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A journal of systematic and evolutionary entomology since 1858

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The 'Tijdschrift voor Entomologie' (Netherlands Journal of Entomology) has a long tradition in the publication of original papers on insect taxonomy and systematics. The editors particularly invite papers on the insect fauna of the Palaearctic and Indo-Australian regions, especially those including evolutionary aspects e.g. phylogeny and biogeography, or ethology and ecology as far as meaningful for insect taxonomy. Authors wishing to submit papers on disciplines related to taxonomy, e.g. descriptive aspects of morphology, ethology, ecology and applied entomology, are requested to contact the editorial board before submitting. Usually, such papers will only be published when space allows.

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THE TAXONOMY AND BIOGEOGRAPHY OF THE *LORIAE* GROUP OF THE GENUS *BAETURIA* STÅL, 1866 (HOMOPTERA, TIBICINIDAE)

Boer, A. J. de, 1993. The taxonomy and biogeography of the *loriae* group of the genus *Baeturia* Stål, 1866 (Homoptera, Tibicinidae). – Tijdschrift voor Entomologie 137: 1-26, figs. 1-102, table 1. [ISSN 0040-7496]. Published 15 July 1994

The *loriae* group is proposed for a presumably monophyletic group of 9 species. Species of the group combine characters seemingly synapomorphic for the species of *Baeturia* Stål, 1866, with characters seemingly synapomorphic for the species of *Gymnotympana* Stål, 1861. Though the generic relationships of the *loriae* group are not clear, it is included here in the genus *Baeturia*, on account of shared male genital characters. One species (*B. loriae* Distant, 1897) is redescribed and eight species (*B. bemmeleni, B. daviesi, B. fortuini, B. hamiltoni, B. hartonoi, B. pigrami, B. silveri*, and *B. wegeneri*) are described as new. *B. loriae* is transferred back from *Gymnotympana* to *Baeturia*. A key to the males is presented. A redescription of *B. tenuispina* Blöte, 1960 is included in this publication, since a character of the clasper indicates a relationship with some species of the *loriae* group. Nevertheless, the attribution of that species to the *loriae* group is far from certain. The *loriae* group is endemic to New Guinea, most species are restricted to the central and eastern mountain ranges of that island.

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Key words. – *Baeturia, loriae* group, taxonomy, biogeography, New Guinea.

Current studies of the tibicinid cicadas of eastern Malesia show, that a number of New Guinean and Australian genera form a monophyletic group: 'the *Baeturia* and related genera complex' (de Boer 1990, 1991). The largest genus of this group, *Baeturia* Stål, 1866, appears to be non-monophyletic in its present concept, but, within that genus, several monophyletic species groups have been recognized. Taxonomic and biogeographic revisions have been published so far for the *B. nasuta* group (de Boer 1982), the *B. conviva* group (de Boer 1986), the *B. bloetei* group (de Boer 1989) and the *B. viridis* group (de Boer 1992).

These pages present the revision of a presumably monophyletic group of nine species, for which the name *Baeturia loriae* group is proposed. This group is of particular interest from a taxonomic point of view, since its species combine several characters regarded apomorphic for *Baeturia*, with characters apomorphic for *Gymnotympana* Stål, 1861. The distribution of these characters within the group is such, that any reconstruction of the in-group relationships will unavoidably show several conflicting characters. The *B. loriae* group is endemic to northern, eastern and central New Guinea.

B. tenuispina Blöte has a character of the clasper in common with some species of the *B. loriae* group, but differs in most other respects. This species is not attributed to the *B. loriae* group, but described here, since it seems more related to this group than to any of the other species groups of *Baeturia*.

MATERIAL AND METHODS

The material used for this study comes from the following institutions:
AMS – Australian Museum, Sydney; BMNH – Natural History Museum [formerly: British Museum (Natural History)], London; BPBM – Bernice P. Bishop Museum, Honolulu; CSIRO – Commonwealth Scientific and Industrial Research Organisation, Australian National Insects collection, Canberra; KBIN – Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussel; MSNG – Museo Civico di Storia Naturale 'G. Doria', Genova; MVM – Museum of Victoria, Melbourne; RMNH – Nationaal Natuurhistorisch Museum (formerly: Rijksmuseum van Natuurlijke Historie), Leiden; SMN – Staatliches Museum für Naturkunde, Stuttgart; ZMA – Institute for Systematics and Population Biology (Zoölogisch Museum), Amsterdam.

The following sources have been used for tracing the localities: 'Atlas van tropisch Nederland' (1938), 'The Times Atlas of the World (Comprehensive Edition)' (1968), 'Papua New Guinea a travel survival kit' by Tony Wheeler, 1988, Lonely Planet Publications, Victoria, Australia 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. Body and tegmen lengths of all specimens were measured, other measurements are based on a maximum of ten specimens, when available.

PHYLOGENY

Classification of the *B. loriae* group

The generic classification of the *loriae* group presents a major problem. As stated above, the species combine characters of *Baeturia* with characters of *Gymnotympana*. Some of these characters appear to be unique for either *Baeturia* or *Gymnotympana* (or part of these genera). The distribution of these characters within the *loriae* group is not homogeneous; some species have more in common with *Baeturia*, others more closely resemble *Gymnotympana*.

The following characters are found in the *loriae* group and indicate a relationship with *Baeturia*, the first four are presumed apomorphies for that genus.

(1) a strongly curved aedeagus, tapering to its apex, with bluntly rounded lateral lobes and oval aedeagus pore. This aedeagus shape is unique for *Baeturia*.

(2) a narrow vertex, with large ocelli close together (fig. 3). Two species of *Gymnotympana* have an even narrower vertex. In other species of the complex, the vertex is broader than in *Baeturia*.

(3) a broad and triangular middle spine on fore femur (fig. 19) is shared by all species of *Baeturia*.

(4) a fairly narrow and frontally bluntly rounded postclypeus, distinctly protruding beyond vertex lobes and, in most species, distinctly and angularly swollen ventrally (figs. 3-4). A similar swelling only occurs in some species of *Baeturia*, the narrow, protruding, and rounded shape of the postclypeus is possibly apomorphic for *Baeturia*.

(5) a rather stout caudodorsal beak, often angularly bent and curved over anal valves. Other species of the complex have a much shorter and erect beak. The curved caudodorsal beak is probably synapomorphic for several of the *Baeturia* species groups together.

(6) almost straight parallel claspers, separated at the base, and with a broad and rounded ventral hollow in the apical part. Such separated claspers are unique for *Baeturia* and *Scottotympana* de Boer, 1991.

(7) a distinct and angular clasper heel (in *B. bemmeleni*, *B. hamiltoni*, and *B. wegeneri*). A clasper heel is found in many species of *Baeturia*, but not in other genera.

(8) rows of setae on veins of tegmina and wings (in *B. hamiltoni* and *B. wegeneri*). Similar rows of setae are found in many *Baeturia* species, but not in any of the related genera. However, such setae also occur, though more distinctly, in several genera of the Prasiini, a possible sister group of the '*Baeturia* and related genera complex'.

(9) dense brown speckling on body (in *B. daviesi* and *B. wegeneri*). Such speckling, though strongly variable in density, only occurs within *Baeturia*.

(10) irregularly shaped brown spots on tegmina (in *B. pigrami* and *B. silveri*, fig. 59). Such spots are only found in some species of *Baeturia* (e.g. *B. guttulinervis*, *B. guttulipennis* and *B. nasuta*).

(11) a distinct crest between the aedeagal lobes. A similar crest occurs in some species of the *B. conviva* group and some species related to that group.

Other characters found in the *B. loriae* group do not occur in other species groups of *Baeturia*, but seem to indicate a relationship with *Gymnotympana*. The first two must possibly be regarded as apomorphies for *Gymnotympana*, others are either restricted to part of that genus, or occur in several other genera as well.

(1) sexual dimorphism in wing venation (males with very slender anal fields, compare figs. 59 and 84) is shared by all species of *Gymnotympana*, but does not occur in other genera of the complex. (Similarly slender anal fields are recorded for *Prasia* Stål and *Plautilla* Stål (Boulard 1975), however. In *Prasia* this character is restricted to the males, but the literature does not record such dimorphism for *Plautilla*).

(2) a sharp ventrolateral fold in tergites 4-7 (more or less distinct in all species) is shared by nearly all species of *Gymnotympana*, but not found in related genera.

(3) an enlarged distal part of male operculum. Both, the broadly rounded shape (as found in *B. bemmeleni*, *B. hamiltoni*, and *B. wegeneri*), as the triangular shape (as found in *B. daviesi*, *B. fortuini*, and *B. pigrami*), are found in *Gymnotympana*, but do not occur in related genera.

(4) a very short, often rudimentary meracanthus

(found in all species with enlarged opercula) is shared by *Venustria* Goding & Froggatt, 1904 and most species of *Gymnotympana*. This character might be coupled to the character described immediately above.

