situation is found in the majority of species of *Savtshenkia* (fig. 7), including the three species added to the present analysis. The characteristically small discal cell of *Mediotipula* was noted before by Mannheims (e.g., in Mannheims & Pechlaner 1963) and Theowald (1973, 1978).

Male terminalia

2. – Gonocoxite, laterally compressed projection on posterodorsal corner: (0) absent; (1) present.

All species of *Mediotipula* are distinguished by the presence of a laterally compressed projection on the upper posterior corner of the gonocoxite. As in *fulvogrisea* (fig. 3), the projection is rather small in most species, but it is dorsoventrally extended as an elongate keel in *nitidicollis.* A similar structure is absent in the species of *Savtshenkia* included in the analysis, but can be found in a subgroup of that subgenus (De Jong 1994, character 24, the range *fragilina* to *subsignata cazorla*). In these species of *Savtshenkia*, the projection is not laterally compressed and is probably not homologous with the projection present in *Mediotipula.*

3. – Gonocoxite, part behind suture x: (0) long; (1) short.

In the Tipulidae, suture x usually separates a relatively large posterior section of the gonocoxite from the remainder of the gonocoxite, a situation found in all species of *Savtshenkia.* Within *Mediotipula*, the posterior part of the gonocoxite is relatively long in *anatoliensis*, *fulvogrisea*, and *mikiana* (fig. 8, arrow). The remainder of species of *Mediotipula* are distinguished by a short caudal part of the gonocoxite (fig. 9).

4. – Gonocoxite, midventral area, ventral extension at midlength; (0) absent; (1) present.

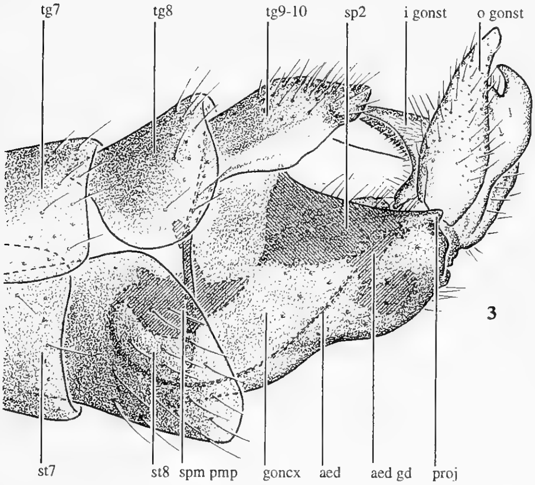
The midventral area in between the gonocoxites is unmodified in a minority of the species studied (fig. 3). *Savtshenkia hartigiana* carries a well-developed cone-shaped extension at about midlength of the midventral area (De Jong 1994, fig. 33). Within *Mediotipula* the midventral area is provided with a bulbous extension in *brolemanni*, *cataloniensis*, *caucasiensis*, *galiciensis*, *mikiana*, *siebkei*, and *stigmatella* (fig. 10). The lobe is relatively small in *caucasiensis*, *mikiana*, and *stigmatella*, whereas it is more pronounced in the other species listed. The homology of the extension in *Savtshenkia hartigiana* and in the species of *Mediotipula* is doubtful, but both are scored 'present' in the data matrix. In *anatoliensis* the entire midventral area is produced as a sclerotized and laterally compressed keel.

5. – Inner gonostylus, anterior part, setae on ventral margin: (0) short; (1) long.

The ventral surface of the anterior part of the inner gonostylus usually carries a vestiture of scattered and rather short setae in the Tipulidae. This is the situation encountered in *Savtshenkia*, including the species added to the data matrix. Within *Mediotipula*, short setae at this part of the inner gonostylus are found in *anatoliensis* and *fulvogrisea* only (figs. 4, 11). In the other species of *Mediotipula*, the ventral margin of the inner gonostylus is covered with strikingly long setae. There is a rather strong concentration of long setae in *mikiana* (fig. 12), *nitidicollis* (fig. 14), *sarajevensis* (fig. 13), and *stigmatella* (fig. 15). In *brolemanni* (fig. 22), *cataloniensis* (fig. 23), *caucasiensis* (fig. 16), *galiciensis* (fig. 20), and *siebkei* (fig. 18), the setae are more sparse.

6. – Inner gonostylus, anterior part, elongate, parallel sided, tip 'double': (0) no ; (1) yes.

Seen in lateral view, the anterior part of the inner gonostylus in the Tipulidae usually terminates in a gradually narrowing tip, a character state found also in the examined species of *Savtshenkia.* Within *Mediotipula*, a gradually narrowing anterior part is present in *anatoliensis* (fig. 11), *fulvogrisea* (fig. 4), *mikiana* (fig. 12), *nitidicollis* (fig. 14), *sarajevensis* (fig. 13), and *stigmatella* (fig. 15). The species *brolemanni* (fig. 22), *cataloniensis* (fig. 23), *caucasiensis* (fig. 16), *galiciensis* (fig. 20), and *siebkei* (fig. 18) have a rostrally stretched anterior part of which the dorsal and ven-



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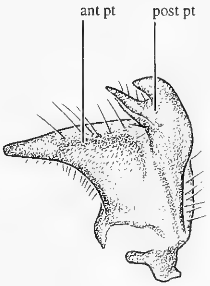

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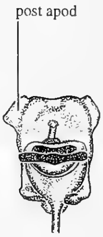

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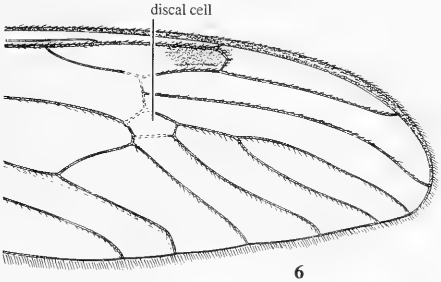

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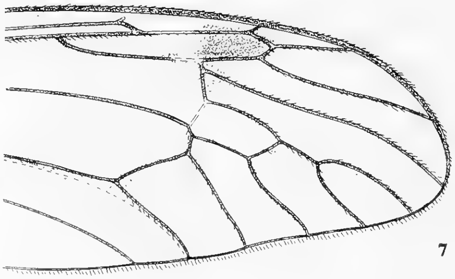

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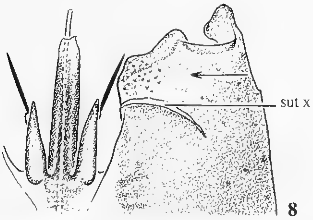

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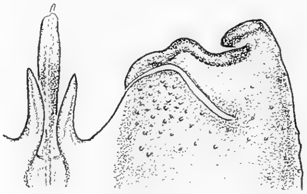

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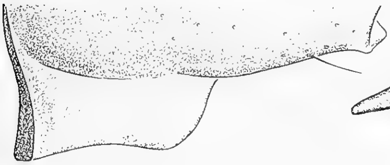

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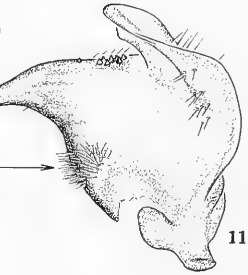

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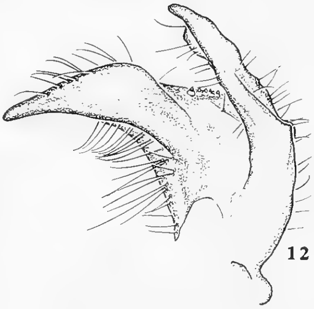

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tral sides run more or less parallel for some distance. The tip of the anterior part laterally carries a low extended rim that gives the apex a two fold appearance (fig. 16, upward arrow).

7. – Inner gonostylus, posterior part, dorsally directed crest: (0) absent; (1) present.

The dorsal margin of the posterior part of the inner gonostylus is usually rounded in the species of the Tipulidae. This situation is present in the studied species of *Savtshenkia* and in most species of *Mediotipula* (figs. 4, 11-16, 18, 20). Both *brolemanni* and *cataloniensis* are distinguished among the members of *Mediotipula* by the presence of a dorsally extended and laterally compressed crest on the posterodorsal surface of the posterior part at the point where the posterior parts curves anteriorly (figs. 22, 23, arrow). The actual size and shape of this crest can vary among specimens of the pertaining species, a feature that led Theowald (1978) to recognize the species *aragoniensis* and *cataloniensis* (figs. 23-27; see Appendix A).

8. – Inner gonostylus, posterior part, posterolateral extension: (0) absent; (1) present.

Two of the species studied, viz., *sarajevensis* and *stigmatella*, are characterized by the presence of a posterolateral extension on the posterior part of the inner gonostylus (figs. 13, 15, arrows).

9. – Inner gonostylus, posterior part, posteromedial extension: (0) absent; (1) present.

The inner gonostylus of the majority of species examined is relatively simple and composed of an anterior and posterior part only. The species *brolemanni, cataloniensis, caucasiensis, galiciensis,* and *siebkei* are distinguished by the presence of a low placed posteromedial extension on the posterior part (figs. 16, 17, 19-23; see next character).

10. – Inner gonostylus, posterior part, posteromedial extension: (0) short; (1) elongate.

The posteromedial extension on the inner gonostylus varies in size between the species that show this structure. The extension is small in *siebkei* (fig. 19, arrow), somewhat more pronounced in *caucasiensis* (figs. 16, 17, downward arrows), and present as an elongate structure in *brolemanni* (fig. 22), *cataloniensis* (fig. 23), and *galiciensis* (figs. 20, 21, arrows).

11. – Sperm pump, posterior apodemes, entirely fused, forming plate: (0) no; (1) yes.

The sperm pump carries a pair of separate posterior apodemes in the majority of species of Tipulidae, a situation found also in *Savtshenkia*, including the species added to the matrix. All species of *Mediotipula* show the total fusion of the posterior apodemes in the horizontal plane; a dorsoventrally flat blade connects the posterior apodemes from the body of the sperm pump up to their posterior apices (fig. 5).

12. – Sp2, medial margin blackish sclerotized: (0) no; (1) yes.

All species of *Savtshenkia* are characterized by the blackish sclerotized medial margin of sp2 (De Jong 1994). Within *Mediotipula*, sp2 is moderately, and usually uniformly, sclerotized throughout (figs. 28-31).

13. – Sp2, dorsal vaulting at anterior margin: (0) absent; (1) present.

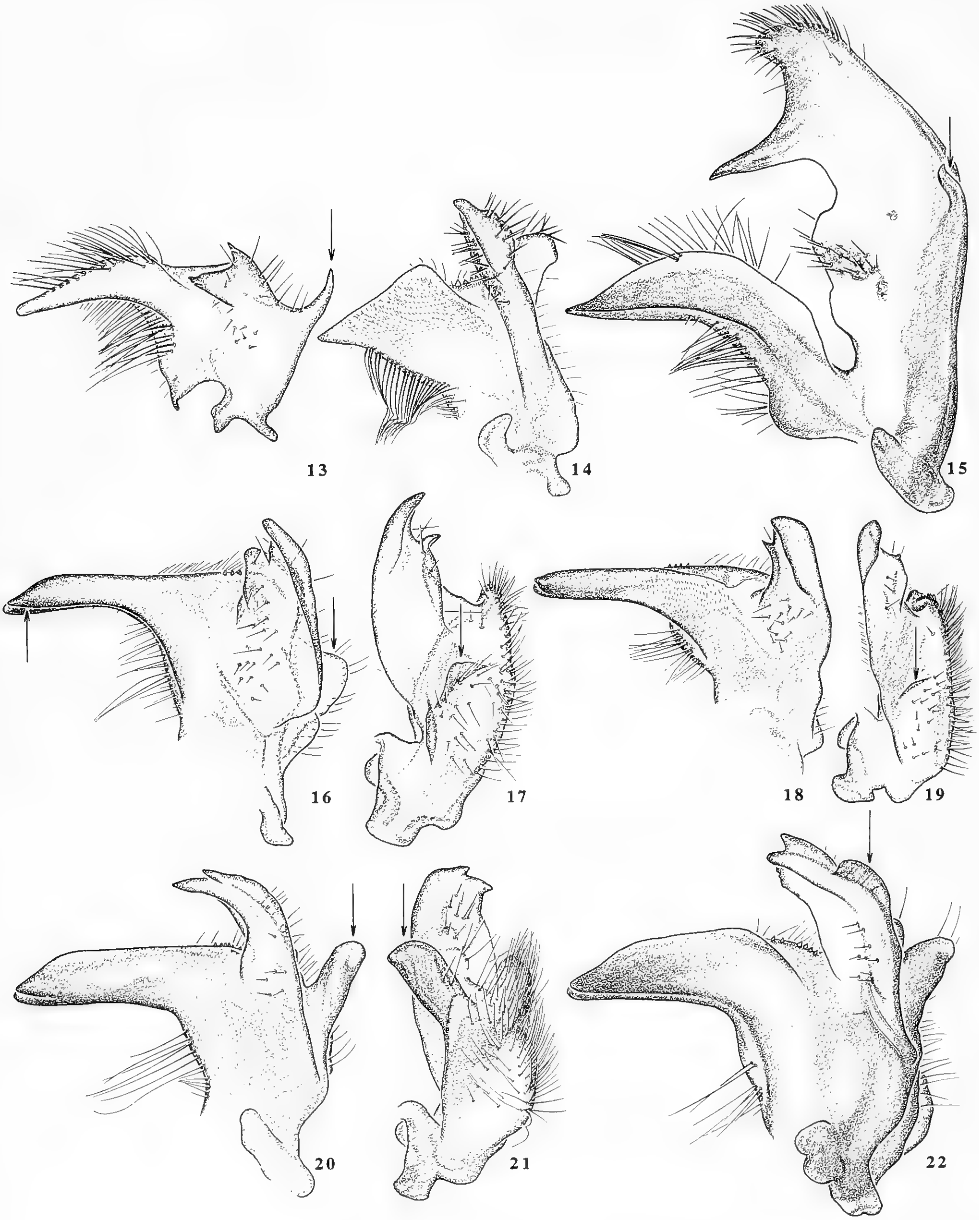
Sp2 usually is present as a relatively flat structure, a situation found in all species of *Savtshenkia*. A relatively flat sp2 is present also in about half of the species of *Mediotipula* (fig. 28). The species *brolemanni, cataloniensis, caucasiensis, galiciensis,* and *siebkei* are distinguished by the presence of a dorsal vaulting at the anterior margin of sp2. The resulting lobe is relatively low and broad-based in *caucasiensis* (fig. 29, arrow), it is more pronounced and relatively narrow-based in *brolemanni, cataloniensis, galiciensis* (fig. 31), and *siebkei* (fig. 30, arrow).

14. – Sp2, membranous area on posterior margin: (0) absent; (1) present.

Sp2 is entirely sclerotized in most Tipulidae that show this structure, a condition found in the species of *Savtshenkia* and in most species of *Mediotipula* (figs. 28-30). The posterior margin of sp2 is partly membranous in *brolemanni, cataloniensis,* and *galiciensis* (fig. 31, arrow).

15. – Sternite 8, posterior margin, U or V-shaped large membranous area: (0) absent; (1) present.

Figs. 3-12. – 3-6, *Tipula* (*Mediotipula*) *fulvogrisea*; 3, male terminalia, lateral view; 4, left inner gonostylus, lateral view; 5, sperm pump, dorsal view; 6, male right wing, dorsal view; 7, *T.* (*Savtshenkia*) *grisescens*, male right wing, dorsal view; 8, 9, posterior part of right gonocoxite, aedeagal guide and appendages, ventral view (gonostyli omitted); 8, *T.* (*M.*) *mikiana*; 9, *T.* (*M.*) *sarajevensis*; 10, *T.* (*M.*) *mikiana*, ventral part of gonocoxite, lateral view; 11, 12, left inner gonostylus, lateral view; 11, *T.* (*M.*) *anatoliensis*; 12, *T.* (*M.*) *mikiana*.
Abbreviations: aed: aedeagus; aed gd: aedeagal guide; ant pt: anterior part of inner gonostylus; goncx: gonocoxite; i gonst: inner gonostylus; o gonst: outer gonostylus; post apod: posterior apodeme of sperm pump; post pt: posterior part of inner gonostylus; proj: projection on posterodorsal corner of gonocoxite; spm pmp: sperm pump; st7 etc.: sternite 7 etc.; sut x: suture x; tg7 etc.: tergite 7 etc.



Figs. 13-22, left inner gonostylus. – 13, *Tipula* (*Mediotipula*) *sarajevensis*, lateral view; 14, *T.* (*M.*) *nitidicollis*, lateral view; 15, *T.* (*M.*) *stigmatella*, lateral view; 16, 17, *T.* (*M.*) *caucasiensis*; 16, lateral view; 17, posterior view; 18, 19, *T.* (*M.*) *siebkei*; 18, lateral view; 19, posterior view; 20, 21, *T.* (*M.*) *galiciensis*; 20, lateral view; 21, posterior view; 22, *T.* (*M.*) *brolemanni*, lateral view.