(5) a laterally elongate basal part of male operculum (in six species) is shared by nearly all *Gymnotympana* species and not found in other genera.

(6) a broad hyaline border along hind margin of tegmen (in *B. fortuini* and *B. loriae*, fig. 84) is shared by all species of *Gymnotympana*, *Scottotympana*, and *Venustria*.

(7) an inwards curving ventral corner of tymbal, with strongly inwards directed connecting bar between abdomen and tymbal (only found in *B. fortuini*) is found in most species of *Gymnotympana*, but not in other related genera.

(8) furthermore, all species except *B. daviesi* and *B. wegeneri* have a more or less distinct colour pattern of dark streaks and spots on head, pronotum, and abdomen (figs. 8-9). This colour pattern is much more distinct than in other species of *Baeturia*. An even more distinct colour pattern is found in many *Gymnotympana* species, in *Scottotympana* and in two species of *Chlorocysta* Westwood, 1851. Since these patterns are very variable between the various species, it is not clear whether the patterns found in the *loriae* group can be considered homologue with those in *Gymnotympana*.

The *loriae* group thus, seems to combine some apparently convincing synapomorphies of *Baeturia* and *Gymnotympana*. At this point of investigation, with several groups of the '*Baeturia* and related genera complex' still undescribed, and with only vague indications as to the possible sister groups of the complex, it is not possible to fully evaluate the meaning of the character distribution in the *loriae* group. Current phylogenetic analysis, involving all species of the '*Baeturia* and related genera complex', however, shows that a monophyletic *loriae* group as part of the genus *Baeturia*, is the most parsimonious solution. Furthermore, this solution is in accordance with the distribution of all male genital characters.

Nevertheless, the remarkable number of conflicting characters concentrated in the *loriae* group is upsetting to any phylogenetic reconstruction. Whatever generic allocation of the *loriae* group is favoured, the parallel evolution and / or the successive gain and loss of several characters must be presumed. Biochemical study of the *loriae* group could be interesting as a test for a hybrid origin of that group.

Monophyly of the *B. loriae* group

The above discussed combination of characters found in the *loriae* group involves all those characters that would, by non-existence of that group, be used as apomorphies for either *Baeturia* or *Gymnotympana*. As a result neither *Baeturia* nor *Gymnotympana* can be properly defined by shared apomorphies in exclusion of the *loriae* group. But also for the *loriae* group itself, no unambiguous apomorphies could be found. The group can be best defined by the unique combination of two characters: sexual dimorphism in wing, and an S-curved aedeagus with lateral lobes at the base of the curvation. Furthermore, there are three characters shared by all, or nearly all, species of the group, and not widely distributed outside the group, that could indicate a close relationship between the species. These characters are: 1) a distinct crest between the lateral lobes of aedeagus, only shared by some species of the *B. conviva* group and two species related to that group; 2) an enlarged and angularly rounded ventral part of the lateral lobe of pygofer, shared by only a few species of *Gymnotympana* (e.g. *G. stridens*); and 3) a rather short and broad eighth apical area of tegmen, tending to be shorter than in *Gymnotympana* or other species of *Baeturia*. The latter character is somewhat variable within the species and cannot be used as a diagnostic character.

Ingroup phylogeny

As long as the problems concerning the phylogenetic position of the *loriae* group, relative to other species groups of *Baeturia* and to the genus *Gymnotympana*, are not satisfactorily solved, characters that occur either in *Baeturia* or *Gymnotympana* and also in some species of the *loriae* group cannot be properly evaluated as plesiomorphous or apomorphous, and can therefore not be used in a phylogenetic reconstruction of the group. Only the distribution of characters that appear to be unique for some species of the *loriae* group allows some remarks on ingroup phylogeny.

B. bemmeleni, *B. hamiltoni*, and *B. wegeneri* almost certainly form a monophyletic group. These species share an almost identical clasper, characterized by a nearly rectangular dorsal corner (figs. 11, 26, and 30), which is regarded synapomorphic. Furthermore, these species share an almost identical male operculum; very broad, slightly domed and broadly rounded at its apex (figs. 14, 22, and 38). A very similar operculum was found in *G. olivacea* Distant, 1905, but in that species the lateral margin of operculum is almost continuous with the lateral crest of operculum base. Some undescribed *Gymnotympana* species, related to *G. olivacea*, have a similarly broad and curved, but more angular, square-shaped, operculum.

B. daviesi, *B. fortuini*, *B. hartonoi*, *B. loriae*, *B. pigrami*, and *B. silveri*, most probably form a monophyletic group on account of a shared dorsal protrusion on the clasper. This protrusion is partly, or complete-

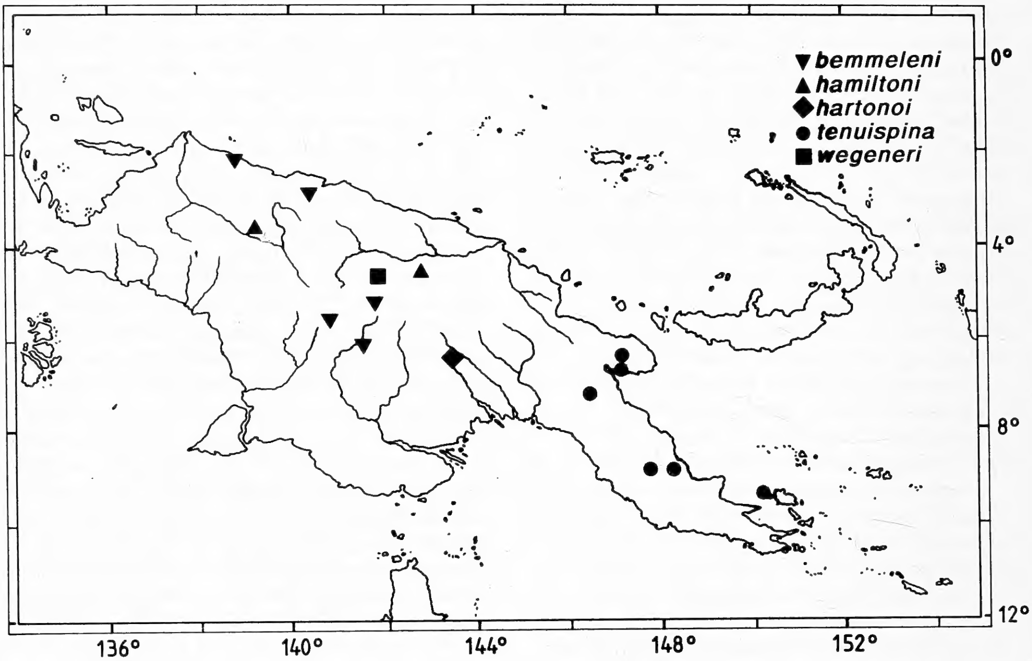


Fig. 1. Localities of *Baeturia bemmeleni*, *B. hamiltoni*, *B. hartonoi*, *B. tenuispina*, and *B. wegeneri*.

ly fused with the upwards curving proximal part of the dorsal margin of clasper, and merges with the clasper base, were in many other *Baeturia* species the clasper heel is formed. *B. tenuispina* Blöte has a similarly shaped protrusion at the corner of its clasper heel (fig. 97) and should possibly be included in this group.

In *B. daviesi*, *B. pigrami*, and *B. silveri* the dorsal protrusion is very distinct and finger-shaped (figs. 40, 50, 64); in *B. hartonoi*, this protrusion is more angular and strongly curved mesiad (fig. 70); and in *B. fortuini* it is rudimentary and only recognizable in the specimens from Mt. Missim (fig. 79). The dorsal protrusion is believed to be lost in the lectotype of *B. loriae* and the remaining specimens of *B. fortuini*.

The clasper of these six species is very broad in lateral view; the dorsal margin of the clasper curves upwards from clasper base, so that no clasper heel is formed. This clasper-shape is probably also synapomorphous.

B. fortuini, *B. loriae*, and *B. hartonoi* possibly form a monophyletic group on account of the shared elongate lateral lobes of aedeagus (figs. 73, 82, 92), and the very broad, angular and laminiform clasper.

B. fortuini and *B. loriae* are very closely related and probably sister species. They share triangular bronzed spots in the tegmina (fig. 84) and a very long and slender aedeagus (figs. 82, 92). Possibly these two species are synonyms, and the lectotype of *B. loriae* is just an aberration.

The relationships between *B. daviesi*, *B. pigrami*, and *B. silveri* are less clear. These species share a triangular clasper, with convex dorsal margin (lateral view), which must probably be regarded more primitive than the squarely laminiform clasper of the three species mentioned above. Especially the claspers of *B. daviesi* and *B. pigrami* are very similar, sharing a broadly rounded and outcurving dorsal lobe, but the clasper of *B. hartonoi* has a very similar outcurving lobe. *B. pigrami* and *B. silveri* are conspicuous by the brown patches along veins of tegmina. But *B. guttulinervis* Blöte and *B. guttulipennis* Blöte, two otherwise very different and not closely related species, have similar patches.