The posterior margin of male sternite 8 is unmodified in the majority of species of the Tipulidae, being evenly convex and entirely sclerotized. This situation is present in the *Savtshenkia* species included in the analysis and in a few species of *Mediotipula* (fig. 32). Within *Mediotipula*, the posterior margin of sternite 8 is incised by a deep and broad U or V-shaped membranous area in *brolemanni, cataloniensis, caucasiensis, galiciensis, nitidicollis* (fig. 33), *siebkei*, and *stigmatella*.

16. – Tergite 9-10, narrow medial longitudinal suture: (0) absent; (1) present.

The medial part of the disk of tergite 9-10 is broadly membranous in *Savtshenkia alpha* and *ignobilis*, as is characteristic of the majority of species of *Savtshenkia*. In *hartigiana*, however, the medial part is entirely sclerotized. Within *Mediotipula*, the disk of tergite 9-10 is evenly sclerotized in *anatoliensis, fulvogrisea, mikiana*, and *nitidicollis* (fig. 34). In *sarajevensis* it is partly membranous as in certain species of *Savtshenkia*. The species *brolemanni, cataloniensis, caucasiensis, galiciensis, siebkei*, and *stigmatella* are distinguished by the presence of a narrow medial longitudinal suture on tergite 9-10 (fig. 35).

17. – Tergite 9-10, posterior margin, medial spinous extension: (0) absent; (1) present.

The majority of species of *Savtshenkia*, including the species added to the data set, carry a pair of spinous caudal extensions on the posterior margin of tergite 9-10. Within *Mediotipula*, a similar situation is found only in *anatoliensis* (fig. 36). The species *fulvogrisea* shows no distinct paired extensions, but has a widely emarginate posterior margin that is covered with black spines (fig. 37). The remainder of *Mediotipula* is distinguished by the presence of a medial spinous extension in between the lateral pair (figs. 34, 35, 38, 39, 40). See also next character.

18. – Tergite 9-10, posterior margin, medial spinous extension ventrally produced: (0) no; (1) yes.

The species of *Mediotipula* that carry a medial extension on the posterior margin of tergite 9-10 can be divided in those with a relatively small extension and those with a relatively large and anteroventrally produced extension. The first category includes *mikiana* (fig. 38), *sarajevensis*, and *stigmatella* (fig. 40), the second *brolemanni, cataloniensis, caucasiensis, galiciensis, nitidicollis* (fig. 39), and *siebkei*. In the species of the first category, the medial extension is of about the same size as the lateral ones, whereas it is much larger than the lateral extensions in the species of the second category. The latter condition is unique among the Tipulidae.

Female terminalia

19. – Cercus, almost straight and apex pointed: (0) no; (1) yes.

The majority of species of *Mediotipula* are characterized by the presence of a slightly downward curved female cercus that terminates in a rounded apex (fig. 41), a situation similar to that of the species of *Savtshenkia*, including those added to the data set. Within *Mediotipula, brolemanni, cataloniensis*, and *galiciensis* are distinguished by the presence of a straight and gradually narrowing cercus that terminates in an acute tip (fig. 42). Theowald (1978) used this character to separate his *brolemanni* group from the remainder of *Mediotipula*.

20. – Hypogynial valves, dorsal margin blackish sclerotized: (0) no; (1) yes.

All species of *Savtshenkia* are characterized by the blackish sclerotized dorsal margin of the hypogynial valves (De Jong 1994). Within *Mediotipula*, the hypogynial valves are moderately sclerotized throughout (fig. 45).

21. – Hypogynial valves, fused for some length: (0) no; (1) yes.

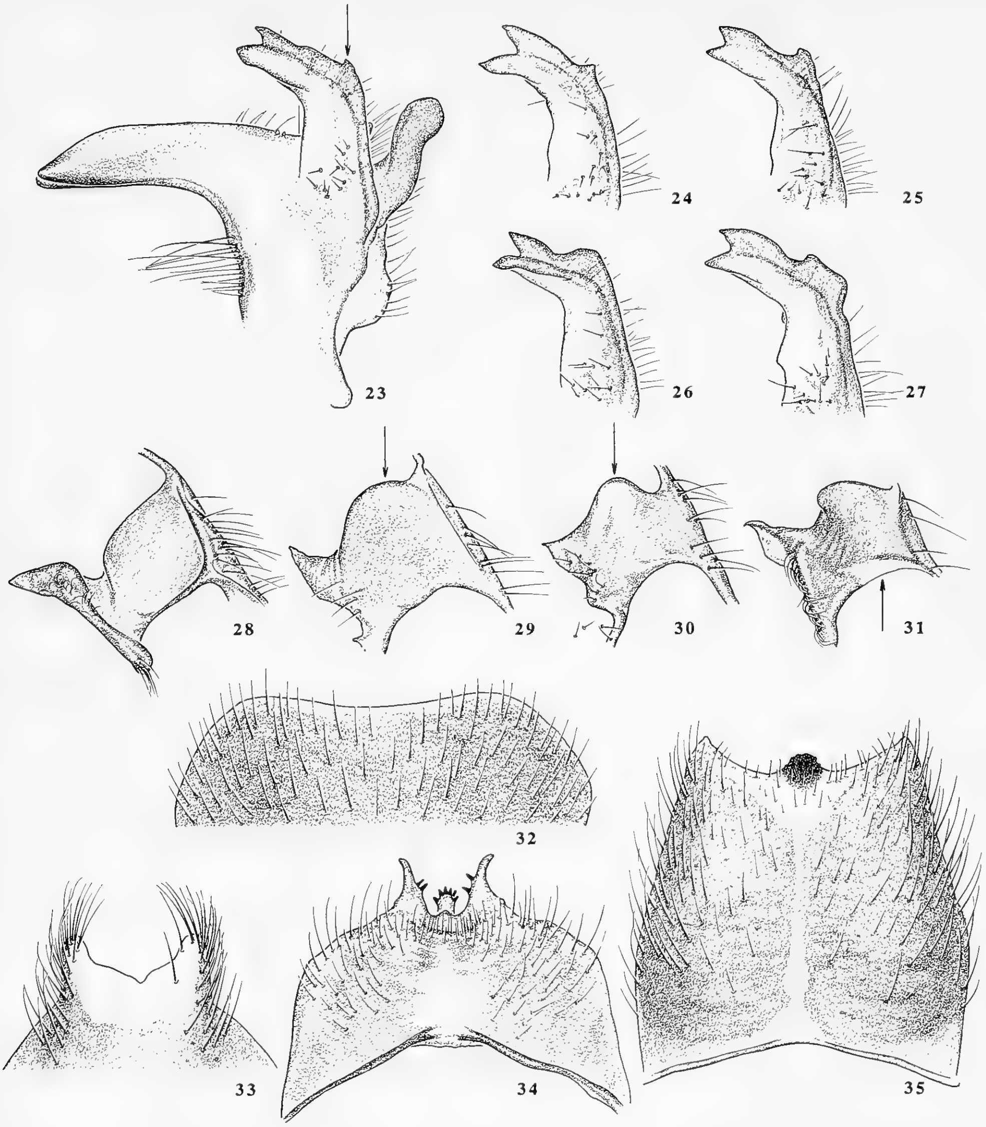
The hypogynial valves in the Tipulidae are separate up to their bases in the majority of species, including those of *Savtshenkia*. All species of *Mediotipula* of which I examined the female sex, have the hypogynial valves ventrally fused for about one half to two thirds of their length (figs. 43, 44, valves fused up to point indicated by upper arrow).

22. – Sternite 8, anterior end of membranous area at base of hypogynial valves: (0) acute; (1) broad, truncate.

The membranous area of sternite 8 at the base of the hypogynial valves narrows gradually and anteriorly terminates in an acute point in the species of *Savtshenkia* and in most species of *Mediotipula*. The end of the membranous area is distinctly acute in the females of *anatoliensis, mikiana, nitidicollis, sarajevensis*, and *stigmatella*. In the female paratype of *caucasiensis*, the only known female specimen of this species, it is less distinct (fig. 43, lower arrow). In the females of *brolemanni, cataloniensis, galiciensis*, and *siebkei*, the anterior end of this membrane is broad and truncate (fig. 44, lower arrow).

23. – Sternite 8, sclerotization at opening of gonopore: (0) absent; (1) present.

All females of *Mediotipula* studied are distinguished by the presence of a sclerotization of the ventral wall of the genital chamber near the opening of the gonopore. The sclerotization consists of a large and dorsally concave sclerite that is anterodorsally lo-

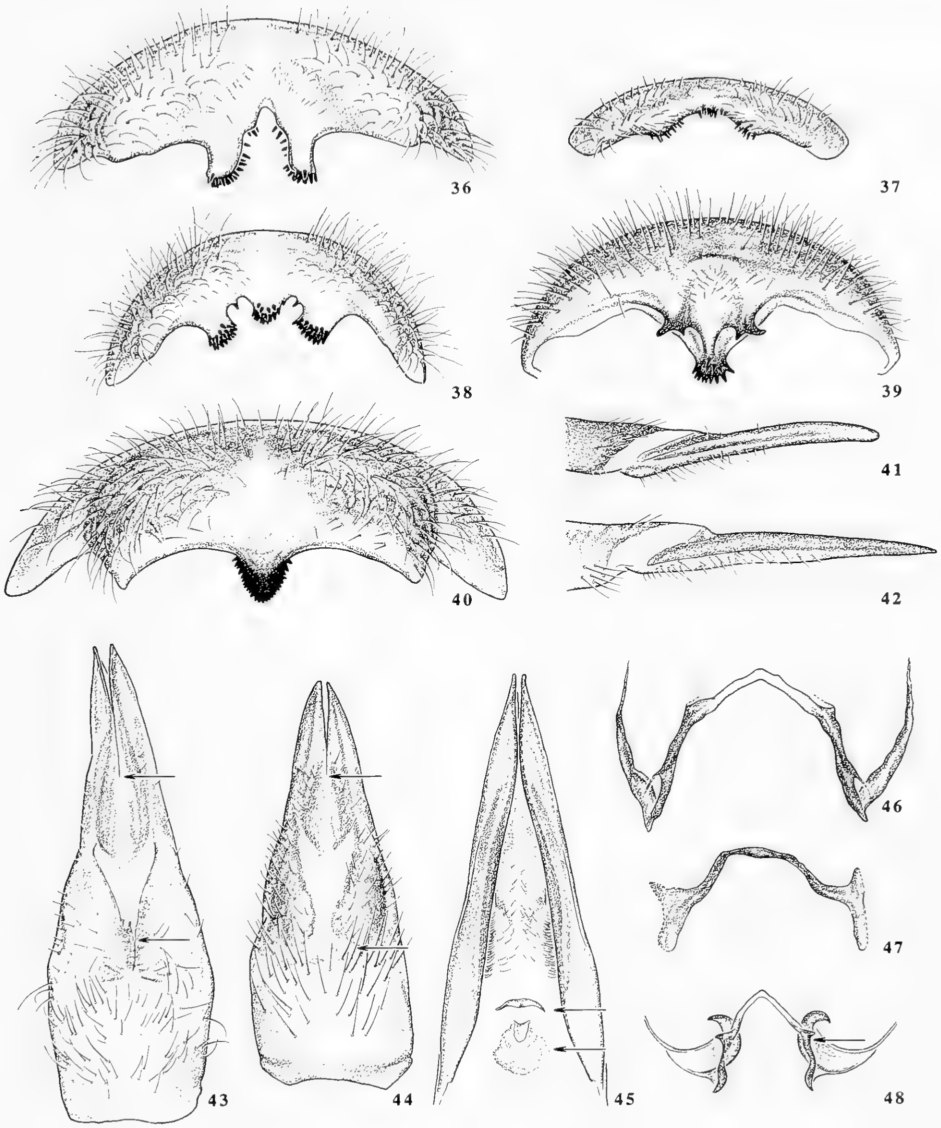


Figs. 23-35. – 23-27, *Tipula* (*Mediotipula*) *cataloniensis*, all Canillo, Andorra, 4-23 June 1979, 1500 m; 23, left inner gonostylus, lateral view; 24-27, posterior part of left inner gonostylus, lateral view; 28-31, right sp2, posterolateral view; 28, *T.* (*M.*) *nitidicollis*; 29, *T.* (*M.*) *caucasiensis*; 30, *T.* (*M.*) *siebkei*; 31, *T.* (*M.*) *galiciensis*; 32, 33, posterior margin of male sternite 8, ventral view; 32, *T.* (*M.*) *sarajevensis*; 33, *T.* (*M.*) *nitidicollis*; 34, 35, male tergite 9-10, dorsal view; 34, *T.* (*M.*) *nitidicollis*; 35, *T.* (*M.*) *stigmatella*.

cated, and a usually less distinct and smaller posteroventral sclerite (fig. 45, arrows). This sclerotization is absent in the species of *Savtshenkia*.

24. – Sternite 9, medial part: (0) entirely sclerotized; (1) membranous over a narrow zone, lateral with sclerotized cavities; (2) membranous over a broad zone.

In most Tipulidae, the medial part of female sternite 9 is produced into a sclerotized elongate and



Figs. 36-48. – 36-40, male tergite 9-10, posterior view; 36, *Tipula* (*Mediotipula*) *anatoliensis*; 37, *T.* (*M.*) *fulvogrisea*; 38, *T.* (*M.*) *mikiana*; 39, *T.* (*M.*) *nitidicollis*; 40, *T.* (*M.*) *stigmatella*; 41, 42, female tergite 10 and left cercus, lateral view; 41, *T.* (*M.*) *siebkei*; 42, *T.* (*M.*) *galiciensis*; 43, 44, female sternite 8 and hypogynial valves, ventral view; 43, *T.* (*M.*) *caucasiensis*; 44, *T.* (*M.*) *siebkei*; 45, *T.* (*M.*) *anatoliensis*, female sternite 8 and hypogynial valves, dorsal view; 46-48, female sternite 9, ventral view; 46, *T.* (*M.*) *anatoliensis*; 47, *T.* (*M.*) *nitidicollis*; 48, *T.* (*M.*) *galiciensis*.

slender extension. Such an extension is present in the species of *Savtshenkia*. Within *Mediotipula*, none of the examined females shows an elongate and posteriorly produced medial section of sternite 9. The sternite is present as a slender and well-sclerotized structure in *caucasiensis*, *nitidicollis* (fig. 47), *siebkei*, and *stigmatella*. It is medially membranous over a relatively narrow zone and incorporates a pair of lateral sclerotized cavities in *brolemanni*, *cataloniensis*, and *galiciensis* (fig. 48, arrow). In *anatoliensis*, *mikiana*, and *sarajevensis* the medial part of sternite 9 is broadly membranous (fig. 46).

Discussion of adopted phylogeny

The character state matrix of table 2 was analyzed with the parsimony programs Hennig86 (Farris 1988) and PAUP (Swofford 1993). For matters of reference, unknown characters are coded '?', inapplicable characters '–' in table 2. Platnick et al. (1991) discussed the potentially different treatment of missing entries by the programs Hennig86 and PAUP, while Maddison (1993) dealt with the consequences of coding inapplicable characters as missing data. All characters were, by default, given the same weight; character 24, the only multistate character in the matrix, was treated unordered. The matrix was run under the ie*; (implicit enumeration) command of Hennig86 and the branch-and-bound algorithm of PAUP. Both methods guarantee to find all optimal trees (Farris 1988; Swofford 1993).

As Hennig86 does not allow the outgroup to be empty (Farris 1988), using this program, the supplementary *alpha*, *hartigiana*, and *ignobilis* were a priori included in the outgroup. A methodologically preferable procedure was employed under PAUP, which is able to simultaneously resolve the phylogenetic relationships of all taxa included in the data set and to compute unrooted trees that can be rooted a posteriori. Outgroup rooting under PAUP was done such that the outgroup is a monophyletic sister group of the ingroup. In this case, *alpha*, *hartigiana*, and *ignobilis* were assigned to the outgroup after the analysis was completed. Recently, Nixon & Carpenter (1993) gave a compact and clear overview of the proper use of outgroups in phylogenetic analysis.

Analysis with Hennig86 resulted in two equally most parsimonious trees with length 30, consistency index 82, and retention index 92; PAUP computed a single most parsimonious tree with length 30, consistency index 0.833, and retention index 0.930. Both programs distinguished *Mediotipula* as a monophyletic taxon. Fig. 2 shows the cladogram produced by PAUP when the outgroup is considered the monophyletic sister group of the ingroup. (Hennig86 declines to resolve the most basal node of a tree on account of implied polarities alone and places the three *Savtshenkia* species in a polytomy).