Table 1. Altitudinal ranges of the species of the *B. loriae* group in meters above sea level.

B. bemmeleni	35-1350
B. fortuini	1100-2100
B. hamiltoni	50-1200
B. hartonoi	100
B. loriae	1300
B. pigrami	120-1260
B. silveri	1800-2590 (8500 ft)
B. wegeneri	250

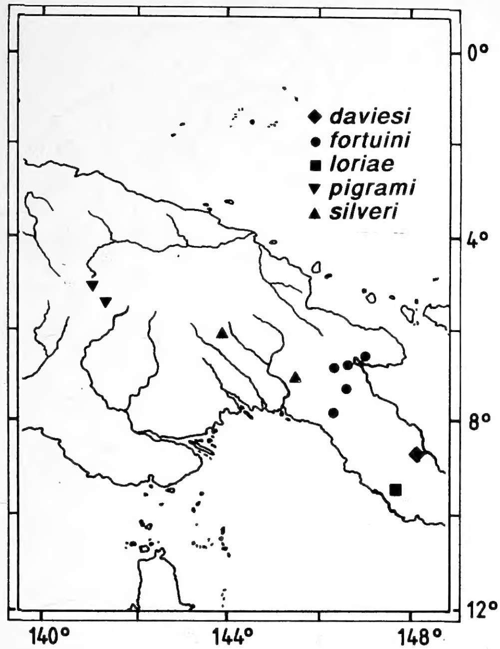


Fig. 2. Localities of *Baeturia daviesi*, *B. fortuini*, *B. loriae*, *B. pigrami*, and *B. silveri*.

BIOGEOGRAPHY

The *B. loriae* group is endemic to New Guinea, and distributed in the northeastern part of Irian Jaya, and in central and eastern Papua New Guinea. Many specimens come from, or close by, the central and eastern mountain ranges. The group seems to consist mainly of montane species, probably with very restricted areas of distribution, often reaching altitudes of over 1000 m (table 1).

It is remarkable, that the subdivision made above, between *B. bemmeleni*, *B. hamiltoni*, and *B. wegeneri* versus the remaining species, is a subdivision between a mainly western and a mainly eastern species group (figs. 1, 2).

TAXONOMY

Description of the *B. loriae* group

The species of the *B. loriae* group are predominantly brown coloured, sometimes greenish tinged. *B. wegeneri* and *B. daviesi* are densely speckled with small brown spots, the other species are conspicuous by a colour pattern of regularly distributed dark markings. These species generally have two dark spots or longitudinal streaks between eyes and lateral ocelli and often darkened lateral corners of postclypeus; a light immaculate middorsal band on pronotum, sometimes bordered by almost black lines, and dark brown streaks in and along the oblique fissures. The dark markings on the mesonotum form two semi-circular paramedian spots, at pronotal collar, two blackened dents in front of cruciform elevation and lateral bands, converging from pronotal collar to edges of elevation. The cruciform elevation and a triangular area in front of the elevation is generally light ochraceous and unmarked. On the male abdomen, dark markings tend to form dorsal, and sometimes lateral bands, while a latero-ventral row of dark spots is often very clear. The dorsal markings tend to be interrupted middorsally by a narrow lighter coloured line. Ventral side of male abdomen generally light ochraceous, segmental hind margins often red. Female abdomen more irregularly dark spotted all over, though the light middorsal band is often more conspicuous.

Females are shorter than males (on average), but have a larger, more robust head and thorax and often longer tegmina.

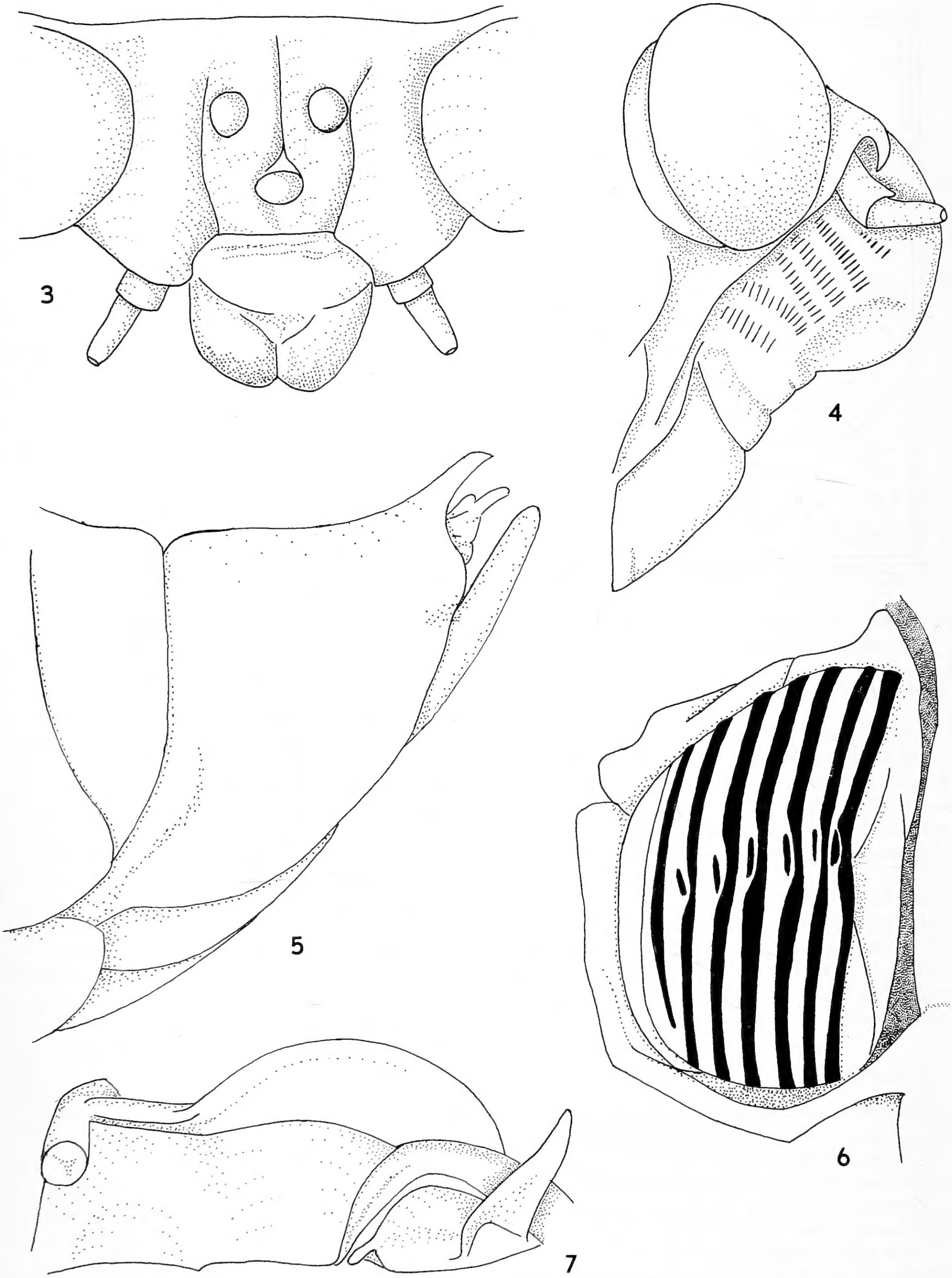
Head in dorsal view (fig. 3): Postclypeus distinctly protruding beyond vertex lobes and broadly rounded at frontal margin. Postclypeus 1.2-2.2 × as broad as long and 0.5-0.7 × as broad as distance between eyes, strongly varying within the species. Head 0.7-0.8 × as wide as pronotal collar and only slightly narrower than anterior width of pronotum. Vertex narrow, ocelli large and close together. Distance between lateral ocelli less than 1.5 × the width of frontal ocellus and 0.7-1.4 × as long as distance between eye and lateral ocellus. Eye 0.6-0.8 × as wide as distance between eyes. Head 0.9-1.2 × as long and 2.2-2.6 × as wide as distance between eyes.

Legs: Ochraceous, sometimes with longitudinal brown stains on femora and tibia. Fore femur (fig. 19) with row of three sharply pointed spines, diminishing in length towards tibia. Proximal spine about as long as distance to middle spine. Middle spine broad, triangular.

Tegmina and wings: Hyaline, though tegmina in some species with brown markings. Venation ochraceous, costa often reddish. Tegmina with 8, wings with 6 apical areas. Costal area of tegmen very narrow. Anal fields of wing in male distinctly narrower than in female (compare figs. 59 and 84).

Tymbal organ (fig. 6): Six or seven parallel transverse sclerotized ridges spanning the tymbal from dorsal to ventral margin. Short intercalary ridges forming a midlateral band across tymbal.

Opercula: Basal part of operculum vaulted, with distinct crest around rectangular distolateral corner. Distal part of male operculum either very long and domed, and completely covering tymbal cavity in ventral view; or short, oblong-shaped, laminiform and flat against body, only partly covering tymbal cavity. Distal part of operculum medially extending



Figs. 3-7. *Baeturia hamiltoni* sp. n. – 3, Head in dorsal view; 4, postclypeus in lateral view; 5, female genital segment in lateral view; 6, tymbal; 7, female operculum.

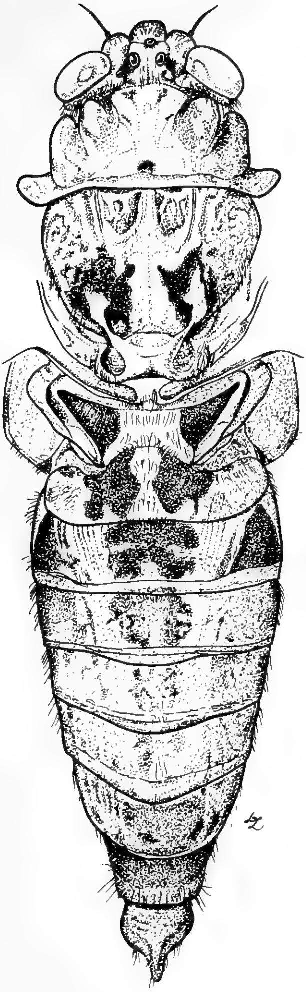


Fig. 8. *Baeturia hamiltoni* sp. n., habitus male.

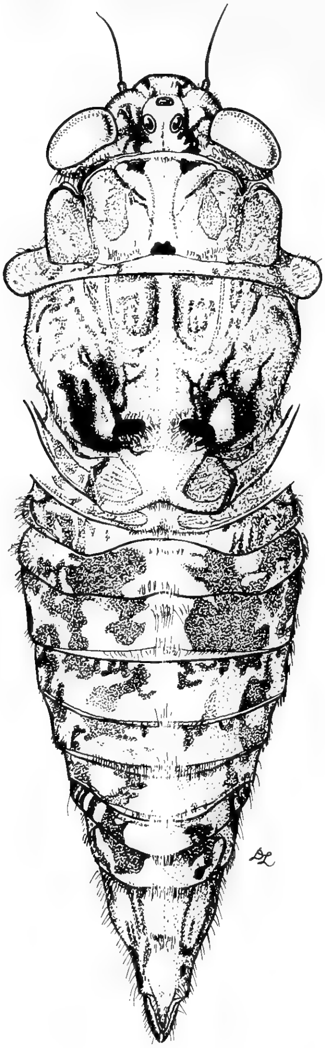


Fig. 9. *Baeturia hamiltoni* sp. n., habitus female.

beyond meracanthus. Distal part of female operculum short, sickle-shaped and erect, medially extending just to base of meracanthus. Basal part of female operculum forming narrow rim around base of meracanthus.

Abdomen: With tergites 4-7 of the male abdomen sharply folded at the ventrolateral edge of abdomen, though these folds are not always distinct an all specimens.

Male genitalia: Pygofer with stout and often angularly bent caudodorsal beak. Lateral lobes of pygofer with small and bluntly rounded protuberances, that do not extend beyond pygofer margin. Lateral lobes strongly folded inwards. Claspers parallel and directed posteriad, slightly bending down towards their apices. Apical part of clasper with small, rounded and sharply edged clasper hollow. Aedeagus strongly S-curved, with two narrowly elongate lateral lobes at base of S-curvation, and a distinct crest between lateral lobes. Aedeagus in lateral view broad at base, gradually narrowing to pointed apex.

Female genitalia: Caudodorsal beak sharply pointed at apex. Ovipositor sheats reaching just beyond apex of beak (fig. 5).

Etymology: This revision is to form part of an area cladistic study of the New Guinean region, in which the general patterns of distribution of organisms are compared to the geological history of that island. The new species described in this publication are named in honour of geologists, who contributed to a paleogeographic reconstruction of the area. The species are named after R. W. van Bemmelen, H. L. Davies, A. R. Fortuin, W. B. Hamilton, H. M. S. Hartono, C. J. Pigram, E. A. Silver, and A. Wegener.

Key to the males

1. Clasper with distinct angular clasper heel; apical part of clasper slender in lateral view, with rectangular dorsal corner (fig. 11). Distal part of operculum broad and long, weakly domed, and broadly rounded at apex (fig.14) 2
– Clasper without clasper heel; apical part of clasper in lateral view broader than clasper base, often with dorsal protrusion, partly fused to proximal part of dorsal margin (fig. 40). Distal part of operculum either oblong and flat (fig. 41), or triangular, domed and pointed (fig. 51) at apex 3
2. Body densely speckled all over, not forming an unspeckled or lighter coloured middorsal band .. ..*B. wegeneri*
– Body not speckled, but with regularly distributed dark markings and an immaculate middorsal band over part or whole length of body 4
3. Body length 25.4-29.7 mm. Caudodorsal beak broad and truncate at apex ....*B. hamiltoni*
– Body length 17.1-21.3 mm. Caudodorsal beak narrowly truncate or pointed at apex ....*B. bemmeleni*
4. Aedeagus very long, with elongate and slender lateral lobes (fig. 82). Clasper quadrangular in lateral view; dorsal part of clasper angular, laminiform (figs. 70, 79, 80, 89) 5
– Aedeagus short and broad, lateral lobes not elongate (fig. 45). Clasper triangular in lateral view; dorsal part of clasper swollen, with weakly convex dorsal margin (figs 40, 50, 64) 7
5. Postclypeus not swollen in lateral view. Tegmen immaculate. Aedeagus angularly bent to apex (fig. 73). Clasper with dorso-lateral lobe (fig. 70) *B. hartonoi*
– Postclypeus distinctly swollen in lateral view. Tegmen with triangular brown spots in apical areas (fig. 84). Aedeagus not angularly bent to apex (fig. 81). Clasper without dorso-lateral lobe (fig. 79) 6
6. Distal part of operculum triangular, domed and narrowly rounded at apex (fig. 77). Margin of aedeagus pore concave at apex (fig. 83) .*B. fortuini*
– Distal part of operculum square-shaped, flat against body (fig. 91). Margin of aedeagus pore not concave at apex (fig. 93) ....*B. loriae*
7. Tegmina with brown markings along veins (fig. 59) 8
– Tegmina immaculate ....*B. daviesi*
8. Postclypeus angularly swollen in lateral view. Distal part of operculum triangular and slightly domed. Hind margin of tegmen with distinct hyaline border ....*B. pigrami*
– Postclypeus not swollen in lateral view. Distal part of operculum square-shaped and flat against body. Hind margin of tegmen with narrow hyaline border ....*B. silveri*

Description of the species

Baeturia hamiltoni sp. n.

(figs. 1, 3-20)

Type material. – Holotype ♂: 'Neth. Ind.-American New Guinea Exped. Rattan camp, 1200 m, 6.iii.1939, L. J. Toxopeus', RMNH. - Paratypes: IRIAN JAYA: NEW GUINEA (W): Araucaria camp, 800 m, 8.iii.1939, L. J. Toxopeus, 1♂, 3♀, RMNH; same data but 9.iii.1939, 1♂, 1♀; 10.iii.1939, 3♀; 11.iii.1939, 1♂; 12.iii.1939, 1♀; 16.iii.1939, 1♂, 2♀; 20.iii.1939, 1♀; 21.iii.1939, 2♂; 22.iii.1939, 2♂, 2♀; 24.iii.1939, 2♀; 25.iii.1939, 1♂; 29.iii.1939, 1♂, all RMNH; same data but 19.iii.1939, 2♀; 28.iii.1939, 2♂, all ZMA; Bernhard camp, 100 m, 11.iv.1939, L. J. Toxopeus, 2♀, RMNH.