The solution for *Mediotipula* produced by PAUP is identical with one of the two alternative trees found by Hennig86. It is also identical with the strict consensus tree of the two equally most parsimonious trees computed by Hennig86. The second most parsimonious tree found by Hennig86 depicts *fulvogrisea* as the sister species of a clade *anatoliensis* to *cataloniensis*, within which *anatoliensis* is the sister species of the clade *mikiana* to *cataloniensis* which has the same topology as in fig. 2. The only support for the monophyly of a clade *anatoliensis* to *cataloniensis* can be given by the female characters 21, 23, and 24. As these characters are unknown in *fulvogrisea* and only characters that have non-missing values affect the location of any taxon on a tree in PAUP (Swofford 1993), they are, contrary to the procedure followed by Hennig86, not employed by PAUP to distinguish a clade *anatoliensis* to *cataloniensis*. Future study of the female terminalia of *fulvogrisea* could lead to a solution of the basal trichotomy in *Mediotipula*. As things are, however, the few known female specimens of this species do not allow for such an examination (see 'Material, methods and terminology', above). Additional material of the Algerian *fulvogrisea* is required, but it will probably take some time before this can be safely amassed.

Savchenko (1961) divided the species of *Mediotipula* he dealt with into two groups, viz., a *siebkei* group containing *caucasiensis* (as *obtusiuscula* Lackschewitz) and *siebkei*, and a *stigmatella* group containing *mikiana* (as *stigmatella*), *sarajevensis*, and *stigmatella* (as *bidens*). Theowald (1978) recognized a *siebkei* group of the same composition as the *siebkei* group of Savchenko. Theowald divided the species of Savchenko's *stigmatella* group over a *stigmatella* group, containing *mikiana*, *stigmatella* and the newly described *anatoliensis*, and a *sarajevensis* group, that besides *sarajevensis* contained *fulvogrisea* and *nitidicollis*. In addition, Theowald recognized a *brolemanni* species group containing *aragoniensis* (here considered a junior synonym of *cataloniensis*; Appendix A), *brolemanni*, *cataloniensis*, and *galiciensis*. Fig. 2 shows that Theowald's *brolemanni* group is the only previously recognized species group that represents a monophyletic unit. The *brolemanni* group together with the species of the *siebkei* group of both authors, viz., *caucasiensis* and *siebkei*, constitute a well-defined monophyletic group. On the basis of the shape of the membranous area of female sternite 8 (character 22), a monophyletic group containing *brolemanni*, *cataloniensis*, *galiciensis*, and *siebkei* can be tentatively distinguished, but, as discussed under character 22, the expression of this character in the female paratype of *caucasiensis* leaves some doubts regarding the interpretation adopted here.

Distribution

Mediotipula is primarily restricted to the Mediterranean subregion of the Palaearctic (fig. 1). The species *anatoliensis* is known from its type locality in the Sultan Daglari mountains in the Turkish province Konya and from a locality in the western province Izmir. The species *fulvogrisea* is known from the type locality Mascara and from Guelt es-Stel in northern Algeria only. The main distribution of *mikiana* lies in the Alps. Besides that, it is known from a few isolated localities in the Czech Republic, Germany, Poland, and Slovakia. The species *sarajevensis* is widely distributed in the central European mountains at levels under 1500 m, ranging from southern England in the west to Rumania and Bulgaria in the east. The range of *nitidicollis* is restricted to central and southern Spain. The distribution area of *stigmatella* extends over most of central Europe, the Caucasus and western Turkey. At present, *caucasiensis* is known from a few localities in the Caucasus only. The widespread distribution area of *siebkei* ranges from southern England and southern Scandinavia over most of the central belt of Europe and reaches southward to the north-eastern part of Sicily and Corsica. The remaining species of *Mediotipula*, viz., *galiciensis*, *brolemanni*, and *cataloniensis*, are confined to the mountainous northern part of Spain and adjacent southern France. The species *galiciensis* has been found in the Spanish provinces Lugo, Oviedo, and Vizcaya, *brolemanni* is known from the French departments Pyrénées Atlantiques and Hautes-Pyrénées only, while *cataloniensis* is known to occur in the Spanish Pyrenean provinces Gerona, Huesca, and Lerida, in Andorra, and in the French department Pyrénées-Orientales. At the moment, no species of *Mediotipula* have been recorded from the Balearic islands and Sardinia, nor from the Rif and Atlas mountains in Morocco. The only species known to occur on the Mediterranean islands Corsica and Sicily is the widespread *siebkei*.

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REFERENCES

Collin, J. E., 1954. *Tipula siebkei* Zetterstedt (1852), an addition to the British Tipulidae (Diptera). – Journal of the Society for British Entomology 5: 72.

Dufour, C., 1986. Les Tipulidae de Suisse (Diptera, Nematocera). – Documenta Faunistica Helvetiae 2: 1-187, + 1-149.

Farris, J. S. 1988. Hennig86, version 1.5 + reference. – Port Jefferson Station, New York.

Höchstetter, L., 1963. Beiträge zur Biologie, Oekologie und Systematik der Tipuliden-Larven (Diptera). – Sitzungsberichten der Physikalisch-Medizinischen Sozietät zu Erlangen 82: 33-112.

Hutson, A. M., 1980. Family Tipulidae. – In: Crosskey, R. W. (ed.), Catalogue of the Diptera of the Afrotropical Region: 47-91. British Museum (Natural History), London.

Jong, H. de, 1994. The phylogeny of the subgenus *Tipula* (*Savtshenkia*) (Diptera: Tipulidae), with special reference to the western Mediterranean fauna. – Tijdschrift voor Entomologie 137: 271-323.

Lackschewitz, P., 1934. Tipuliden-Studien III. (Dipt., Nematoc. polyn.). – Konowia 13: 117-144, pl. I.

McAlpine, J. F., 1981. Morphology and terminology - adults. – In: McAlpine, J. F. et al. (eds.) Manual of Nearctic Diptera. Volume 1. Research Branch, Agriculture Canada, Monograph 27: 9-63.

Maddison, W. P., 1993. Missing data and missing characters in phylogenetic analysis. – Systematic Biology 42: 576-581.

Mannheims, B. & E. Pechlaner, 1963. Die Tipuliden Nordtirols (Dipt.). – Stuttgarter Beiträge zur Naturkunde 102: 1-29.

Nixon, K. C. & J. M. Carpenter, 1993. On outgroups. – Cladistics 9: 413-426.

Oosterbroek, P., 1989. Family Tipulidae. – In: Evenhuis, N. L. (ed.), Catalog of the Diptera of the Australasian and Oceanian Regions: 53-116.

Oosterbroek, P. & B. Theowald, 1992. Family Tipulidae. – Catalogue of Palaearctic Diptera 1: 56-178.

Pierre, C., 1924. Tipulidae nouveaux d'Algérie. – Encyclopédie Entomologique, Série B II, Diptera 1: 9-12.

Pierre, C., 1926. Diptera, Fam. Tipulidae, Subfam. Tipulinae. – Genera Insectorum 186: 1-68, pls. 1-5.

Platnick, N. I., C. E. Griswold & J. A. Coddington, 1991. On missing entries in cladistic analysis. – Cladistics 7: 337-343.

Savchenko, E. N., 1961. Crane flies (Fam. Tipulidae), subfam. Tipulinae: genus *Tipula* L. (part 1). – Fauna SSSR (N.S. 79) Two-winged insects II (3): 1-486. (In Russian).

Savchenko, E. N., 1966a. Crane flies. – Fauna Ukraini 14 (1): 1-552. (In Ukrainian).

Savchenko, E. N., 1966b. On the distribution, ecology and preimaginal phases of the crane fly *Tipula* (*Mediotipula*) *bidens* Bergr. (Diptera, Tipulidae). – Entomologicheskoe Obozrenie 45: 286-293. (In Russian, English summary). English translation in Entomological Review 45: 157-160.

Savchenko, E. N. (as Savtshenko), 1979. Phylogenie und Systematik der Tipulidae. – Tijdschrift voor Entomologie 122: 91-126. (Translation of Savchenko 1966a: 63-88).

Savchenko, E. N., 1983. Crane flies of the family Tipulidae. General part and beginning of systematic part. Subfam. Dolichopezinae; subfam. Tipulinae (part). – Fauna SSSR (N.S. 127) Two-winged insects II (1-2): 1-585. (In Russian).

Stubbs, A. E., 1992. Provisional atlas of the long-palped craneflies (Diptera: Tipulinae) of Britain and Ireland: 1-134. – Biological Records Centre, NERC Institute of Terrestrial Ecology, Monks Wood, Huntingdon, UK.

Swofford, D. L., 1993. PAUP, Phylogenetic Analysis Using Parsimony, version 3.1. – Illinois Natural History Survey, Champaign, Illinois.
Tangelder, I. R. M., 1985. Phylogeny of the *Nephrotoma dorsalis* species-group (Diptera, Tipulidae), mainly based on genital characters. –Beaufortia 35: 135-174.
Theowald, B. 1957. Die Entwicklungsstadien der Tipuliden (Diptera, Nematocera), insbesondere der west-palaearktischen Arten. – Tijdschrift voor Entomologie 100: 195-308.
Theowald, B. 1967. Familie Tipulidae. (Diptera, Nematocera). Larven und Puppen. – Bestimmungsbücher zur Bodenfauna Europas 7: 1-100.
Theowald, B. 1973. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 300: 321-404.
Theowald, B. 1978. Tipulidae. – Fliegen der Palaearktischen Region 15, Lieferung 318: 405-436.
Zetterstedt, J. W., 1852. Diptera Scandinaviae, disposita et descripta 11: XII, 4091-4546. Lundae (Lund).

Appendix A

Synonymy

aragoniensis Theowald, 1978 = ***cataloniensis*** Theowald, 1978 **syn. n.**

In his revision of *Mediotipula*, Theowald (1978) described three species from northern Spain as new and assigned them, together with *brolemanni*, to his *brolemanni* species group. In Theowald's concept, the *brolemanni* group contained the species *aragoniensis*, *brolemanni*, and *cataloniensis* from the Pyrenees and *galiciensis* from northern Spain. According to Theowald, a constant character separating *aragoniensis* and *cataloniensis* could be found in the structure of the posterior part of the inner gonostylus. Its tip should be more acute in *aragoniensis* and short and *brolemanni*-like in *cataloniensis*, whereas the dorsal crest of the posterior part ('Buckel' in Theowald 1978; character 7 in the present paper) should be placed somewhat laterally on the posterior part in *aragoniensis*, while it should have an acute dorsal angle in *cataloniensis*. The collection of ZMAN contains a series of 22 identical labelled males, giving Canillo in Andorra at 1500 m as locality and dates of capture 4 to 23 June 1979. Within this series, the posterior part of the inner gonostylus shows a range of forms intermediate between those considered typical of *aragoniensis* and *cataloniensis*. A number of these forms are shown in figs. 23-27. Considerable variation in the shape of the posterior part is observed in other species of *Mediotipula* as well (see for instance Theowald 1978 on *sarajevensis*). I therefore conclude that both *aragoniensis* and *cataloniensis* are names that pertain to the same species. At the moment, the range of this species is known to extend in Spain from the north-eastern part of Aragón eastward to the Mediterranean coast of northern Cataluña. To the north it has been recorded from Andorra and the French department Pyrénées-Orientales. As the major part of its range seems to cover the Pyrenean northern portion of Cataluña, I prefer to denote this species *cataloniensis*. The species is most easily distinguished from the other species of *Mediotipula* by the medially curved corners on the posterior margin of male sternite 8 that are covered by medially directed strong setae.

Appendix B

Autapomorphies of the species of *Tipula* (*Mediotipula*)

anatoliensis: midventral area of gonocoxites present as a well-developed keel; inner gonostylus anterolaterally with a cluster of short setae (fig. 11, arrow).

brolemanni: anterior part of inner gonostylus relatively robust and short compared with that of close relatives (cf. fig. 22 with figs. 16, 18, 20, 23).

cataloniensis: posterior margin of male sternite 8 with medially directed tips, tips with long and strong medially directed setae; outer gonostylus with concentration of long setae at posterior margin.

fulvogrisea: male antenna extremely elongate.

galiciensis: no autapomorphy recognized.

mikiana: shape of posterior part of inner gonostylus (fig. 12).

nitidicollis: surface of thorax shining; branched gonapophysis; gonocoxite ring interrupted.

sarajevensis: shape of low posterior part of inner gonostylus (fig. 13).

siebkei: no autapomorphy recognized.

stigmatella: inner gonostylus about two times as high as inner gonostyli of other species of *Mediotipula* (fig. 15); sensory area on posterior part of inner gonostylus instead of dorsally on anterior part as in other species of *Mediotipula*; female sternite 8 bulbous.

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SCIOPHILA MEIGEN, 1818 FROM THE ORIENTAL REGION (DIPTERA, MYCETOPHILIDAE)

Söli, G. E. E. 1995. *Sciophila* Meigen, 1818 from the Oriental region (Diptera, Mycetophilidae). – Tijdschrift voor Entomologie 138: 283-289, figs. 1-11 [ISSN 0040-7496]. Published 15 November 1995.

Sciophila bilobata sp. n., *S. fistulata* sp. n. and *S. suthepensis* sp. n. are described and male genitalia are illustrated; for *S. suthepensis* also the female. These species are the first three confirmed species of *Sciophila* from the Oriental region. It is pointed out that the only species previously recorded from this region, *S. bicolor* Brunetti, 1912, should be considered a nomen dubium. Some tentative remarks are made about the systematical position of the new species.

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Key words. – Diptera, Mycetophilidae, Sciophila, new species, Thailand.

During an expedition arranged by the Museum of Zoology, University of Bergen, to the montane evergreen forests in Northern Thailand in April 1991, more than 1000 specimens of Mycetophilidae (s. str.) were collected. Among others the material held five specimens belonging to the genus *Sciophila* Meigen, 1818, representing three species, all of which proved to be undescribed.

Species of the genus *Sciophila* can be identified in having their wing membrane densely clothed by large, decumbent trichia, a very short median fork, and a cubital fork branching out very close to the wing margin. A small, closed cell is present between Rs and R_{2+3}. These two veins may, however, occasionally fuse.

Altogether 113 species belonging to this genus are recognized, of which 48 are Nearctic, 34 Palaearctic (including 2 species from the Canary Island and 5 species from Nepal), 8 Holarctic, 2 Afrotropical, 1 Oriental and 20 Neotropical. The number of Neotropical species is, however, uncertain as more than half of the species may belong to other genera (Papavero 1978). One Australasian species, *Austrosciophila solitaria* (Tonnoir, 1929) from Tasmania, was originally described as a subgenus of *Sciophila*, but the subgenus has later been raised to generic rank (Matile 1989).

The single Oriental species, *S. bicolor* Brunetti, 1912, is described from Darjiling, India (Brunetti 1912) based on 4 females. The species is not commented on by Edwards (1924) in his review of Brunetti's types of Mycetophilidae. Neither, has it been possible to trace the type specimens, and they are probably lost. Consequently, *S. bicolor* should be regarded a nomen dubium.

The world fauna of *Sciophila* has not been revised, but the Holarctic species, which constitute the greater part of the genus, are treated by Zaitzev (1982).

METHODS AND TERMINOLOGY

All specimens were cleared and slide mounted in Canada balsam.

The general terminology follows Vockeroth (1981) and McAlpine (1981), except for the clypeus and the female genitalia. Clypeus is here regarded as being secondarily divided in Mycetophilidae, consisting of an upper postclypeus and a lower anteclypeus (see also Matile 1990). The interpretation of the female genitalia is mainly in accordance with Sæther (1977), and will be further dealt with in a forthcoming paper.

Cubital ratios are given as the length of CuA_1 and CuA_2, respectively, to the length of CuA-petiole. Two ratios are given for the fore, mid and hind leg each: the length of femur to tibia, and the length of tibia to first tarsomere. The lengths of the tibial spurs are given in relation to the tibial diameter, measured apically.

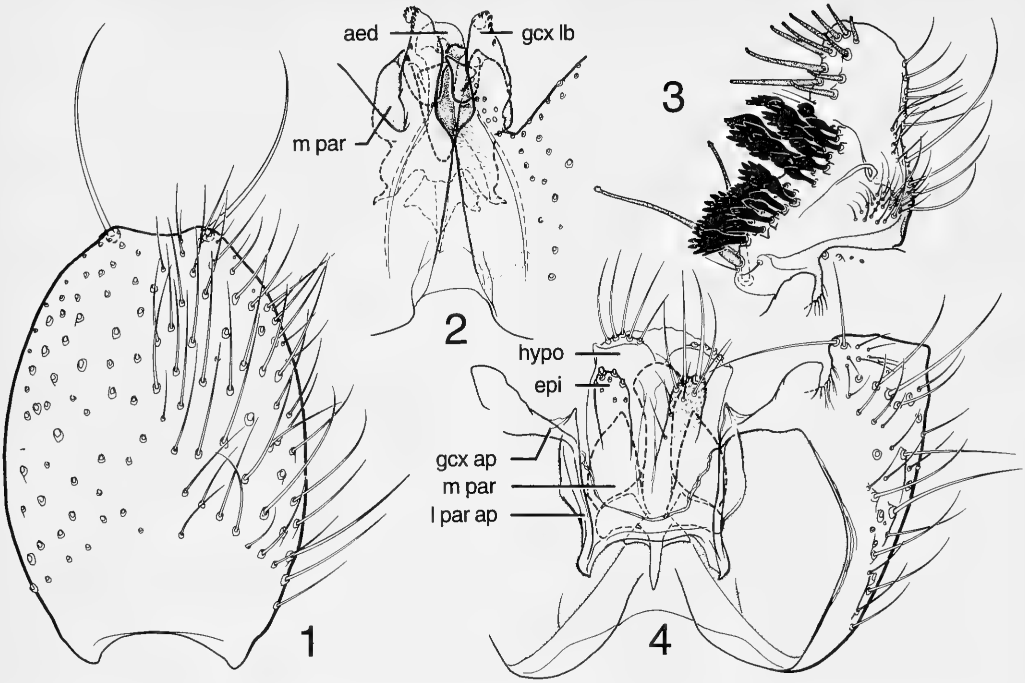
Sciophila bilobata **sp. n.**

(figs. 1 - 4)

Type material. – Holotype ♂: Thailand, Chiang Mai region, Doi Suthep, 9.-15.04.1991, G. Söli (Malaise trap) (ZMBN No. 224).

Diagnostic characters. – Metakatepisternum setose; male gonocoxites with two well developed medioventral lobes.

Etymology. – From Latin, *bi-*, two, and *lobate*, with lobes, referring to the two medioventral lobes of the male gonocoxites.



Figs. 1-4. Male terminalia of *Sciophila bilobata* sp. n. – 1, tergite 9, dorsal view; 2, median lobes of gonocoxite, ventral view; 3, gonostylus, dorsal view; 4, gonocoxite and proctiger, dorsal view.
Abbreviations: aed, aedeagus; epi, epiproct; hypo, hypoproct; gcx ap, gonocoxal apodemes; gcx lb, gonocoxal lobe; l par ap, lateral parameral apodeme; m par, median paramere.

Description

Male (n=1). – Total length about 3.8 mm. Flagellum 1.19 mm, or 1.4 times as long as scutum and scutellum together.

Coloration. Head, incl. antennae and mouthparts, light brown. Thorax, legs and abdomen yellowish.

Head. Lateral ocelli about twice as large as median, and separated from the eye margin for a distance of about 1.5 times their diameter. Frons with 29 setae in front of ocelli. Frontal suture nearly complete, not reaching median ocellus. Frontal tubercle broad, bilobate. Stipes with 6-9 setae. Fused face-postclypeus with 10 setae. Anteclypeus ovate, about 1.3 times as long as broad, with 56 setae. Relative lengths of the palpomeres: 1 : 1.2 : 1.3 : 2.7 : 7.5. Sensory pit on third palpomere shallow. Lacinia tapered, about 1.2 times as long as first palpomere, with a few small trichia.

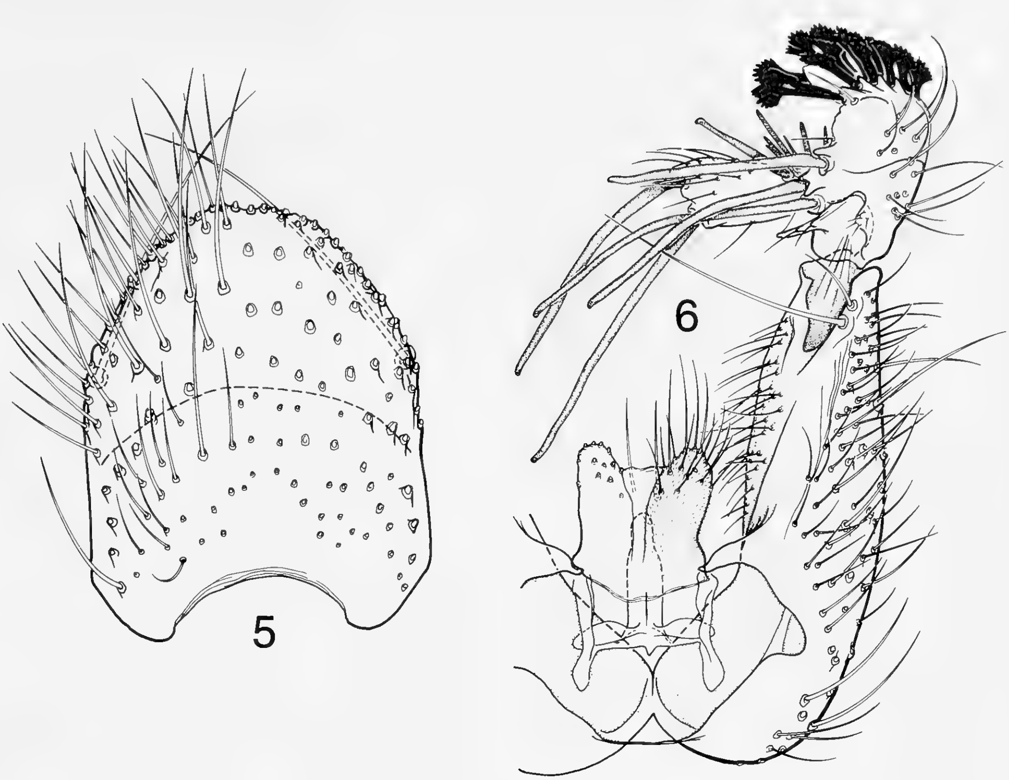
Thorax. Anepisternum with 12-14 setae situated anterodorsally. Katepisternum bare. Laterotergite with 8-9 setae. Mediotergite with 4-5 lateral and 5 posterior setae. Metakatepisternum with 11 setae.

Wings. Wing length 2.39 mm. Length to width 2.3. Sc 0.41 times as long as wing. Sc-r located in front of Rs. M-petiole about as long as r-m. M-basis 0.56 times as long as CuA-petiole. CuA-ratios: 0.71 and 0.51. Anal vein well developed, 1.15 times as long as CuA-petiole.

Legs. Apical triangular, depressed area on fore tibia with two distinct rows of setae. Ratio femur to tibia: 0.97; 0.96; 0.85. Ratio tibia to tarsus: 1.17; 1.50; 1.98. Spur lengths: 2.6; 2.6, 3.5; 2.3, 3.3.

Abdomen. Sternite 8 about 0.7 times as long as sternite 7, and 5.0 times as long as tergite 8.

Terminalia (figs. 1-4). Gonocoxites short, fused medioventrally for about half of their length; fusion weakly sclerotized. Two distinct, notched lobes are formed where the two gonocoxites meet medioventrally. Apical half of each lobe with several small, blunt setae. Gonocoxite with a rounded, flat outgrowth above the gonocoxal apodeme. Gonostylus with numerous dark, rather short-stalked furcated megasetae. Apicomedial part of gonostylus with numerous straight, thick setae. Two pairs of parameres present, the lateral pair less developed than the median. Lateral parameres short, not protruding beyond the gonocoxal apodemes; the medians partly fused with the basal portion of aedeagus, each broad with a conspicuous bend apically. Aedeagus with a club-



Figs. 5-6. Male terminalia of *Sciophila fistulata* sp. n. – 5, tergite 9, dorsal view; 6, gonocoxite, gonostylus and proctiger, dorsal view.

shaped head, and well developed aedeagal apodemes. Tergite 9 about 1.4 times as long as broad. Two long setae situated posterodorsally. Proctiger situated above the parameres and aedeagus, distinctly connected to the gonocoxal apodemes. Hypoproct protruding beyond the epiproct, apically bilobed with numerous setae.

Sciophila fistulata sp. n.
(figs. 5, 6)

Type material. – Holotype ♂: Thailand, Chiang Mai region, Doi Suthep, 9.-15.04.1991, G. Söli (Malaise trap) (ZMBN No. 223).

Diagnostic characters. – Male gonostylus with a well developed, elongated ventral lobe, and equipped with several long, pipe-like megasetae.

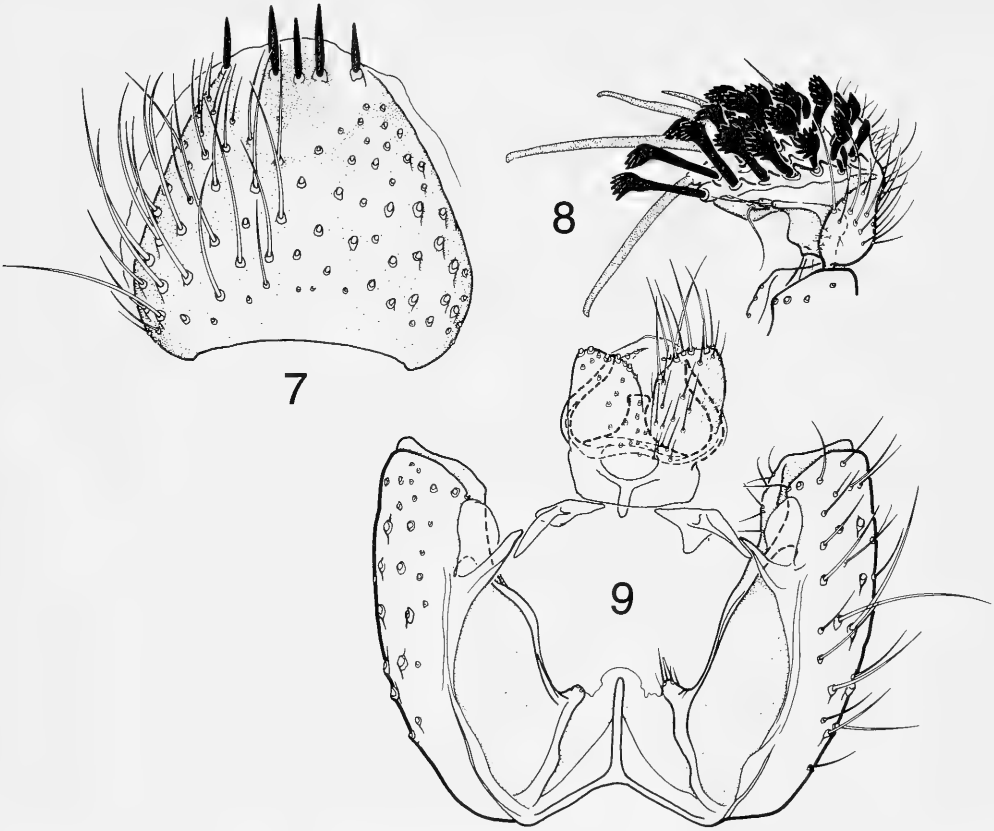
Etymology. – From Latin, *fistulatus,* with pipes, referring to the well developed pipe-like megasetae on the male gonostylus.

Description

Male (n=1). – Total length about 3.5 mm. Flagellum 1.36 mm, or 1.8 times as long as scutum and scutellum together.

Coloration. Head, including antennae and mouthparts, light brown. Thorax light brown. Coxae yellowish, hind coxa brownish apically. Abdomen light brown, somewhat lighter laterally.

Head. Median ocellus slightly smaller than laterals. Lateral ocelli separated from the eye margin for a distance of about 2.5 times their diameter. Frons with 14 setae in front of ocelli. Frontal suture short, produced halfway along the distance from frontal tubercle towards median ocellus. Frontal tubercle broad, bilobate. Stipes with 7 setae. Fused face-postclypeus 1.4 times as long as broad, with 12 setae. Anteclypeus ovate, about 1.2 times as long as broad, with 28 setae. Relative lengths of the palpomeres: 1 : 1.2 : 1.6 : 3.1 : 6.4. Sensory pit on third palpomere shallow. Lacinia tapered, about as long as first palpomere, with a few small trichia.



Figs. 7-9. Male terminalia of *Sciophila suthepensis* sp. n. – 7, tergite 9, dorsal view; 8, gonostylus, dorsal view; 9, gonocoxite and proctiger, dorsal view.

Thorax. Anepisternum with 15 setae situated anterodorsally. Katepisternum bare. Laterotergite with 7 setae. Mediotergite with 4 lateral and 4 posterior setae. Metakatepisternum bare.

Wings. Wing length 2.43 mm. Length to width 3.0. Sc 0.39 times as long as wing. Sc-r located in front of Rs. M-petiole about as long as r-m. M-basis 0.54 times as long as CuA-petiole. CuA-ratios: 0.63 and 0.44. Anal vein well developed, 1.20 times as long as CuA-petiole.

Legs. Apical triangular, depressed area on fore tibia with one distinct row of setae, and no setae above these. Ratio femur to tibia: 0.93; 0.88; 0.85. Ratio tibia to tarsus: 1.11; 1.43; 1.71. Spur lengths: 2.2; 2.4, 3.5; 2.4, 3.3.

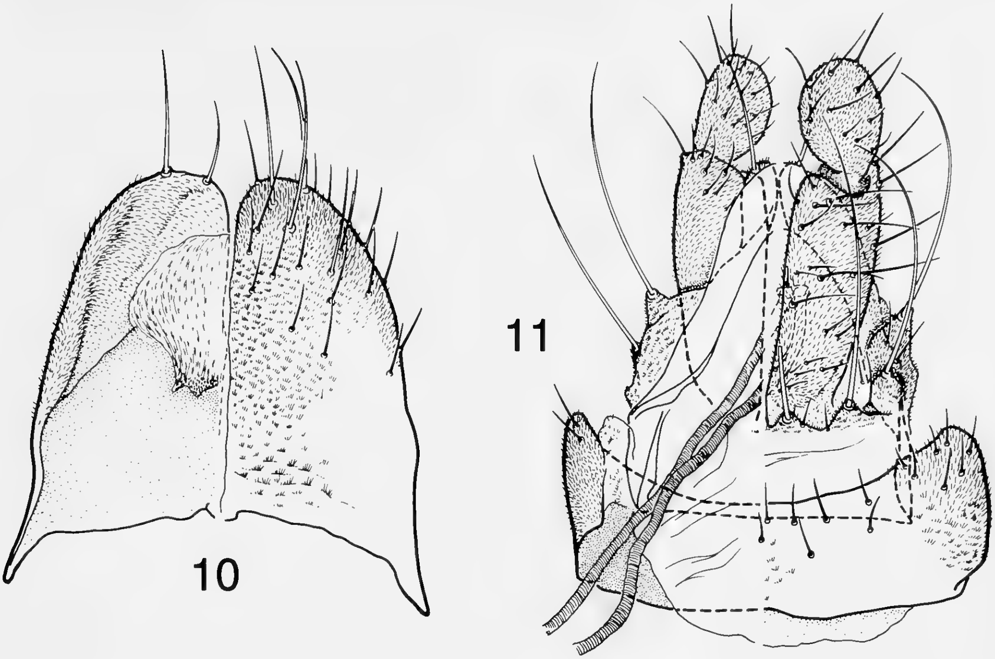
Abdomen. Sternite 8 about as long as sternite 7, and 2.3 times as long as tergite 8.

Terminalia (figs. 5, 6). Gonocoxites narrow and elongated, fused medioventrally for a very short distance only. Gonostylus with a distinct, elongated ventral lobe. Three long and thick tube-like megasetae situated dorsally, and two more on the apicoventral surface of the ventral lobe. Apical portion of gonostylus with numerous dark, rather long-stalked furcated megasetae. One pair of lateral parameres only, very short, not protruding beyond the gonocoxal apodemes; parameral apodemes well developed. Aedeagus short, aedeagal apodemes apparently forming a transverse bridge between the two parameral apodemes. Tergite 9 about 1.3 times as long as broad. Two very long setae situated lateroventrally. Proctiger situated above the parameres and aedeagus, distinctly connected to the gonocoxal apodemes. Hypoproct weakly sclerotized, with 2 posterior setae.

Sciophila suthepensis **sp. n.**

(figs. 7 - 11)

Type material. – Holotype ♂: Thailand, Chiang Mai region, Doi Suthep, 9-15.04.1991, G. Söli (Malaise trap)



Figs. 10-11. Female terminalia of *Sciophila suthepensis* sp. n. – 10, sternite 8, left: dorsal view, rigth: ventral view; 11, tergite 8 and proctiger, left: ventral view, rigth: dorsal view.