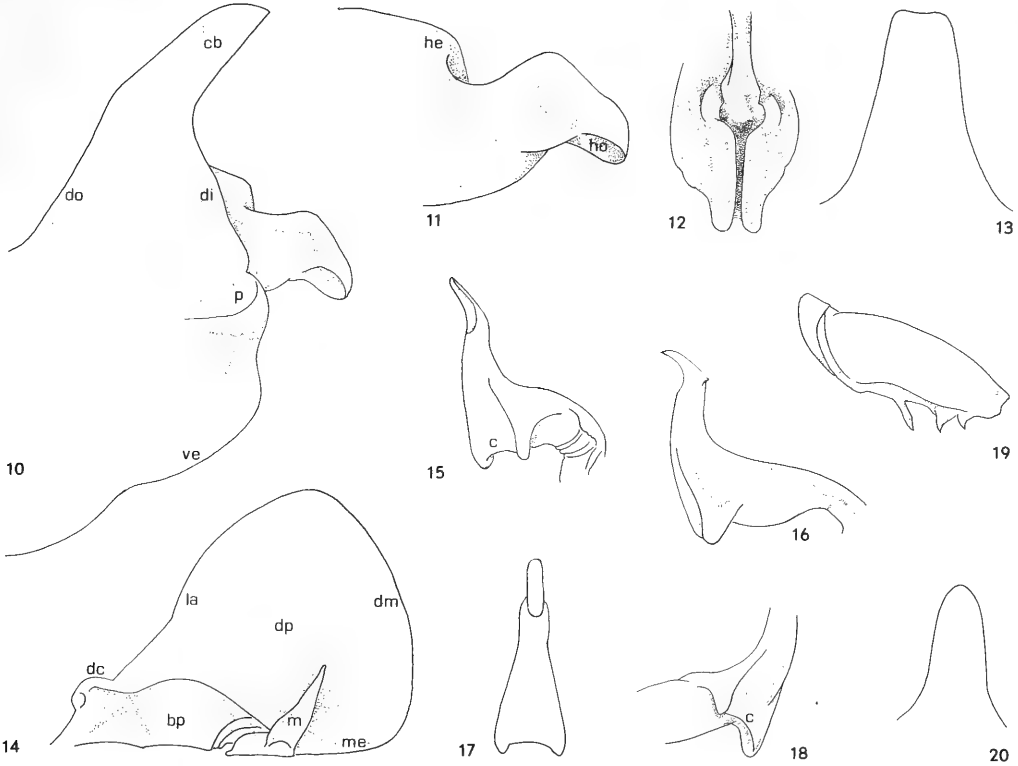
Other material. – PAPUA: NEW GUINEA (NE): Ambunti, Sepik R., 50 m, 10.v.1963, R. Straatman, 1♂, BPBM.

B. hamiltoni is a large brown coloured, species with a light middorsal band on head and thorax, sometimes continuing over abdomen. The species is easily recognized by a small and almost black medial spot on pronotum, at pronotal collar. Females have a glistering middorsal band of silvery setae on the abdomen, making the light and immaculate middorsal band more conspicuous than in males.

Description

Body of males brown, abdomen sometimes reddish, with distinct colour pattern of darkened markings and an immaculate middorsal band on head and thorax, sometimes continuing over abdomen. Females on average slightly smaller than males, with more robust head and thorax, but shorter abdomen and considerably longer tegmina. Male abdomen 1.3-1.4× as long as head and thorax, of female 0.9-1.0×. Tegmina of males 1.1-1.2× as long as total body length, of females 1.4-1.5×.

Head (fig. 3): Light brown, with traces of red around ocelli, longitudinal dark brown to black streaks on vertex lobes, between eyes and lateral ocelli, and often brown spots at margins of postclypeus. Postclypeus very stout, 1.3-1.9× as long as broad, distinctly protruding beyond vertex lobes and broadly rounded at anterior margin. Postclypeus in lateral view (fig. 4) strongly inflated, and angularly protruding; dorsal part of anterior margin (lateral view) al-



Figs. 10-20. *Baeturia hamiltoni* sp. n. – 10, pygofer in lateral view; 11, clasper in lateral view; 12, clasper in dorsal view; 13, male caudodorsal beak in dorsal view; 14, male operculum; 15, aedeagus from aslant; 16, aedeagus in lateral view; 17, aedeagus from behind; 18, detail crest between lateral lobes of aedeagus; 19, fore femur; 20, female caudodorsal beak in dorsal view. Lettering: bp = basal part of operculum; c = crest between lateral lobes of aedeagus; cb = caudodorsal beak; dm = distomedial margin of operculum; di = distal margin of pygofer; dc = crest around distolateral corner of basal part of operculum; do = dorsal margin of pygofer; dp = distal part of operculum; he = clasper heel; ho = clasper hollow; la = lateral margin of operculum; m = meracanthus; me = medial margin of operculum; p = protuberance on lateral lobe of pygofer; ve = ventral margin of pygofer.

most straight, ventral part strongly concave. Head very narrow between eyes, distance between lateral ocelli only slightly larger than width of frontal ocellus. Distance between lateral ocelli 0.8-1.2× distance between eye and lateral ocellus. Head narrower than anterior part of pronotum.

Thorax: Pronotum brown, with broad dark brown streaks, in and along oblique fissures, and broad, immaculate medial band. Markings variable in intensity and shape, and sometimes completely absent. All specimens with a small dark brown or black middorsal spot at margin of pronotal collar. Mesonotum light brown, with two paramedian dark spots at pronotum margin, darkened lateral streaks converging from pronotal collar to corners of cruciform elevation and two black spots in front of elevation. Cruciform elevation, and a narrow triangular area in front of elevation, often reaching to pronotal collar, light ochraceous and immaculate.

Legs: Fore femur (fig.19) with row of three erect spines, diminishing in length towards tibiae.

Tegmina and wings: Hyaline, though slightly bronzed, venation ochraceous or reddish tinged, but costa often bright red. Veins densely set with short setae. Tegmina with very short apical areas, 8th area almost square-shaped, and with a very narrow hyaline border along hind margin.This border slightly broader in wings.

Tymbal organs (fig. 6): Tympanum not curving inwards; connecting bar between tymbal and abdomen quite short and almost parallel to body axis. Six transverse sclerotized ridges spanning the tymbal, from dorsal to ventral margin. A 7th ridge, close to proximal tymbal margin, almost reaching ventral margin.

Six short intercalary ridges seem to form a band across tymbal.

Opercula: Male operculum (fig. 14) ochraceous brown with darkened streaks. Basal part of operculum almost oblong-shaped, but at half-width slightly longer than at lateral or medial margin. Distal part of operculum very broad, shell-shaped, and almost flat against body. Operculum broadly rounded at apex and reaching to, or beyond, margin of abdominal segment 3. Distomedial margin and distal ⅔ of lateral margin convex, proximal ⅓ of lateral margin straight. Medial margin short and straight, recurving to base of meracanthus. Opercula well separated medially; 1st sternite slightly elevated between opercula, with distinct distal lobe. Meracanthus very short, reaching to about ⅓ the operculum length. Female operculum (fig. 7) sickle-shaped and erect, with weak crest along distal margin; area between operculum and base of meracanthus broad and flat.

Abdomen: Male abdomen light brown, with some darker brown spots on lateral sides and latero-ventral rows of dark spots on segments 3-7. Segments 2-7 darkened dorsally as well, though these markings often interrupted by a narrow lighter middorsal band. Segment 8 almost entirely dark brown, but pygofer ochraceous. Ventral side of abdomen light brown, immaculate. Segmental hind margins often reddish. Anterior margin of 2nd tergite convex medially; anterolateral sides of 2nd tergite distinctly swollen adjacent to tymbal. Female abdomen more irregularly spotted all over. Light middorsal band more conspicuous than in males, often glistering with short, silvery setae. Ovipositor sheaths reaching just beyond apex of caudodorsal beak (fig. 5). Female caudodorsal beak (fig. 20) stout, slightly erect and rounded at apex.

Male genitalia: Pygofer slender in lateral view as in fig. 10. Dorsal margin straight, angularly bending into stout, short and slightly erect caudodorsal beak. Distal margin straight angularly bending into margin of beak. Lateral lobes of pygofer strongly curved inwards, with bluntly rounded lateral protuberances. Ventral margin angularly convex, but concave near base of pygofer. Caudodorsal beak in dorsal view (fig. 13) broad and truncate at apex. Clasper in lateral view (fig. 11) broad at base, with very distinct and angular clasper heel, strongly bent down at half-length, forming almost right angled dorsal corner. Dorsal margin of clasper concave between clasper heel and this dorsal corner. Distinct crest running along ⅔ of dorsal margin, and bending outwards around aedeagus towards clasper base. Clasper hollow short, broadly rounded at apex. Clasper in dorsal view (fig. 12), with dorsal margins of clasper bases very close together, leaving only a narrow gap for anal valves. Aedeagus in lateral view (fig. 16) strongly concave around aedeagus pore, lateral lobes long and slender. Distinct crest, at base of S-curvation, between lateral lobes (figs. 15, 18). Aedeagus pore (fig. 16) large and oval-shaped.