(ZMBN No. 225). Allotype ♀: Thailand, Chiang Mai region, Doi Suthep, 15.04.1991, J. Kjærandsen (ZMBN). Paratype: ♂, as for allotype (ZMBN).

Diagnostic characters. – Third palpomere with a distinct sensory pit; lateral ocelli widely separated from eye margin. Males with 4-5 black spine-like setae attached to the posterodorsal portion of tergite 9.

Etymology. – Named after the type locality, the mountain Doi Suthep.

Description

Male (n=2). – Total length 2.6-3.2 mm. Flagellum 1.22-1.28 mm, or 1.5 times as long as scutum and scutellum together.

Coloration. Head and antennae brown, mouthparts light brown. Thorax and abdomen brown. Legs yellowish to light brown.

Head. Median ocellus slightly smaller than laterals. Lateral ocelli separated from the eye margin for a distance about 4 times their diameter. Frons with 25-34 setae in front of ocelli. Frontal suture complete. Frontal tubercle broad, bilobate. Stipes with 7-10 setae. Fused face-postclypeus 0.9-1.0 times as long as broad, with 18-23 setae. Anteclypeus ovate, about 0.9 times as long as broad, with 31-42 setae. Relative lengths of the palpomeres: 1 : 1.0 : 1.3-1.5 : 2.3-2.8 : 5.1-5.3. Sensory pit on third palpomeres distinct and deep. Lacinia tapered, about as long as first palpomere, with a few small trichia.

Thorax. Anepisternum with 8-9 setae situated anterodorsally. Katepisternum bare. Laterotergite with 6-7 setae. Mediotergite with 6-7 lateral and 2-4 posterior setae. Metakatepisternum bare.

Wings. Wing length 2.07-2.25 mm. Length to width 2.3. Sc 0.35-0.38 times as long as wing. Sc-r located in front of Rs. M-petiole slightly shorter than r-m. M-basis 0.53-0.55 times as long as CuA-petiole. CuA-ratios: 0.71-0.76 and 0.54-0.56. Anal vein well developed, 1.09-1.15 times as long as CuA-petiole.

Legs. Apical triangular, depressed area on fore tibia with one distinct row of setae, and 4-6 weak, thin setae above these. Ratio femur to tibia: 0.91-0.97; 0.93-0.97; 0.87-0.88. Ratio tibia to tarsus: 1.18-1.21; 1.58-1.59; 2.02-2.12. Spur lengths: 2.4-2.5; 2.8, 3.3-3.5; 2.4-2.6, 3.4-3.6.

Abdomen. Sternite 8 about 0.6 times as long as sternite 7, and 4.0 times as long as tergite 8.

Terminalia (figs. 7-9). Gonocoxites rather narrow, separated by a weakly sclerotized area medioventrally. Each gonocoxite with a small setose knob ventrobasally, and a thin, rounded rim above the gonocoxal apodeme. Gonostylus with numerous dark furcated megasetae, and some longer tube-like setae ventrally. Two pairs of parameres present, the lateral pair less developed than the median. Median parameres partly fused with the basal portion of aedeagus, each thin and curved. Aedeagus small, not protruding beyond the median pair of parameres. Tergite 9 about as long as broad. 4-5 bristle-like setae present posterodorsally. Proctiger situated above the parameres and aedeagus. Hypoproct weakly sclerotized, with 8-9 setae posteriorly.

Female (n=1). – Total length 3.2 mm. Flagellum 0.89 mm, or about as long as scutum and scutellum together.

Coloration. As for males.

Head. Position of ocelli as in males. Frons with 29 setae in front of ocelli. Stipes with 10-12 setae. Fused face-postclypeus 0.9 times as long as broad, with 20 setae. Anteclypeus 0.9 times as long as broad, with 35 setae. Relative lengths of the palpomeres: 1 : 1.0 : 1.3 : 2.7 : 5.7.

Thorax. Anepisternum with 12 setae situated anterodorsally. Laterotergite with 6-7 setae. Mediotergite with 5-7 lateral and 3 posterior setae. Katepisternum and metakatepisternum bare.

Wings. Wing length 2.29 mm. Length to width 2.33. Sc 0.38 times as long as wing. Sc-r located slightly in front of Rs. M-petiole about as long as r-m. M-basis 0.60 times as long as CuA-petiole. CuA-ratios 0.83 and 0.68. A well developed, 1.00 times as long as CuA-petiole.

Legs. Apical triangular, depressed area on fore tibia with one row of setae, and no setae above these. Ratio femur to tibia: 0.95; 0.96; 0.88. Ratio tibia to tarsus: 1.16; 1.67; 2.06. Spur lengths: 2.3; 2.6, 3.4; 2.7, 3.6.

Terminalia (figs. 10, 11). Sternite 8 bearing two large and broad posterior lobes (gonocoxites 8) with numerous setae. A pair of well developed labia is present above and in between these lobes. Tergite 8 with some minute setae along posterior margin. Eight strong protuberances posterior of tergite 8, each with a very long, curved seta. The spermathecal ducts end separately in the gonopore. Epiproct reduced; hypoproct more or less triangular. A thin plate, sternite 10, is situated ventrally of the hypoproct. Cercus I elongated and separated to base; cercus II small, rounded.

DISCUSSION

As there have been no attempts to outline the phylogeny of the genus, it is difficult to comment on the systematic position of the three new species. Among the new species *S. fistulata* is similar to *S. nepalensis* Zaitzev, 1982, from Nepal, in having a well developed ventral lobe of the gonostylus. Furthermore, both species have strongly reduced parameres. The presence of distinctly serrated setae along the posterior border of tergite 9 is a common feature of Holarctic species, present also in the three Nepalese species *S. admiranda* Zaitzev, 1982, *S. kashmirensis* Zaitzev, 1982 and *S. propria* Zaitzev, 1982, but absent in the species here described.

Among the 3 new species, *S. bilobata* and *S. suthepensis* seem to be most closely related because of the presence of two pairs of parameres, a ventral protrusion where the two gonocoxites meet ventrally, and a rounded outgrowth close to the gonocoxal apodemes.

Judging from to the present material, collected by use of sweep net and one Malaise trap operated for less than one week at one locality, specimens belonging to *Sciophila* do not appear particularly rare in the area. Lack of previous records of this genus from the Oriental region is thus probably best explained by the limited number of studies dealing with fungus gnats in this region.

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REFERENCES

Brunetti, E. 1912. The Fauna of British India. Diptera Nematocera (excluding Chironomidae and Culicidae). – Reprinted (without year), Today & Tomorrow's Printers & Publishers, New Delhi, 582 pp +12 plates.

Edwards, F. W. 1924. Notes on the types of Diptera (Mycetophilidae and Tipulidae) described by Mr. E. Brunetti. – Records of the Indian Museum 26: 291-307.

Matile, L. 1989. Family Mycetophilidae. Pp. 135-145 in Evenhuis, N. L. (Ed.) Catalog of the Diptera of the Australasian and Oceanic Regions. – Bishop Museum Press and E. J. Brill. 1155 pp.

Matile, L. 1990. Recherches sur la systématique et l'évolution des Keroplatidae (Diptera, Mycetophiloidea). – Mémoires du Muséum national d'Histoire Naturelle (Zoologie) 148: 1-682.

McAlpine, J. F. 1981. Morphology and terminology - adults. Pp. 9-63 in McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R. & Wood, D. M. (Eds.) Manual of Nearctic Diptera. Vol.1. – Research Branch Agriculture Canada. Monogr. 27. Ottawa, Ontario.

Papavero, N. 1978. Family Mycetophilidae. – A catalogue of the Diptera of the Americas south of the United States. 19E: 1-78. Museu de Zoologia, Universidade de São Paolo.

Sæther, O. A. 1977. Female genitalia in Chironomidae and Other Nematocera: morphology, phylogenies, keys. – Bulletin of the Fisheries Research Board of Canda 197: 1-210.

Tonnoir, A. L. 1929. Australian Mycetophilidae. –

Proceedings of the Linnean Society of New South Wales 54: 584-614.

Vockeroth, J. R. 1981. Mycetophilidae Pp. 223-247 in McAlpine, J. F., Peterson, B. V., Shewell, G. E., Teskey, H. J., Vockeroth, J. R. & Wood, D. M. (Eds.) Manual of Nearctic Diptera. Vol.1. – Research Branch Agriculture Canada. Monograph 27. Ottawa, Ontario.

Zaitzev, A. I. 1982. Fungus gnats of the genus Sciophila Meig. of the Holarctic. – Akademia Nauk USSR. Moscow. 76 pp. (In Russian.)

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BOOK ANNOUNCEMENTS AND REVIEWS

M. Olmi, 1994. The Dryinidae and Embolemidae (Hymenoptera: Chrysidoidea) of Fennoscandia and Denmark. – Fauna Entomologica Scandinavica, 30: 1-100, 38 colour plates, 60 text-figs. E.J. Brill, Leiden etc. [ISBN 90-04-10224-8]. Price Nlg. 70.– (US $ 40).

The 30th volume of this well known series on North-European insects deals with two families of primitive Hymenoptera Aculeata: 1 species of Embolemidae and 34 species in Dryinidae. These are curious small wasps of 1-5 mm, with remarkable chelate fore tarsi in the females of many Dryinid species: with these they can grasp the hosts: nymphs or adults of cicadas or leafhoppers (Auchenorrhyncha). The dryinid larvae develop in or on these hosts.

The introduction deals with morphology, bionomics, classification and evolution. The main part of the book is devoted to keys and descriptions of the species, following the normal lay-out of volumes in this series. Text figures (by the author and Nicolò Falchi) show mainly male genitalia and female chelae (tarsus), plus some habitus figures. The colour plates include a few photos of parasitized leafhoppers and beautiful water colours (by Monica Cirillo and Luca Palermo) of many species. The book concludes with a systematic list of hosts and a distribution catalogue.

[E. J. van Nieukerken]

V. I. Tobias, S. A. Belokobylskii & A. G. Kotenko, 1995. Keys to the insects of the European part of the USSR. Volume III – Hymenoptera. Braconidae: Part IV.[translated from Russian]. Science Publishers, Inc., Lebanon, New Hampshire, USA. [ISBN 1-886106-23-1]. Price US$ 147.50. Ditsributed in Europe by Universal Book Services, PO Box 321, NL-2300 AH Leiden, fax +31-71-5171856.

This part provides keys for 20 subfamilies of braconids, covering 1700 species belonging to 165 genera; 123 species have been described for the first time. Besides species reported for the European part of the former USSR, the *keys* . . . includes species known from Western Europe, Kazakhstan, Central Asia and the Caucasus. For all the species, information is provided on their geographic distribution and (if available) synonymy. The introduction briefly outlines the morphology, biology, general features of geographic distribution and economic significance of braconids.

This book is the first compendium since the last century on the Palaearctic braconids and may be used for their identification throughout the former USSR and as a reference book.

[from information provided by the publisher]

Zdeněk Laštůvka & Aleš Laštůvka, 1995. An illustrated key to European Sesiidae (Lepidoptera). – Faculty of Agronomy MUAF, Brno, 174. pp., 8 colour plates, 105 text-figs and maps. [ISBN 80-7157-151-2]. Price DM 34.–, postage DM 6.–. To be ordered from Dep. of Zoology and Apiculture, Fac. of Agronomy MUAF, Zemědělská 1, CZ-61300 Brno, Czech Republic.

This booklet provides a key to European genera and species of clearwing moths, 105 in all. For each species a diagnosis of externals and genitalia is given, plus notes on bionomics (hostplants, fenology), habitat, and distribution. The male and female genitalia are illustrated as line drawings, the distribution is given as black area on a small map of Europe. The colour plates depict adults of all species in natural size. The hostplants are also listed in alphabetic order of families and species, together with the sesiid species. The keys are based on external characters.

The book provides the first comprehensive treatment of the European Sesiidae since the beginning of the century. It is nicely printed, the black and white illustrations are satisfactorily, the colour plates are reasonibly well printed, although the moths are sometimes rather small in natural size.

A very useful and cheap booklet.

[E. J. van Nieukerken]

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ZWEI NEUE ARTEN DER GATTUNG *HELOTREPHES* STÅL AUS CHINA (HETEROPTERA: HELOTREPHIDAE)

Zettel, H., 1995. Two new species of the genus *Helotrephes* Stål from China. – Tijdschrift voor Entomologie 138: 291-295, figs. 1-15 [ISSN 0040-7496]. Published 15 November 1995.
Helotrephes jendeki sp. n. is described from Jianxi and *H. sausai* sp. n. from Yunnan. A key to the *Helotrephes* species is provided for the Chinese mainland.
Dr. H. Zettel, Naturhistorisches Museum, 2. Zoologische Abteilung, Burgring 7, A-1014 Vienna, Austria.
Key words. – Helotrephidae, *Helotrephes*, new species, key, China

Die Gattung *Helotrephes* Stål, 1860, wurde nach einer Art, *Helotrephes semiglobosus* Stål, 1860, aus 'China (Wampoa)' (heute Guangdong) beschrieben. Derzeit ist nur eine weitere Art, *H. formosanus* Esaki & Miyamoto, 1943, von Taiwan bekannt, welche mit *H. semiglobosus* sehr nahe verwandt ist (Polhemus 1990), und deren Unterschiede sehr gering sind: Beim ♂ von *H. formosanus* ist die Spitze des Aedaeagus feiner als bei *H. semiglobosus* und die querliegende Apikalplatte schmäler, die hakenförmige Spitze der rechten Paramere geringfügig stumpfer und die linke Paramere distal etwas stärker gebogen; beim ♀ ist das 7. Sternit distal etwas weniger stark abgesetzt; die dunkle Zeichnung am Kopf ist bei ♂ und ♀ kräftiger entwickelt (nach Untersuchung von Paratypen im BMNH; siehe auch Esaki & Miyamoto 1943: Abb. 6C, D, G). *Helotrephes lundbladi* China, 1935, ebenfalls aus China beschrieben ('Che Kiang Province, coast opposite Tygosan Island', heute Zhejiang), wurde von Polhemus (1990) als Synonym zu *H. semiglobosus* gestellt. Alle übrigen in der Gattung beschriebenen Arten wurden von China (1932, 1935) in die Gattungen *Esakiella* China, 1932, (afrikanische und madagassische Arten) und *Hydrotrephes* China, 1935, (orientalische Arten) überstellt. Polhemus (1990) beschreibt auch die Variabilität einiger Merkmale bei *H. semiglobosus.* Ob die Gattung *Hydrotrephes*, die sich durch das Fehlen eines Sternalkieles auf den Abdominalsterniten 4 - 6 von *Helotrephes* unterscheidet, tatsächlich als Schwestergruppe von *Helotrephes* aufzufassen ist oder in ihrem heutigen Umfang eine paraphyletische Gruppe bildet, kann erst nach einer Analyse der zahlreichen, meist noch unbeschriebenen *Hydrotrephes*-Arten entschieden werden.

Das derzeit bekannte Verbreitungsbild der Gattung *Helotrephes* beschränkt sich also auf China einschließlich Taiwan und das nördliche Vietnam (*H. semiglobosus*). Allerdings bemerkt Polhemus (1990: 54), daß ihm zwei noch unbeschriebene Arten der Gattung aus Thailand und Malaysia vorliegen. Jedenfalls dürfte die Gattung weder Vorderindien, noch die Sunda Inseln und die Philippinen erreicht haben.

Zwei bisher unbeschriebene chinesische *Helotrephes*-Arten liegen vor und werden in Folge beschrieben. Freilich ist noch eine größere Zahl unbeschriebener Arten aus China zu erwarten.

Abkürzungen wissenschaftlicher Sammlungen

BMNH = The Natural History Museum, London, England; CASS = Chinese Academy of Sciences, Shenyang, VR China; CNT = Coll. N. Nieser, Tiel, Niederlande; CJP = Coll. J.T. Polhemus, Englewood, Colorado, U.S.A.; CPC = Coll. P.P. Chen, Beijing, China; NMW = Naturhistorisches Museum in Wien, Österreich; UBCB = University of South Bohemia, Ceské Budejovice, Tschechien.

BESTIMMUNGSSCHLÜSSEL ZU DEN ARTEN DES CHINESISCHEN FESTLANDES

1. Prosternalkiel hinten tief ausgerandet, zweispitzig (Abb. 4); Körperlänge über 3,5 mm; Kopfzeichnung mit gelber Fläche in der Mittellinie des Frontoclypeus (Abb. 3); Genitalia des ♂ (Abb. 8): Aedaeagus mit langgestreckter apikaler Querplatte, rechte Paramere präapikal sehr breit, linke Paramere einfach zugespitzt ....*H. sausai* sp.n.