Measurements: Body length ♂: 25.4-29.7 mm ($\bar{x}$ 27.6 mm ± 1.3), ♀: 23.5-28.7 mm ($\bar{x}$ 26.6 mm ± 1.4); tegmen length ♂: 28.0-35.0 mm ($\bar{x}$ 32.5 mm ± 1.8), ♀: 32.1-40.5 mm ($\bar{x}$ 37.7 mm ± 2.3); head length ♂: 2.3-2.6 mm ($\bar{x}$ 2.4 mm), ♀: 2.4-3.1 mm ($\bar{x}$ 2.6 mm); pronotum length ♂: 3.1-3.8 mm ($\bar{x}$ 3.5 mm), ♀: 3.5-4.3 mm ($\bar{x}$ 4.0 mm); mesonotum length ♂: 5.8-6.6 mm ($\bar{x}$ 6.3 mm), ♀: 6.5-7.8 mm ($\bar{x}$ 7.1 mm); head width ♂: 5.5-6.2 mm ($\bar{x}$ 5.8 mm), ♀: 5.9-6.9 mm ($\bar{x}$ 6.6 mm); width of pronotal collar ♂: 7.1-8.5 mm ($\bar{x}$ 8.0 mm), ♀: 8.3-9.9 mm ($\bar{x}$ 9.2 mm).

Distribution (fig. 1). – *B. hamiltoni* is known from a very restricted area in Irian Jaya and from one locality in NW Papua.

Etymology. – The species is named in honour of the geologist W. B. Hamilton.

Remark. – Three females from Araucaria camp that have been described as *B. guttulinervis* Blöte (allo- and paratypes) are very similar in size and colour pattern to the females of *B. hamiltoni*, but have darkened patches along the venation of tegmen, are slightly brown speckled on the pronotum and miss the dark middorsal spot at pronotal collar.

Baeturia bemmeleni **sp. n.**

(figs. 1, 21-29)

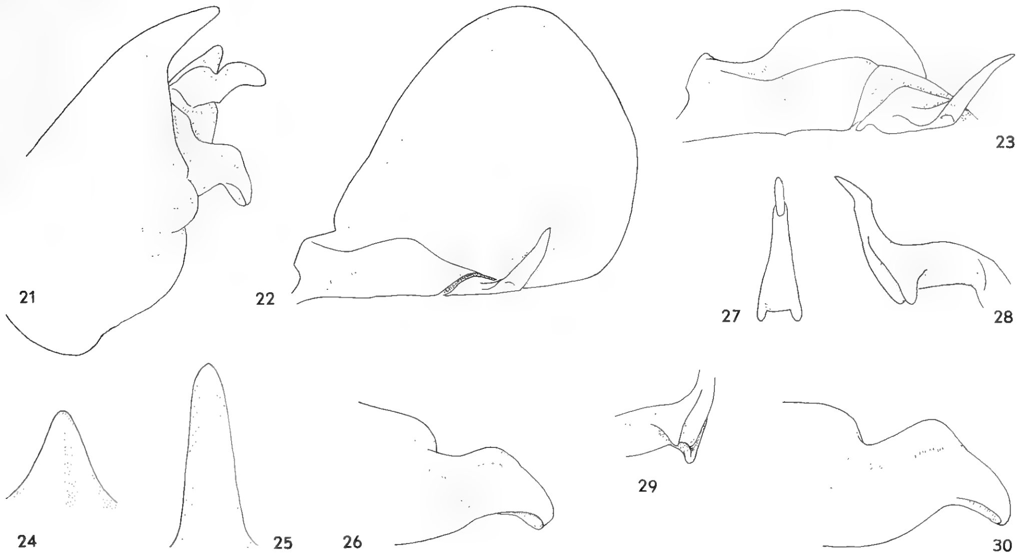
Type material. – Holotype ♂: 'NEW GUINEA NETH. Bodem, 100 m, 11 km SE of Oerberfaren, July 7- 17. 1959'; 'T. C. Maa Collector', BPBM. – Paratypes: IRIAN: NEW GUINEA (W): Boven Digul gebied [Upper Digul area], 400 km N. Merauke, Dr A. Kalthofen, legit 1926, 1♂, ZMA; Boven Sermowai riv., ± 400 m, 8.iv.1911, K. G. [K. Gjellerup], 2♂, RMNH.

Other material. – PAPUA: NEW GUINEA (NE): Eliptamin valley, 1200-1500 m, 16-31.vii.1959, W.W. Brandt, 1 ♀, BPBM; NEW GUINEA (SE): Kiunga, Fly riv., 35 m, viii.1969, J. and M. Sedlacek, 1♀, BPBM.

B. bemmeleni closely resembles *B. hamiltoni* in shape of male operculum and clasper, but is considerably smaller and less intensely coloured. The female from Eliptamin Valley deviates somewhat in shape and colour pattern, but the shape of its 8th apical area of tegmen suggests that this specimen belongs to the *B. loriae* group and it presumably belongs to this species.

Description

Body of males ochraceous or reddish brown, with light brown patches, smaller than in foregoing species. Distribution of patches resemble markings in *B. hamiltoni*; leaving a light middorsal band on head and



Figs. 21-30. 21-29: *Baeturia bemmeleni* sp. n. – 21, pygofer in lateral view; 22, male operculum; 23, female operculum; 24, male caudodorsal beak in dorsal view; 25, female caudodorsal beak in dorsal view; 26, clasper; 27, aedeagus from behind; 28, aedeagus in lateral view; 29, detail crest between lateral lobes of aedeagus. – 30: *Baeturia wegeneri* sp. n., clasper.

thorax immaculate. This band sometimes interrupted by a vaguely darkened middorsal spot, at margin of pronotal collar. Females greenish brown, specimen from Eliptamin Valley densely brown speckled. Both females show the light brown middorsal marking on pronotum. Male abdomen 1.3-1.6× as long as head and thorax, of females 1.1×. Male tegmen 1.1-1.2× as long as total body length, of females 1.3×.

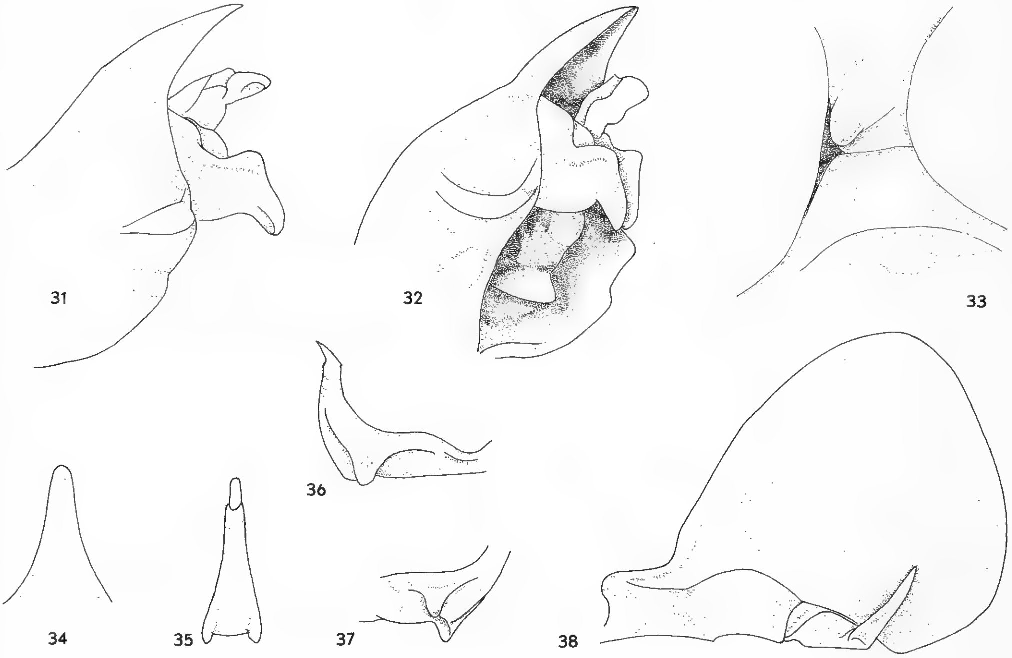
Head: Ochraceous, with brown markings on vertex lobes and along sides of postclypeus, but densely speckled in female of Eliptamin Valley. Postclypeus strongly protruding, almost triangular in dorsal view, 1.8-2.3× as wide as long. Postclypeus in lateral view, angularly inflated as in *B. hamiltoni*, though in some specimens more rounded at anterior margin. Head about as wide as anterior part of pronotum. Distance between lateral ocelli 0.7-0.9× as long as distance between eye and lateral ocellus.

Thorax: Pronotum light brown, with dark brown spots along oblique fissures and a light, but narrow, middorsal band. Female from Eliptamin Valley brown speckled between medial fissures and showing this band only on proximal half of pronotum. Slightly darkened middorsal spot, at margin of pronotal collar, marking end of immaculate band; this spot less clear than in B. *hamiltoni*. Spot U-shaped in one male from Sermowai riv. and the female from Kiunga riv.; connecting two dark lines, running partly along the immaculate middorsal band. Mesonotum variable in colour pattern between individual specimens, though always with a light, immaculate cruciform elevation and, with exception of the densely speckled female from Eliptamin Valley, with a light middorsal band or narrow triangular area in front of elevation. Two dark spots in front of cruciform elevation.

Tegmina and wings: Hyaline, veins slightly reddened. Tegmina with short 8th apical area, and with narrow hyaline border along hind margin. Wings with slightly broader hyaline border.