– Prosternalkiel hinten gerade oder ausgewölbt, recht- oder stumpfwinkelig (Abb. 5, 6); Körperlänge unter 2,9 mm; Kopfzeichnung anders

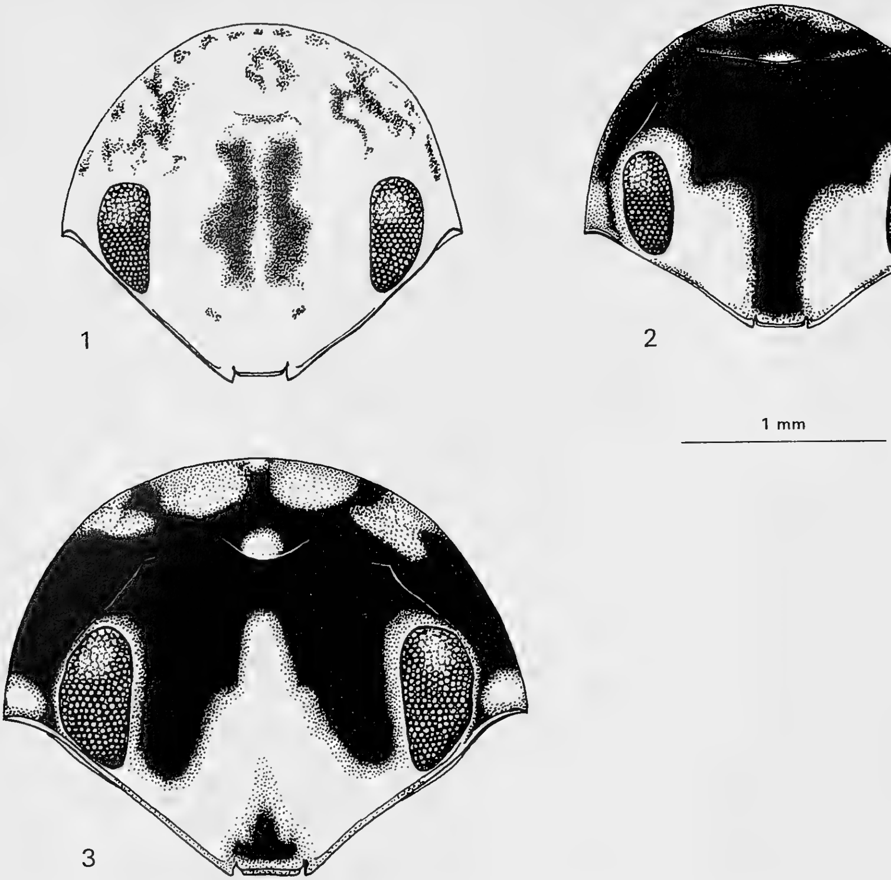


Abb. 1-3. – Frontalansicht der Cephalonota von (1) *H. semiglobosus* (helles Exemplar), (2) *H. jendeki* sp. n. und (3) *H. sausai* sp. n.

(Abb. 1, 2); Genitalia der ♂♂ (Abb. 7, 9): Aedaeagus ohne oder mit kurzer Querplatte, rechte Paramere präapikal schmal 2

2. Kiel am 3. Sternit apikal zugespitzt (Abb. 6), am 6. Sternit des ♀ zu einem Körnchen am Vorderrand reduziert; Kopfzeichnung mit zwei braunen Längsflecken in der Mitte des Frontoclypeus (Abb. 1); laterale Pronotalplatte tief eingebuchtet (Abb. 13); Genitalia des ♂ (Abb. 9): Aedaeagus mit einer breiten apikalen Querplatte, linke Paramere apikal gebogen, rechte Paramere lang und schlank; 7. Sternit des ♀ mit einen abgehobenen Mittelteil (Abb. 12) .... *H. semiglobosus*

– Kiel am 3. Sternit apikal ausgerandet (Abb. 5), am 6. Sternit des ♀ deutlich ausgebildet; Kopfzeichnung mit schwarzer Mittellinie am Frontoclypeus (Abb. 2); laterale Pronotalplatte leicht eingebuchtet (Abb. 14); Genitalia des ♂ (Abb. 7): Aedaeagus einfach zugespitzt, linke Paramere einfach abgerundet, rechte Paramere kürzer und breiter; 7. Sternit des ♀ einfach, gewölbt (Abb. 10) .... *H. jendeki* sp. n.

Beschreibung der Arten

Helotrephes sausai sp. n.
(Abb. 3, 4, 8, 11, 15)

Typenmaterial: Holotypus (♂, hinterflügelmakropter) und 1 Paratypus (♀, hinterflügelmikropter) [China. Yunnan 14.-21.6./ 100 km W Baoshan, 1993/ Gaoligongshan Nat. Res./ E. Jendek & O. Sausa leg.] (nmw).

Weiteres Material: 8 Larven vom gleichen Fundort (nmw, ubcb).

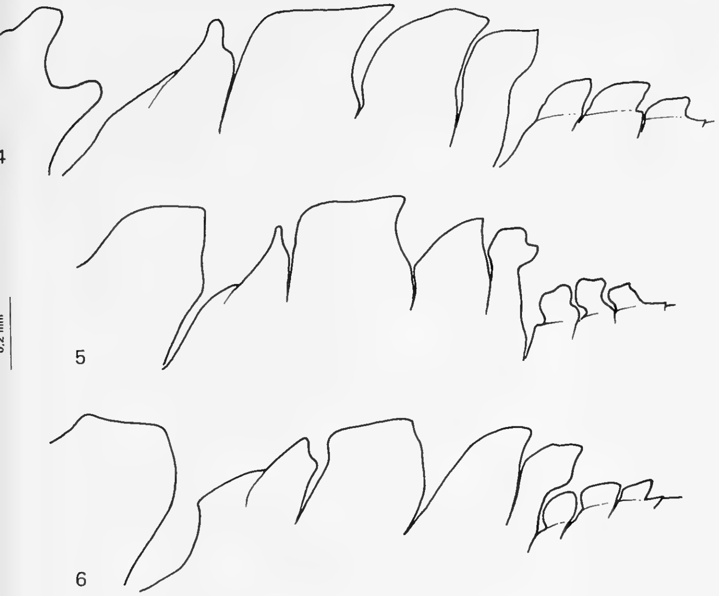


Abb. 4-6. – Ventralkiele der ♂♂ von (4) *H. sausai* sp. n., (5) *H. jendeki* sp. n. und (6) *H. semiglobosus* (Ansicht von rechts bei nach oben gerichteten Venter).

Beschreibung

Körperlänge 3,55 - 3,6 mm; größte Körperbreite über dem Pronotum 2,6 mm; schokoladebraun; Kopf vorne, um die Augen und entlang der Mittellinie gelb (Abb. 3); hinterer Bereich des Pronotum, Scutellum und Hemielytren mit feiner, gelber Sprenkelung; Pro-, Meso- und Metapleuren und alle Beine ab den Femora gelb.

Kopf fein punktiert, zwischen den Punkten mit feiner Mikropunktur, die am Vorderrand des Kopfes runzelig ist; daher ist der Kopf vorne matt; Pronotum fein punktiert, zwischen den Punkten glatt oder zart retikuliert, stark glänzend; Scutellum gröber und dichter punktiert und retikuliert; Hemielytren des ♂ wie bei allen hinterflügelmakropteren Helotrephiden mit Clavalsutur, wie das Scutellum skulptiert, aber die Punktur etwas gröber und die Retikulierung kräftiger, und daher matt; Skulptur insgesamt feiner und weniger dicht als bei *H. semiglobosus.*

Sternalkiel wie in Abb. 5, bei ♂ und ♀ bis zum 6. Sternit reichend; charakteristisch sind der tief ausgebuchtete Prosternalkiel und der besonders beim ♂ hinten scharf zugespitzte Metasternalkiel; laterale Prosternalplatte innen weniger tief eingebuchtet als bei *H. semiglobosus*; Propleuralplatte innen schwach abgestutzt (Abb. 15); Metafemora bei ♂ und ♀ in der distalen Hälfte schwach dorsad gebogen.

Genitalia des ♂ siehe Abb. 8: Aedaeagus in lateraler Ansicht präapikal stark verschmälert und apikal scharf zugespitzt, mit langgestreckter apikaler Querplatte; rechte Paramere präapikal sehr breit dann plötzlich verschmälert, viel kürzer als die linke Paramere; diese einfach zugespitzt.

Subgenitalplatte (7. Sternit) des ♀ sehr breit, hinter der niedergedrückten Basis hochgewölbt (Abb. 11).

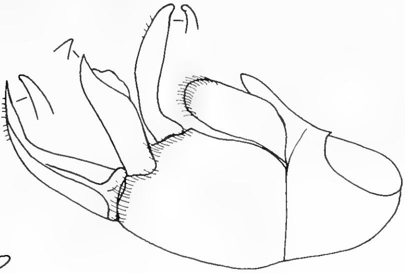
Larven (5. Stadium): Körperlänge 2,9 - 3,0 mm; dunkel schokoladebraun; Kopfränder, hintere Abdominalsegmente und Beine gelb; 'w-förmige' Cephalonotalsutur in der Mitte fast gerade, also kaum nach vor gezogen.

Helotrephes jendeki sp. n.
(Abb. 2, 5, 7, 10, 14)

Typenmaterial: Holotypus (♂, hinterflügelmikropter) und 42 Paratypen (♂♂ und ♀♀, hinterflügelmikropter) [CHINA: Jiangxi W/ Jinggang Shan/ Ciping env./ 2-14.VI.1994] (Holotypus in NMW, Paratypen in CASS, CJP, CNT, CPC, NMW, UBCB). [Zahlreiche Larvenstadien vom gleichen Fundort können dieser Art nicht eindeutig zugeordnet werden, da 1 Exemplar von *H. semiglobosus* zusammen mit *H. jendeki* sp.n. gefangen worden ist.]

Beschreibung

Körperlänge 2,4 - 2,55 mm; größte Körperbreite über dem Pronotum 1,8 - 1,95 mm; schwarzbraun; am Kopf die Augenränder und der vordere Bereich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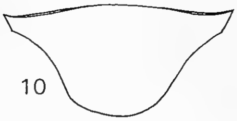
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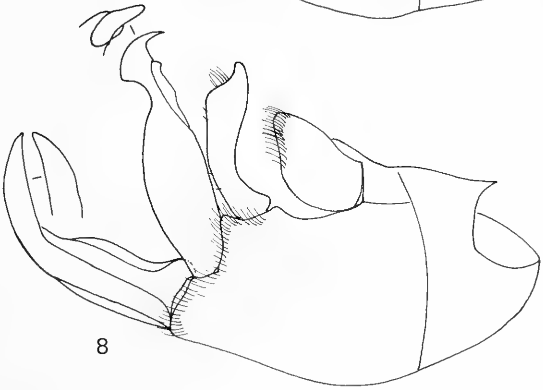
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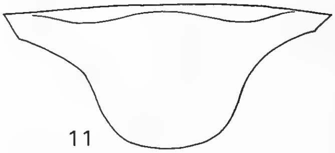
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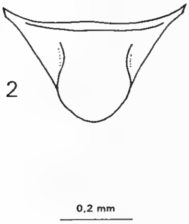
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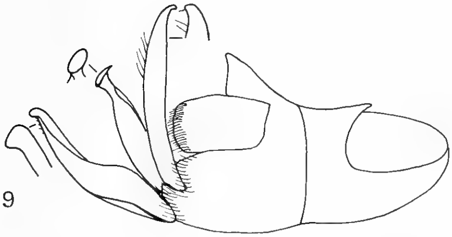
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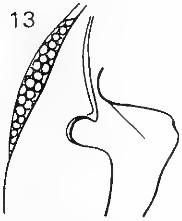
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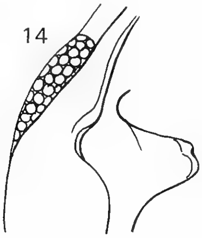
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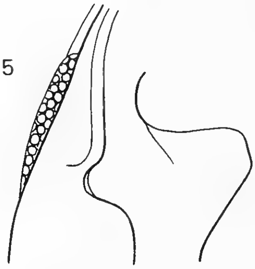
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Abb. 7-9. – Genitalia der ♂♂ von (7) *H. jendeki* sp. n., (8) *H. sausai* sp. n. und (9) *H. semiglobosus*; Details: Ansicht der Parameren vertikal auf die Seitenfläche der Spitze, Ansicht des Aedaeagus vertikal auf die Spitzenfläche.

Abb. 10-12. – 7. Sternite der ♀♀ von (10) *H. jendeki* sp. n., (11) *H. sausai* sp.n. und (12) *H. semiglobosus* (Hinterrand nach unten gerichtet).

Abb. 13-15. – Ventralansicht der rechten lateralen Pronotalplatten und Propleuralplatten bei (13) *H. semiglobosus*, (14) *H. jendeki* sp. n. und (15) *H. sausai* sp. n.

mit Ausnahme der immer dunklen Mittellinie gelb (Abb. 2); hintere Bereiche des Pronotum, Scutellum und Elytren mit unterschiedlich stark ausgeprägter, jedoch fast nie (und wenn, dann geringfügig) überwiegender, gelber Sprenkelung; (bei *H. semiglobosus* ist die Oberseite hingegen immer (bräunlich-)gelb, die braune Fleckenzeichnung nicht so dunkel und immer flächenmäßig deutlich geringer ausgebildet als die gelbe Grundfärbung;) laterale Pronotalplatte, Meso- und Metapleuren gelb; Beine ab den Femora gelb.

Kopf fein und spärlich punktiert, die feine Mikropunktur hinten in der Mitte reduziert; Pronotum vor allem in der Mitte sehr spärlich und fein punktiert, zwischen den Punkten glatt und stark glänzend; Scutellum zwischen den groben Punkten schwach retikuliert und glänzend; Hemielytren dichter retikuliert, matter als das Scutellum; Skulptur insgesamt feiner und spärlicher, die Oberseite daher glänzender als bei *H. semiglobosus*.

Sternalkiel wie in Abb. 5, bei ♂♂ und ♀♀ bis zum 6. Sternit ausgebildet; Pronotalkiel hinten rechtwinkelig; Kiel des 3. Sternit hinten mit einer Ausrandung, beim ♀ etwas stärker nach hinten gezogen als beim ♂; laterale Pronotalplatte seichter eingebuchtet als bei *H. semiglobosus*; Propleuralplatte innen schwach abgestutzt (Abb. 14); Metafemora bei ♂♂ und ♀♀ in der distalen Hälfte schwach dorsad gebogen.

Genitalia des ♂ siehe Abb. 7: Aedaeagus in lateraler Ansicht präapikal nicht verschmälert und apikal einfach zugespitzt, ohne apikale Querplatte; rechte Paramere gleichmäßig zur Spitze hin verschmälert, apikal schwach umgebogen, wenig kürzer als die linke Paramere; diese einfach, schmal zugespitzt.

Subgenitalplatte (7. Sternit) des ♀ einfach, gewölbt (Abb. 11).

Helotrephes semiglobosus Stål, 1860
(Abb. 1, 6, 9, 12, 13)

Helotrephes semiglobosus Stål, 1860 Eugenies Resa, Zool. I., Ins.: 268. – Polhemus 1990: 54.

Helotrephes lundbladi China, 1935 Ann. Mag. Nat. Hist, ser. 10, 15: 599 (synomymisiert durch Polhemus 1990).

Untersuchtes Typenmaterial: Holotypus (♂, hinterflügelmikropter) von *Helotrephes lundbladi*: [Type], [China/ 92-196.], [7785], [Helotrephes/ lundbladi/ China/ TYPE / det.W.E.China.1934] (BMNH).

Weiteres Material (alle Exemplare hinterflügelmikropter): 2 ♂, 1 ♀ [HONGKONG (7) 1992/ N.T.- Tai Po N.Res./ 27.VI. leg. Jäch] (NMW); 1 ♂ [CHINA: Guangxi, 10 km NE/ Liuzhou,2km E Shanmenjiang/ Forest Farm,150m,10.11./1993, leg. Schönmann (17)] (NMW); 1 ♀ [CHINA: Guangxi, Bez. Liuzhou/ Shanmenjiang Forest Farm/ 10 km NE Liuzhou/ 10.11.1993, 200 m / leg. H. Schillhammer (17)] (NMW); 1 ♂, 1 ♀ [CHINA: SE Guangxi, Yulin/ Liuwan Forest Farm / 350-400 m, 16.11./ 1993, leg. Schönmann (20)] (NMW); 1 ♀ [CHINA: SE Guangxi, Yulin/ Liuwan Forest Farm / 600-700 m, 17.11./ 1993, leg. Schillhammer (21)] (NMW); 1 ♂ [CHINA: SE Guangxi, Yulin/ Liuwan Forest Farm/ 500 m, 20.11./ 1993, leg. Schillhammer (26)] (NMW); 1 ♀ [CHINA: Jiangxi W / JINGGANG SHAN/ Ciping env./ 2.-14.VI.1994] (NMW).