Tymbal organs: As in *B. hamiltoni*, not curving inwards, but with connecting bar between tymbal and abdomen distinctly longer and more curved inwards. Six transverse sclerotized ridges spanning the tymbal, from dorsal to ventral margin. A 7th ridge, close to proximal tymbal margin, almost reaching ventral margin. Six short intercalary ridges seem to form a band across tymbal.

Opercula: Male operculum (fig. 22) closely resembling that of *B. hamiltoni*, broadly rounded, shell-shaped, and ochraceous brown with some darkened streaks. Basal part of operculum almost oblong, but weakly tapering mesiad at half its width. Distal part weakly domed, almost flat against body, its rounded apex reaching well beyond margin of abdominal segment 3. Distomedial margin and distal ⅔ of lateral margin weakly convex, proximal ⅓ of lateral margin more strongly convex. Meracanthus very short, reaching to about ¼ the operculum length. Female opercu-



Figs. 31-38. *Baeturia wegeneri* sp. n. – 31, pygofer in lateral view; 32, pygofer from aslant; 33, first sternite; 34, caudodorsal beak in dorsal view; 35, aedeagus from behind; 36, aedeagus in lateral view; 37, detail crest between lateral lobes of aedeagus; 38, operculum.

lum (fig. 23) sickle-shaped and erect, with broad and flat area between base of meracanthus and medial edge of operculum.

Abdomen: Male abdomen ochraceous brown, stained with dark brown spots, concentrated in nearly continuous middorsal band. Sternites immaculate. A latero-ventral row of clear dark spots on segments 3-7. Segmental hind margins bright red. Anterior margin of 2nd tergite convex medially; sides of 2nd tergite distinctly swollen and adjacent to tymbal. Female abdomen darker brown with irregular brown markings. Latero-ventral row of dark spots less conspicuous than in males. Segmental hind margins ochraceous. Female caudodorsal beak (fig. 25) long, slender, and pointed at apex.

Male genitalia: Pygofer (fig. 21) closely resembling that of *B. hamiltoni*, slender in lateral view. Dorsal margin straight, angularly bending into straight, stout and slightly erect caudodorsal beak. Distal margin straight, angularly bending into margin of beak. Lateral lobes of pygofer strongly incurved, with well-developed, bluntly rounded lateral protuberances. Ventral margin angularly convex, but concave near base of pygofer. Caudodorsal beak (fig. 24) short, sharply pointed or narrowly truncate at apex. Clasper in lateral view (fig. 26) almost identical to that of *B. hamiltoni*, with very distinct angular clasper heel, and rectangular dorsal corner. Dorsal margin of clasper concave between clasper heel and this dorsal corner. Distinct crest running along ⅔ of dorsal margin, and bending outwards around aedeagus towards clasper base. Clasper hollow short, broadly rounded at apex. In dorsal view, dorsal margins of clasper bases wider apart than in *B. hamiltoni*. Aedeagus in lateral view (fig. 28) slender, strongly concave along margin of pore. Lateral lobes long and slender. Distinct crest at base of S-curvation, between lateral lobes (fig. 29). Aedeagus seen from behind (fig. 27) very slender. Aedeagus pore narrow and oval.

Measurements: Body length ♂: 17.1-21.3 mm (x̄ 18.4 mm ± 1.7), ♀: 19.3 and 21.7 mm; tegmen length ♂: 19.8-20.4 mm, ♀: 27.8 and 28.6 mm; head length ♂: 1.5-1.8 mm (x̄ 1.7 mm), ♀: 1.9 and 2.2 mm; pronotum length ♂: 1.9-2.2 mm (x̄ 2.1 mm), ♀: 2.8 and 3.2 mm; mesonotum length ♂: 3.4-3.8 mm (x̄ 3.7 mm), ♀: 5.0 and 5.3 mm; head width ♂: 4.2-4.5 mm (x̄ 4.3 mm), ♀: 5.0 and 6.0 mm; width of pronotal collar ♂: 5.2-5.4 mm (x̄ 5.3 mm), ♀: 6.9 and 7.2 mm.

Distribution (fig. 1). – *B. bemmeleni* is known from several localities in the northern and central parts of Irian Jaya.

Etymology. – The species is named in honour of the geologist R. W. van Bemmelen.

Baeturia wegeneri sp. n.

(figs. 1, 30-38)

Type material. – Holotype ♂: 'NEW GUINEA: NE, May R. Petrol sta., 250 m, 3.vi.1963' [print]; 'Dry Forest' [print]; 'R. Straatman Collector BISHOP' [print], BPBM. – Paratype: same locality and collector as holotype but 100 m, 31.v.1963, 1♂, BPBM.

B. wegeneri is an ochraceous brown coloured species, with densely brown speckling all over its body, as characteristic for many *Baeturia* species, and in this respect quite different from most other species of the *B. loriae* group. However, *B. wegeneri* is very similar to the two foregoing species in shape of male operculum and genitalia.

Description

Body ochraceous brown, densely brown speckled all over. Abdomen strongly inflated, 1.7× as long as head and thorax. Tegmina about as long as body length.

Head: Ochraceous, brown speckled. Postclypeus broad and oblong in dorsal view, 1.4-1.6× as broad as long. Postclypeus angularly inflated ventrally (as in fig. 4). Head narrower than anterior part of pronotum. Distance between lateral ocelli 0.8-1.0× distance between eye and lateral ocellus.

Thorax: Pronotum ochraceous, brown speckled in middorsal band and on pronotal collar. Mesonotum grey-brown, densely brown speckled. Two dark spots in front of speckled cruciform elevation, almost lost in speckling.

Tegmina and wings: Hyaline, veins ochraceous or slightly reddish and set with short setae. Tegmen with short and squarish 8th apical area, and narrow hyaline border along hind margin. Wing with slightly broader hyaline border.

Tymbal organs: Not curving inwards, connecting bar between tymbal and abdomen quite short and almost parallel to body axis. Six transverse sclerotized ridges spanning the tymbal, from dorsal to ventral margin. A 7th ridge, close to proximal tymbal margin, almost reaching ventral margin. Six short intercalary ridges seem to form a band across tymbal.

Operculum (fig. 38): Broad and rounded as in foregoing species, ochraceous with some darkened stains near lateral margin. Basal part of operculum almost oblong, but weakly tapering towards mesiad at half its width. Distal part slightly domed, almost flat against body, broadly rounded at apex and reaching just beyond margin of abdominal segment 3. Distomedial margin and distal ⅔ of lateral margin convex, proximal ⅓ of lateral margin more strongly convex. Opercula well separated medially, by distinctly smaller and anteriorly lobate first sternite (fig. 33). Meracanthus short, reaching to about ⅕ of operculum length.

Abdomen: Ochraceous brown, tergites densely brown speckled all over, sternites unspeckled. Lateroventral row of dark spots almost inconspicuous, by speckling. Segmental hind margins bright red. Anterior margin of 2nd tergite convex middorsally; sides of 2nd tergite weakly swollen and adjacent to tymbal.

Genitalia: Pygofer in lateral view (fig. 31) resembling that of foregoing species. Dorsal margin straight, angularly bending into stout and slightly erect caudodorsal beak. Distal margin straight and more gradually bending into margin of beak. Lateral lobes of pygofer strongly curved inwards, with well-developed, bluntly rounded, lateral protuberances. Ventral margin straight, not concave to base; ventral margins converge to sharp angle at base of pygofer opening (fig. 32). Caudodorsal beak slightly longer than in *B. bemmeleni*, very slender in dorsal view (fig. 34) and sharply pointed apically. Clasper in lateral view (fig. 30) strongly resembling that of two foregoing species, with a very distinct angular clasper heel and rectangular dorsal corner. Clasper strongly bent down to apex at half-length. Distinct crest running along ⅔ of dorsal margin. Clasper hollow short and broadly rounded at apex. Dorsal margins of clasper bases wider apart than in *B. hamiltoni*. Aedeagus in lateral view (fig. 36) concave along margin of pore, with broader basal lobes than in *B. bemmeleni*. Distinct crest at base of S-curvation, between basal lobes (fig. 37). Aedeagus from behind (fig. 35) broader than in *B. bemmeleni*, with a short and broad oval pore.

Measurements: Body length: 26.0 and 27.3 mm; tegmen length: 26.4 and 26.6 mm; head length: 2.0 and 2.3 mm; pronotum length: 2.6 and 2.7 mm; mesonotum length: 5.3 mm; head width: 4.7 and 4.8 mm; width of pronotal collar: 6.4 and 6.5 mm.

Distribution (fig. 1). – *B. wegeneri* is only known from May river, in central west Papua New Guinea.