Eine umfassende Beschreibung der Art findet man bei China (1935), und zwar die Beschreibung des ♀ als '*Helotrephes semiglobosus* Stål' und des ♂ als '*Helotrephes lundbladi* sp. n.'. Es wird deshalb auf eine neuerliche Beschreibung der Art hier verzichtet. Als Hilfe für die Unterscheidung von den neubeschriebenen Arten sei auf die Abbildungen verwiesen. Die Kopfzeichnung des *Helotrephes lundbladi* ähnelt in der Abbildung von China (1935: Fig. 3a) der des *H. jendeki* sp. n. Die Untersuchung des Holotypus konnte diese Abbildung jedoch nicht bestätigen: Die dunklen Makeln am Kopf sind nicht schwarz, kleiner und keineswegs so deutlich abgegrenzt, sondern fallen durchaus in die Variabilität des *H. semiglobosus*.

Bisher bekannte Verbreitung: CHINA: Zhejiang, Jiangxi, Guangdong, Hong Kong, Guangxi; VIETNAM: Tam Dao.

DANK

Meinen slowakischen Kollegen E. Jendek und O. Sausa (beide Bratislava) danke ich für das Insektenmaterial, das den Neubeschreibungen zugrunde liegt, Frau Dr. J. Margerison-Knight (BMNH) für die leihweise Zusendung der Typen von *Helotrephes lundbladi* und *H. formosanus*, Dr. M. Papacek (UBCB) und Dr. J.T. Polhemus (Englewood, Colorado) für kritische Anmerkungen zum Manuskript.

ZUSAMMENFASSUNG

Zwei bisher unbekannte Arten der Gattung *Helotrephes* werden aus China beschrieben: *Helotrephes jendeki* sp. n. aus Jiangxi und *H. sausai* sp.n. aus Yunnan. Ein Bestimmungsschlüssel zu den chinesischen Arten ist beigefügt.

LITERATUR

China, W. E., 1932. Notes on the African Helotrephidae (Hemiptera, Helotrephidae). – Entomologist 65: 270-273.

China, W. E., 1935. New and little-known Helotrephidae (Hemiptera, Helotrephidae). – Annals and Magazin of Natural History (10) 15: 593-614.

Esaki, T. & S. Miyamoto, 1943. A new species *Helotrephes* from Formosa (Hemiptera: Helotrephidae). – Transactions of the Natural History Society of Taiwan 33: 485-494.

Polhemus, J. T., 1990. A new tribe, a new genus and three new species of Helotrephidae (Heteroptera) from Southeast Asia, and a world checklist. – Acta Entomologica Bohemoslovaca 87: 45-63.

Stål, C., 1860. Hemiptera. Species novas descripsit. In: Kongliga svenska fregattens Eugenies resa omkring jorden under befäl af C.A. Virgin aren 1851 - 1853. 2 (Zoologi 1. Insekter). – Norstedt & Söner, Stockholm, pp. 219-298.

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EUSTIGMAEUS JOHNSTONI, NEW SPECIES (ACARI: STIGMAEIDAE), PARASITIC ON PHLEBOTOMINE SANDFLIES (DIPTERA: PSYCHODIDAE)

Zhang, Z.-Q., & U. Gerson, 1995. *Eustigmaeus johnstoni*, new species (Acari: Stigmaeidae), parasitic on phlebotomine sandflies (Diptera: Psychodidae). – Tijdschrift voor Entomologie 138: 297-301, fig. 1-6. [ISSN 0040-7469]. Published 15 November 1995.

Eustigmaeus johnstoni sp. n. (Acari: Stigmaeidae) is described from several species of phlebotomine sandflies (Diptera: Psychodidae) in tropical areas. Adult females of this species were found on *Phlebotomus papatasi* (Scopoli), *Sergentomyia magna* (Sinton) and *Sergentomyia dreyfussi* (Parrot) in Yemen, on *P. papatasi*, *Sergentomyia africana* Newstead and an undetermined species of *Sergentomyia* in Saudi Arabia, on *P. papatasi* in Cyprus, Israel, and Pakistan, and on *Phlebotomus longicuspis* Nitzulescu in Tunisia. Both males and females of sandfly hosts were parasitized. The new species is eyeless and is separated from other eyeless species of *Eustigmaeus* in an artificial key.

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Key words. – Asia, Africa, phlebotomine sandflies, ectoparasites, *Eustigmaeus johnstoni*, new species, Stigmaeidae

Mites of the genus *Eustigmaeus* Berlese, 1910 (= *Ledermuelleria* Oudemans, 1923) (Prostigmata: Stigmaeidae) comprise a group of globate, red acarines whose bodies are covered by ornamental armour. In females this dorsal armour is separated into propodosomal and hysterosomal plates, the latter being often subdivided in the males. Females carry 13 variously-shaped dorsal setae, of which three are often ventrally displaced: the humerals (c_2) laterally and the posteriormost h_1 and h_2 caudally. Most species have one pair of eyes, located between propodosomal setae *ve* and *sci*. The eyeless species include *E. lirella* (Summers & Price), *E. coronaria* (Kuznetzov), *E. parasitica* (Chaudhri), *E. gamma* (Chaudhri), *E. gorgasi* (Chaudhri) and the new species described in this paper.

The species *E. lirella* and *E. coronaria* were collected from `soil and screenings from the nest of woodrat' (Summers & Price 1961) and from the hollow of an ash tree (Kuznetzov 1977), respectively. The species *E. parasitica*, *E. gamma*, and *E. gorgasi* were found associated with phlebotomine sandflies (Diptera: Psychodidae) and were presumed ectoparasitic (Chaudhri 1965). This association was challenged by Gerson (1972) who argued that as some species of *Eustigmaeus* feed on mosses (bryophytes), a habitat wherein many sandflies rest, the mites' occurrence on the flies might be only a fortuitous phoretic association.

This argument is no longer tenable in view of the many additional sandfly-parasitizing specimens of *Eustigmaeus* which have since been collected (Abonnenc 1970, Lewis & Macfarlane 1982, Martinez-Ortega et al. 1983). The evidence presented in there patently shows that these *Eustigmaeus* mites actually feed on the flies, leaving feeding wounds or scars on hosts' bodies. Abonnenc (1970) has described a new sandfly-associated species, *Eustigmaeus dyemkoumai*, which does have eyes, and herein we describe a new species which is eyeless. Setal terminology follows Kethley (1990). All measurements are of the holotype female and are in micrometers.

TAXONOMY

Eustigmaeus johnstoni sp. n.
(Figs. 1-6)

Type material. – Holotype female (ZQZ941012-1a) and two paratype females (ZQZ941012-1, b &c), YEMEN: Zabid, ex. female *Sergentomyia magna* (Sinton), 10.xii.1970, B. Deringhi. Paratype female (ZQZ941012-2), YEMEN: Zabid, ex. male *Sergentomyia dreyfussi* (Parrot), 2.xii.1970, B. Deringhi. Paratype female (ZQZ941012-6), SAUDI ARABIA, ex. male of *Sergentomyia* sp., 2.iii.1979, W. Büttiker. Holotypes and paratypes are deposited in the Natural History Museum, London (BMNH). One paratype is in the collection of Uri Gerson, Department of Entomology, The Hebrew University of Jerusalem.

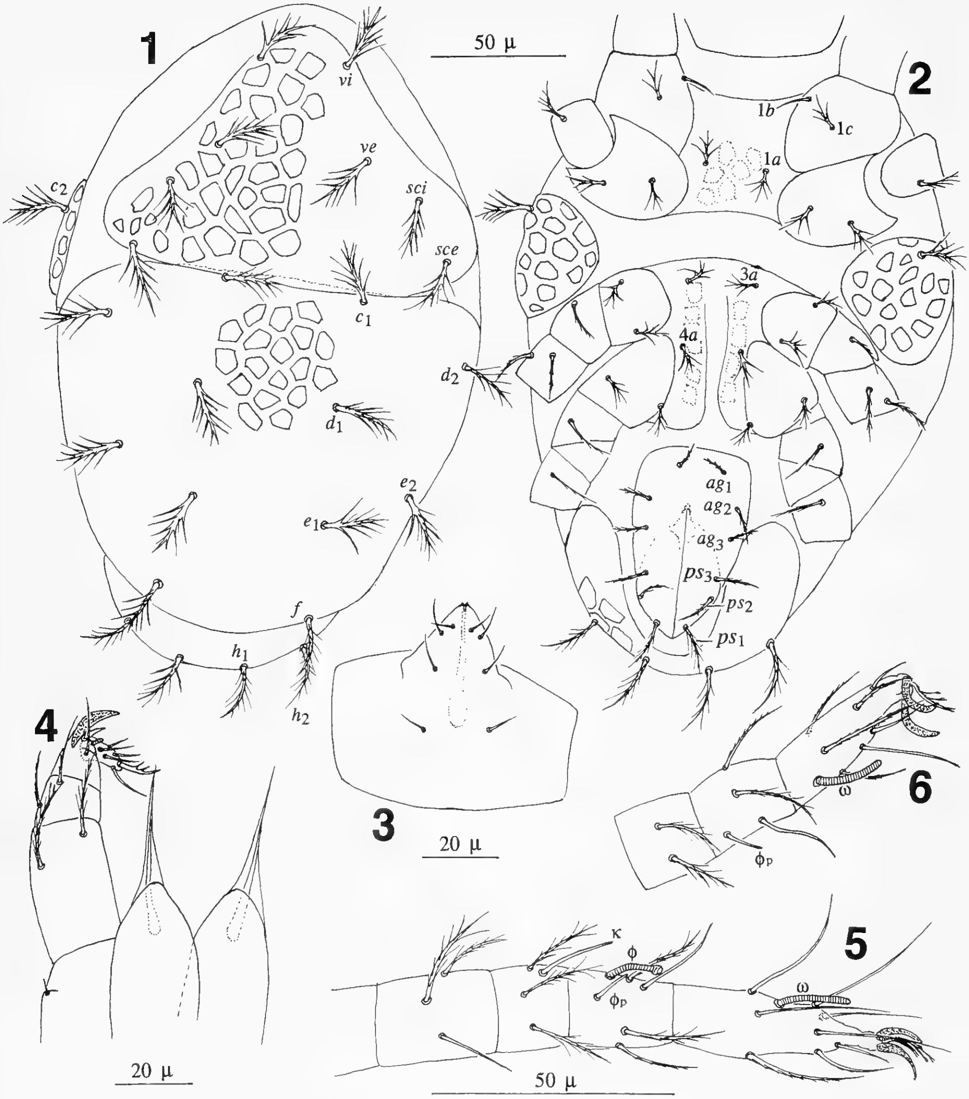

Fig. 1-6. *Eustigmaeus johnstoni* sp. n. (Holotype female). – 1, Idiosoma, dorsal view; 2, Idiosoma, ventral view; 3, Subcapitulum; 4, Palp and chelicera; 5, Leg I; 6, Leg II.

Other material. – Other examined specimens (all females) were excluded from the type series because of poor slide mount. SOUTH YEMEN: Hadramawt, ex. female *Phlebotomus papatasi* (Scopoli), D. M. Minter (ZQZ941012-4). CYPRUS: Larnaca, ex. male *P. papatasi*, 21.ix.1980, M. Jennings (ZQZ941012-3). SAUDI ARABIA, ex. *P. papatasi*,. W. Büttiker 10.x.1977,1978, 28.iii.1978, 2.vii.1976, 16.x.1978, 10.iii.1979 (ZQZ941012-5, 8, 9, 10, 11, 12), ex. female *Sergentomyia africana* Newstead, 10.iii.1979 (ZQZ941012-7). PAKISTAN: Janodola, ex. female *P. papatasi*, 18.viii.1923 (ZQZ941012-14); Lahore, ex. *P. papatasi*, 29.x.1923 (ZQZ941012-15); ex. *P. papatasi*, 4.xi.1923 (ZQZ941012-16). TUNISIA: Tunis, ex. *P. longicuspis* Nitzulescu, 19-26.vi.1969, P.D. Massa (ZQZ941012-17; CIE A4003). Additional female specimens from *P. papatasi* (collected by Y. Schlein in the summer of 1984 in Gilgal, Jordan Valley, Israel) were examined by U. Gerson.

Diagnosis. – Eyeless species of medium size. Dorsal setae subequal, each 15-35 long, with 10-15 long

Table 1. Measurements (in μ) of dorsal setae and setal distances in *Eustigmaeus johntoni* females from different areas.

	Yemen	Saudi Arabia	Cyprus	Tunis	Pakistan	mean ± se	n
vi	22- 32	19- 23	24	21	21	22.3 ± 1.0	14
ve	23- 28	19- 21	23	22	21	21.9 ± 0.8	15
sci	18- 23	15- 20	21	21	19	19.2 ± 0.7	13
sce	22- 28	19- 23	21	21	21-23	21.8 ± 0.9	14
c_1	22- 26	19- 23	21	23	21	21.5 ± 0.5	15
c_2	22- 28	19- 23	22	23	22-23	22.6 ± 0.6	14
d_1	19- 28	19- 21	21	23	21-22	21.3 ± 0.7	15
d_2	19- 26	17- 21	21	21	20-21	20.6 ± 0.6	14
e_1	22- 28	21- 23	23	21	20-21	22.4 ± 0.5	15
e_2	20- 23	19- 23	23	19	20-21	20.8 ± 0.5	14
f	24- 35	21- 25	28	24	23-24	25.5 ± 1.1	15
h_1	22- 32	20- 26	24	21	24	24.4 ± 1.0	13
h_2	23- 24	19- 23	21	19	21	21.5 ± 0.5	13
vi-vi	32- 34	23- 32	30	28	26-27	28.8 ± 1.0	13
ve-ve	54- 56	41- 49	47	47	42-50	47.8 ± 1.4	13
sci-sci	91- 95	80- 86	86	86	78-81	85.0 ± 1.5	13
sce-sce	112-120	100-114	109	103	105	107.0 ± 1.8	12
c_1-c_1	51- 60	41- 54	50	50	52-53	50.5 ± 1.3	13
d_1-d_1	40- 56	43- 52	54	53	47-52	49.8 ± 1.4	13
d_2-d_2	133-140	106-128	126	116	116	122.0 ± 3.0	12
e_1-e_1	44- 49	34- 45	43	42	40	42.1 ± 1.1	12
e_2-e_2	110-116	84- 111	100	92	90	99.5 ± 3.2	11
f-f	56- 59	48- 60	54	50	52-57	54.0 ± 1.0	12
h_1-h_1	24- 26	19- 25	23	22	17-21	22.0 ± 0.8	12
h_2-h_2	56- 71	49- 63	58	54	54	58.2 ± 1.8	11

branches. Intercoxal setae 1*a*, 3*a*, and 4*a* subequal, each 9-11 long and with 4-6 long branches. Coxal setae similar to intercoxal setae except for the nude 1*b*. Dorsal solenidion (ϕ) on tibia I with a characteristic bulbous tip.

Description

Female. – Idiosoma 240 long, 160 wide. Dorsal plates covered with prominent polygonal cells (Fig. 1). Propodosoma with ten polygonal cells arranged transversely between setae *sce* and eight or nine cells longitudinally. No eyes present between setae *ve* and *sci* on propodosoma. Hysterosoma with 12-13 transverse cells between setae d_2 and 12-14 cells longitudinally. Humeral plates large, with 12-14 polygonal cells and setae c_2. Dorsal idiosoma with 13 pairs of setae, each with 10-15 branches emerging along entire shaft and not clustered together. Measurements of setae: *vi* 22; *ve* 23; *sci* 18; *sce* 22; c_1 22; c_2 22; d_1 22; d_2 19; e_1 22; e_2 20; *f* 24; h_1 22; h_2 24. Distances between alveoli of setae: *vi-vi* 32; *ve-ve* 55; *sci-sci* 91; *sce-sce* 112; c_1-c_1 51; d_1-d_1 40; d_2-d_2 133; e_1-e_1 49; e_2-e_2 110; *f-f* 56; h_1-h_1 24; h_2-h_2 65. Variations of setal measurements for specimens from different areas are summarized in Table 1.

On ventral side of idiosoma, intercoxal plate with weak outlines of polygonal cells, continuous across mid-ventral line, separated beyond coxae II by transverse striae (Fig. 2). Intercoxal plate between coxae III and IV with similar weak outlines of polygonal cells, but divided by longitudinal striae between coxae III. Intercoxal setae 1*a*, 3*a*, and 4*a* subequal, each 9-11 long and with 4-6 branches. Coxal setae similar to intercoxal setae in structure except the nude 1*b*. Three pairs of aggenital setae present; ag_1 (9) slightly shorter than ag_2 and ag_3 (both 10-11). Anal valve with three pairs of *ps* setae; ps_1 longest (17), with longer barbs than ps_2 and ps_3.

Gnathosoma. Subcapitulum with two pairs of adoral setae distally and two pairs of subcapitular setae proximally (Fig. 3). These setae each very weakly branched. Palp 64 long from base of femur to tip of tibia (Fig. 4). Paplfemur with three setae, two dorsal, strongly barbed, and the third ventral, weakly branched. Palpgenu and palptibia each with two setae. Palptibial claw 13 long, almost reaching the end of palptarsus. Accessory claw 5 long. Palptarsus cylindrical, with seven setae, including subbasal solenidion and apical trifid sensillum (Fig. 4). Cheliceral base 49 long, 23 wide. Stylet 47 long.

Legs. Each tarsus terminating in a pair of strong claws and an empodium bearing three paired branches. Length of legs I, II, III and IV (from base of trochanter to tip of claw) 127, 106, 106, and 121, respectively. Number of ordinary setae and sensillae (in parentheses) on legs I-IV: coxae 2-2-2-2; trochantera 1-1-1-1; femora 6-5-3-2; genua 3(1)-3(1)-1-1; tibia 5(2)-5(1)-5(1)-5(1); tarsi 12(1)-8(1)-7(1)-7. Dorsal solenidion ϕ on leg I with a characteristic bulbous tip and *p* on leg I about half as long as normal setae on tibia I (Fig. 5). Numerous dorsal setae on podomeres strongly branched (Figs. 5, 6). Microseta κ on leg I nearly as long as other setae on genu I. Microseta κ on leg II normal, visible only in well preserved and positioned specimens.

Males and immatures not seen.

Etymology. – This species is named to commemorate our esteemed late colleague, the prominent acarologist Prof. Donald E. Johnston of the Ohio State University, Columbus, Ohio, USA.

Remarks. – This new species is a very widespread species, at least present in Yemen, Saudi Arabia, Israel, Cyprus, Tunis, and Pakistan. Within species variation in the lengths of and distances between dorsal seta are evident in specimens from different countries. This new species shows a striking resemblance to *E. dyemkoumai*, which is parasitic on *Phlebotomus duboscqi* Neveu-Lemaire in Upper-Volta and Mali (Abonnenc 1970). Both species have characteristic dorsal setae with long branches and their intercoxal setae (1a, 3a and 4a) carry similar structures (Figs. 1-2). *E. dyemkoumai* was only briefly described, but an examination of a type specimen revealed that *E. johnstoni* differs from *E. dyemkoumai* by its relatively larger size, by the absence of eyes, by the bulbous tip of ϕ on leg I, and by having more branches on the dorsal setae. Like *E. johnstoni*, five other species of *Eustigmaeus* have also lost their eyes. They can be separated by using the following key, which serves to emphasize the lack of other features common to these mites. Species found in association with phlebotomine sandflies are denoted by an asterisk.

Key to eyeless *Eustigmaeus*

1 Dorsal hysterosomal setae c_1 and d_1 short, not reaching the bases (alveoli) of any neighbouring setae 2
– Dorsal hysterosomal setae c_1 and d_1 long, overreaching the bases (alveoli) of at least two neighbouring setae 4
2 Distance between alveoli of dorsal setae pairs, c_1-c_1, d_1-d_1, and e_1-e_1, subequal 3
– Distance c_1-c_1 and d_1-d_1 subequal, both much less than e_1-e_1 (setae e_1 laterally displaced) ... .*gamma**
3 Dorsal setae flat, with short barbs on distal 3/4; all intercoxal setae (1*a*, 3*a*, and 4*a*) weakly barbed ....*lirella*
– Dorsal setae thin, with long branches throughout; intercoxal setae (1*a*, 3*a*, and 4*a*) with long branches .... *johnstoni* sp. n.*
4 Femur IV with two setae 5
– Femur IV with three setae .... *parasitica**
5 Dorsal setae c_1, d_1, and e_1 of uniform width, not flattened near the base; setae ps_1 to ps_3 subequal .... *gorgasi**
– Dorsal setae c_1, d_1, and e_1 flattened near their bases; length of seta ps_3 1.5 times that of ps_1 or ps_2 .... *coronaria*

The fact that four species of *Eustigmaeus* were found to parasitize phlebotomine sandflies indicates that this is not a fortuitous occurrence. This statement is supported by the presence of two additional undescribed species, one from *Phlebotomus cruciatus* Coquillett in Honduras and the other from *Phlebotomus longipes* Parrot & Martin in Ethiopia, in the collections of the Natural History Museum (they were not described in this paper because only a single specimen each was available). Although phlebotomine sandflies are also parasitized by other mites (Lewis & Macfarlane 1982), no species of *Eustigmaeus* have ever been found on other animal hosts. The nature of *Eustigmaeus*-sandfly association, however, remains obscure. No males or immatures of *Eustigmaeus* have been collected on phlebotomine sandflies, nor have any been found in alcohol-preserved museum specimens. This suggests that the phlebotomine-associated *Eustigmaeus* species develop and mate elsewhere, probably in the habitat where sandflies breed and rest; parasitism may thus be only one phase in the life history of these mites.

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We thank Mr. Donald Macfarlane for comparing the new species with *E. lirella* and for making the type of *E. dyemkoumai* available for study, Dr. Sabina of the Bishop Museum for reviewing the manuscript, and Prof. Y. Schlein, Hadassah Medical School of the Hebrew University of Jerusalem, Israel, for making mite specimens available to us. The use of facilities by Z.-Q. Zhang at The Natural History Museum, London, was made possible by the Keeper of Entomology, Dr. R. P. Lane.

REFERENCES

Abonnenc, E., 1970. Notes sur les Acariens parasites des Phlébotomes. – Cahiers L'office de la Recherche Scientifique et Technique Outer-Mer. Série Entomologie médicale et Parasitologie 8: 89-94.

Chaudhri, W.M., 1965. New mites of the genus *Ledermuelleria*. – Acarologia 7: 467-486.

Gerson, U., 1972. Mites of the genus *Ledermuelleria* (Prostigmata: Stigmaeidae) associated with mosses in Canada. Acarologia 13: 319-343

Kethley, J., 1990. Acarina: Prostigmata (Actinedida). – In: D. L. Dindal (ed), Soil Biology Guide, John Wiley, New York. pp. 667-756.

Kuznetzov, N. N., 1977. New species of the family Stigmaeidae from Crimea. – Zoologicheskii Zhurnal 56: 635-638 [in Russian].

Lewis, D. J., & D. Macfarlane, 1982. The mites of Phlebotomine sandflies (Diptera: Psychodidae). – In: E. U. Canning (ed), Society of Protozoologists Special Publication No. 1, Allen Press, Kansas. pp. 177-183.

Martinez-Ortega, E., C. E. Conesa-Gallego, D. Macfarlane, & R. D. Ward, 1983. Ectoparasitic mites on phlebotomine sandflies (Diptera: Psychodidae) from Spain. – Annals of Tropical Medicine and Parasitology 77: 545-546.

Summers, F. M. & D. W. Price, 1961. New and redescribed species of *Ledermuelleria* from North America (Acarina: Stigmaeidae). – Hilgardia 31: 369-387.

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BOOK REVIEWS

LEPIDOPTERA CHECKLISTS

Zdeněk Laštůvka, 1993. Katalog von Faltern der mährisch-schlesischen Region. (Lepidoptera). - Agronomická fakulta Vysoké školy zemědělské v Brně, Brno. 130 pp. [in czech and german].

Povilas Ivinskis, 1993. Check-list of Lithuanian Lepidoptera. - Ekologijos Institutas, Vilnius. 210 pp. [in english and lithuanian].

Peter Huemer & Gerhard Tarmann, 1993. Die Schmetterlinge Österreichs (Lepidoptera). Systematisches Verzeichnis mit Verbreitungsangaben für die einzelnen Bundesländer. - Veröffentlichungen des Museum Ferdinandeum, Beilageband 5. 224 pp. [in german].

A. Vives Moreno, [1994]. Catalogo sistematico y sinonimico de los Lepidopteros de la peninsula Iberica y Baleares (Insecta: Lepidoptera) (Segunda Parte). - Ministerio de Agricultura, pesca y Alimentacion, Madrid. 775 pp. [in spanish and french].

In a short time four new lepidopteran checklists of European countries appeared on my desk. Since one of the authors asked me to review his work, I take the opportunity to review and compare all these checklists together. They treat respectively very different faunas: from Lithuania (2213 species), Moravia (part of the Czech Republic) (3087 species), Austria (3963 species) and the Iberian Peninsula (number of species not given, probably more than 5000).

The aim of local checklists is usually twofold: providing an up-to-date list of the local fauna and providing the valid names in the light of the recent views on systematics. Obviously, as fauna lists all these books have their own value, and give an up-to-date account of the various faunas. The lists of Lithuania and Austria also provide details about the distribution within the countries, the Austrian one most clearly in tabulated form. Vives-Moreno only indicates the ocurrence in Spain, Portugal, Andorra or the Balear Islands. Ivinskis provides also data on food-plants, albeit often taken from foreign literature, including mistakes. The Moravian list is interesting, because it presents sources for the inclusion of all species by referring to a literature reference or a collection by a number. This important feature is usually lacking in other checklists. None of the lists here provides detail about the present status of the species in their countries (such as extinct, breeding, migrant, import), nor do they indicate endemism (which is high in the Iberian peninsula), but Ivinskis provides indications of abundance (rare, common etc.). Huemer & Tarmann also provide a list of excluded species.

The second aim of checklists: up-to-date nomenclature, is a topic for dispute. Nowadays there are checklists for most European countries, and new ones are on their way for France (P. Leraut) and Italy (A. Minelli ed.) (both in press now) or in preparation (Greece, Netherlands). Also a European checklist (J. Razowski ed.) is in press now, but all these lists, including the four reviewed here still differ greatly as to nomenclature of families, genera, species and subspecies. It often seems that authors try to be even more modern than previous lists by including all nomenclatorial and systematical changes which have recently been published. Unfortunately the quality of published systematical works is very different indeed, and one can wonder about the acceptation of certain changes in classification. There seems to be little effort in Europe to reach a common view on some of these changes, and most lists just follow the personal preference of the author Some recently published classifications seem to be more a challenge for new research than a basis for a sound classification. So, Minet's new classification of Gelechioidea definitely raises some interesting questions and tries to solve some existing problems, but being so radically different from former ones, and still based on the cladistic analysis of one lifestage only, it seems a little too premature to incorporate such a tentative classification in checklists to be used by non-systematists as well. Yet, this classification is completely followed by Huemer & Tarmann, thereby risking that a next edition will show yet another family classification. There are several other examples in these lists of such differences.

The lists are more consistent in the rejection of the view of some authors that many of the long-used Denis & Schiffermüller names are nomina nuda and should be replaced. Both Vives Moreno and Huemer & Tarmann suggest a ruling by the ICZN on this problem. Another hot topic in lepidopteran nomenclature is the agreement in gender between genus name and specific epitheton. Only the Moravian list tries to completely follow up the agreement in gender, even in names ending in non-latin endings -ella, -ata, etc. They stand alone in this practice: most lepidopterists treat such names as nouns and keep the original spelling. This practice will probably become rule in the next issue of the Code of which a draft is now circulating for discussion (i.e. on INTERNET).

All the noted differences between lists, issued almost at the same time, appeal for a more European approach of the problem. I would suggest that all lists combine into one basic European list, which follows a rather conservative approach as to classification, but indicates where there are problems and different views. Such a list should be prepared by specialists and local faunists in close cooperation. Needless to say that such lists should be distributed in digitized form and become available on internet. It is rather strange that even in 1993-1994 so many checklists can appear without an electronic counterpart! Electronic publishing will also make updating of lists much easier.

A final word on the four lists:

Ivinskis: Lithuania. – A handy booklet, unfortunately with many inaccuracies in nomenclature. Gives details about distribution, abundance and hostplants. No nomenclatorial notes.

Laštůvka: Moravia. – A practical list without many synonyms and with clear references for each species. With nomenclatorial notes, also in german.

Huemer & Tarmann: Austria. – The most handy of the four lists with the distribution of 'Bundesländer' (provinces) in tabulate form and not more than three synonyms per species. Clear notes. Follows all recent systematic changes, even if the authors themselves have a different opinion about these changes (Huemer pers. comm.).

Vives-Moreno: Iberian peninsula. – By far the largest list. Rather impractible by the large number of synonyms, which seems partly superfluous to me. Follows a volume one (partida primera) on Microlepidoptera, published in 1992, but these are all repeated in the present list (partly in changed form). However, for the faunistic remarks one should refer to vol. 1. Notes also in french.

[E. J. van Nieukerken]

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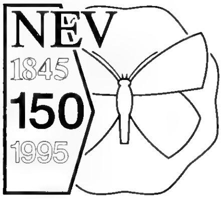

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New paragraphs should *not* be indented in wordprocessors. Scientific names of genera and species should be typed in *italics* or underlined. No underlining or italics are allowed for any other text. Abbreviations of museums ('codens'), computer programs etc. should be typed in SMALL CAPS, if available.

References

In the text they are given as Lopes (1982a), (Lopes 1982) or (Brown & White 1975: 24). All cited papers should be listed alphabetically at the end of the paper under the heading 'References', papers not cited in the text should be omitted from the list of references. Examples for format:

Boer, P. J. den, 1970. On the significance of dispersal power for populations of carabid-beetles (Coleoptera, Carabidae). – Oecologia 4: 1-28.
Karsholt, O. & E. S. Nielsen, 1976. Systematisk fortegnelse over Danmarks sommerfugle. – Scandinavian Science press, Klampenborg, 128 pp.
Johansson, R. & E. S. Nielsen, 1990. Tribus Nepticulini. – In: Johansson, R. et al. The Nepticulidae and Opostegidae (Lepidoptera) of NW Europe. – Fauna entomologica scandinavica 23: 111-238, pls.

Titles of journals should not be abbreviated. Type long dashes as double dash '- -', or in WordPerfect use 'en dash (4,33)'. Do not try to type indentation, just end each reference with a hard return.

Nomenclature

The latest edition of the ICZN Code should be followed. The composition of new names should preferably be explained in a paragraph 'Etymology', including indication of gender of generic names and kind of specific name (adjective, noun in apposition, etc.). Use standard abbreviations: Sp. n., gen. n., comb. n., syn. n., sp. rev., nom. n., etc. For all genus and species-group names the authority (preferably with year of description) should be mentioned once. Author's names are not abbreviated.

In new taxa the type material should be listed immediately after the name. Only holotype, lectotype, neotype, paratype and paralectotype are allowed. Label data should not be quoted literally (except for primary types), but arranged in a standardized sequence. Material should be listed alphabetically or chronologically under the present day countries or other geographical units. Long lists of non-type material should be summarized. Geographical names should be written according to present day spelling, original spelling or label names may be given in brackets. Use standard transcription for non-latin scripts (e.g. Pinyin for chinese, BSI for cyrillic, etc.) or refer to recent editions of the `Times Atlas of the World'.

Abbreviations (Codens) for depositories preferably follow Arnett & Samuelson (1986: The insect and spider collections of the world. E.J. Brill/Flora & Fauna publications, Gainesville). Otherwise, they should be listed under 'Material and methods' or in the introduction.

Data for primary types of previously described species follow directly the reference to the original description as:

Elachista subnitidella Duponchel, [1843]: 326, pl. 77: 8. Lectotype ♂ [designated by van Nieukerken & Johansson 1987: 471]: [Austria, Vienna region], Duponchel coll., Genitalia slide EvN 2522 (MNHN) [examined].

Illustrations

All illustrations, including photographs, graphs, maps, etc. should be serially numbered as figures. No subdivision with letters is recommended. Illustrations are to be reduced to column width (65 mm), 1.5 × column width (102.5 mm) or text width (135 mm). Line figures should be mounted in blocks, or are printed singly. When all figures are mounted in full-page blocks (after reduction: 135 × 195 mm including caption), they may be printed after the text, otherwise the approximate place in the text should be indicated with pencil in the margin of the manuscript. Line-drawings are numbered with pre-stencilled or preprinted figures, which should not be too large after reduction, preferably using a font like 'Garamond' or 'Times'. Photographs should be unmounted glossy prints. Numbering of photos should be left to the discretion of the editors. Captions should be typed on a separate sheet (or in a separate file), consult a recent issue for style. Colour plates will only be printed at the author's expense. It is possible to submit line illustrations as computer files, using well known formats, such as TIFF.

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Tables should be typed in separate files [or on separate sheets], starting with the captions. When using a wordprocessor: start with a practical TAB setting, and use only one [TAB] code for each next column. No formatting with spaces is allowed. No lines should be added. Extensive and long tables should be avoided.

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