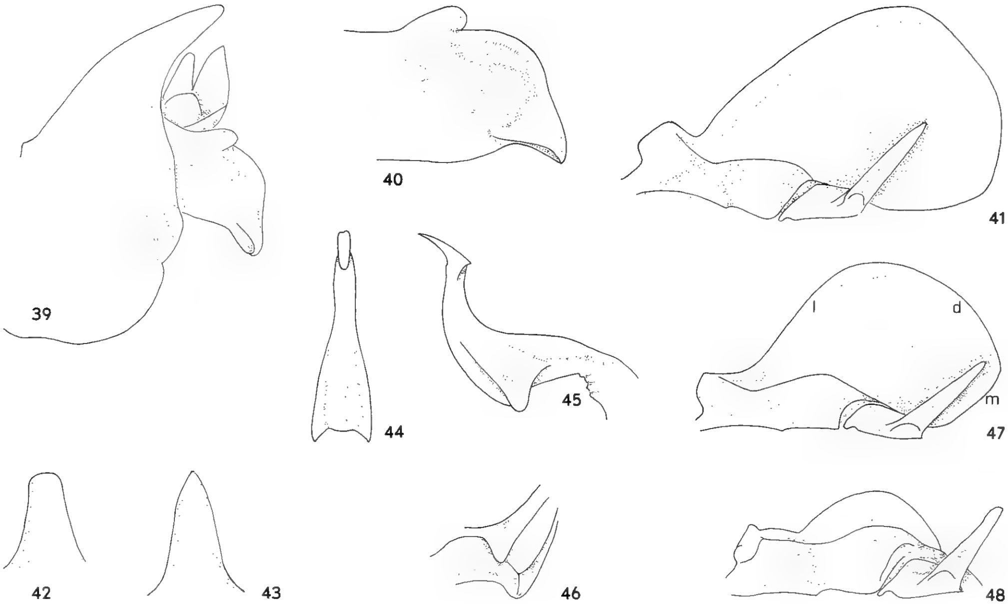
Etymology.– The species is named in honour of the geologist A. Wegener.

Baeturia silveri sp. n.

(figs. 2, 39-48)

Type material. – Holotype ♂: 'NEW GUINEA: NE Purosa, 20-26 km SE Okapa, 1800-2020 m, 28.viii.1964' [print]; 'J. and M. Sedlacek Collectors BISHOP' [print], BPBM. – Paratypes: same data as holotype 1♂, 1♀, BPBM.

Other material. – PAPUA: NEW GUINEA (NE): Kandep,



Figs. 39-48. *Baeturia silveri* sp. n. – 39, pygofer in lateral view; 40, clasper; 41, male operculum, Kandep; 42, male caudodorsal beak in dorsal view; 43, female caudodorsal beak in dorsal view; 44, aedeagus from behind; 45, aedeagus in lateral view; 46, detail crest between lateral lobes of aedeagus; 47, male operculum, holotype; 48, female operculum. Lettering: d = distal margin of operculum; l = lateral margin of operculum; m = medial margin of operculum.

Western Highlands, 8000 ft, 23.xii.1961-14.ii.1962, W. W. Brandt, 1♂, CSIRO.

B. silveri can be recognized by the brown speckled tegmina and short, oblong male operculum.

Description

Body of males light brown or ochraceous, with a colour pattern of dark brown spots and a narrow, immaculate, middorsal band as characteristic for most species of the *B. loriae* group. Female slightly reddish brown with irregularly distributed dark spots. Male abdomen 1.4-1.6× as long as head and thorax, of female 1.1×. Tegmina of males 1.2-1.4× as long as total body length, of female 1.5×.

Head: Ochraceous brown, with dark brown streaks on vertex lobes, almost black between eyes and lateral ocelli. Female with black markings between pronotum and ocelli. Postclypeus sometimes darkened towards lateral margins, 1.6-1.9× as broad as long and broadly rounded at anterior margin. Postclypeus not, or only slightly, swollen ventrally, anterior margin (lateral view) straight or weakly convex. Head narrower than anterior part of pronotum. Distance between lateral ocelli 0.9-1.3× distance between eye and lateral ocellus.

Thorax: Pronotum light brown, darkened along fissures; with a lighter, ochraceous, middorsal band, sharply bordered by irregular black streaks. Middorsal band abruptly widening near pronotal collar, and ending at a vaguely darkened middorsal spot. Middorsal band reddish brown and brown speckled in the female, but clearly recognizable by its black lining. Pronotal collar red-brown, brown speckled. Mesonotum with two distinct semi-circular dark spots at pronotum margin and darkened, greenish tinged, broad lateral streaks, converging from pronotum margin to corners of cruciform elevation. Elevation and narrowly pointed triangular area in front of elevation, light ochraceous. Mesonotum of female, including cruciform elevation, reddish tinged and densely brown speckled.

Tegmina and wings: Hyaline, venation reddish ochraceous. Tegmen with irregular brown markings, predominantly along venation. Hyaline border along hind margin of tegmen broader than in foregoing species and almost as broad as in wing. The 8th apical area of tegmen slightly longer, more slender, than in other species of this group.

Tymbal organ: Not curving inwards, connecting bar between tymbal and abdomen quite short and almost parallel to body axis. Five transverse sclerotized ridges spanning the tymbal, from dorsal to ventral margin. A 6th ridge almost reaching ventral margin, and a 7th, most proximal, ridge running from dorsal margin to about half the tymbal width. Six intercalary ridges seem to form a band across tymbal. Traces of red between tymbal ridges.

Opercula: Male operculum (fig. 47) quite different from that of the three foregoing species, more resembling the opercula found in other groups of *Baeturia.* Basal part of operculum oblong, equally long at lateral and medial margins. Distal part angularly oblong, wider than long and flat against the body, almost completely covering tymbal cavity. Lateral and medial margin almost straight, distal margin weakly convex. Distolateral corner broadly rounded, distomedial corner angular. Opercula wide apart medially, separated by broad and rounded 1st sternite. Meracantus almost as long as operculum. Operculum of Kandep specimen (fig.41) much longer and more directed mesiad, with longer lateral margin. Female operculum (fig. 48) sickle-shaped and erect. Distal margin convex.

Abdomen: Male abdomen light brown, ochraceous in Kandep specimen. Two parallel dorsal rows of dark spots along a narrow light middorsal band and a very clear latero-ventral row of dark spots on segments 3-7. Lateral and ventral sides of abdomen slightly brown stained. Abdomen of Kandep specimen with midlateral band of dark spots, as in *B. fortuini* and *B. loriae.* Anterior margin of 2nd tergite convex medially; sides of 2nd tergite distinctly swollen and adjacent to tymbal. Female abdomen irregularly brown spotted all over, though with unstained light middorsal band. Female caudodorsal beak (fig. 43) pointed at apex.

Male genitalia: Pygofer in lateral view rounded, with stout caudodorsal beak (fig. 39). Dorsal margin straight almost continuous with erect caudodorsal beak. Distal margin straight or slightly concave, broadly rounded into margin of beak. Lateral lobes of pygofer curved inwards, with well-developed, bluntly rounded protuberances, that curve slightly upwards towards pygofer margin. Ventral margin angularly convex, but concave near base of pygofer. Caudodorsal beak (fig. 42) rounded, almost truncate at apex. Clasper in lateral view (fig. 40) strongly rounded and quite different from the three foregoing species. Clasper gradually widening distad to clasper base, so that no clasper heel is formed. Dorsal margin of clasper rounded, forming an almost globular, slightly inwards curved, protrusion at about ¼ its length and, distad to this protrusion, convex to apex. Clasper slightly curved outwards, towards dorsal margin and around aedeagus. Clasper hollow narrow triangular, narrowly rounded at apex. Aedeagus longer than in foregoing species, in lateral view (fig. 45) strongly concave along margin of pore, with long and slender basal lobes. Distinct crest at base of S-curvation between basal lobes (fig. 46). Aedeagus pore (fig. 44) large and oval-shaped, but truncate at apex.

Measurements: Body length ♂: 20.0-22.0 mm ($\bar{x}$ 20.9 mm), ♀: 18.8 mm; tegmen length ♂: 25.9-28.8 mm ($\bar{x}$ 27.2 mm), ♀: 28.6 mm; head length ♂: 1.5-1.7 mm, ♀: 1.8 mm; pronotum length ♂: 2.2-2.5 mm, ♀: 2.5 mm; mesonotum length ♂ 4.2-4.6 mm, ♀: 5.0 mm; head width ♂: 3.8-4.3 mm, ♀: 4.4 mm; width of pronotal collar ♂: 5.4-6.2 mm, ♀: 6.2 mm.

Distribution (fig. 2). – *B. silveri* is known from only two localities, both in the central mountain ranges of Papua New Guinea.

Etymology. – The species is named in honour of the geologist E.A. Silver.

Baeturia pigrami sp. n.

(figs. 2, 49-59)

Type material. – Holotype ♂: 'Museum Leiden Neth New Guinea Exp. Star Range, 1260 m, Sibil, 21.viii.1959, op licht' [print], RMNH.

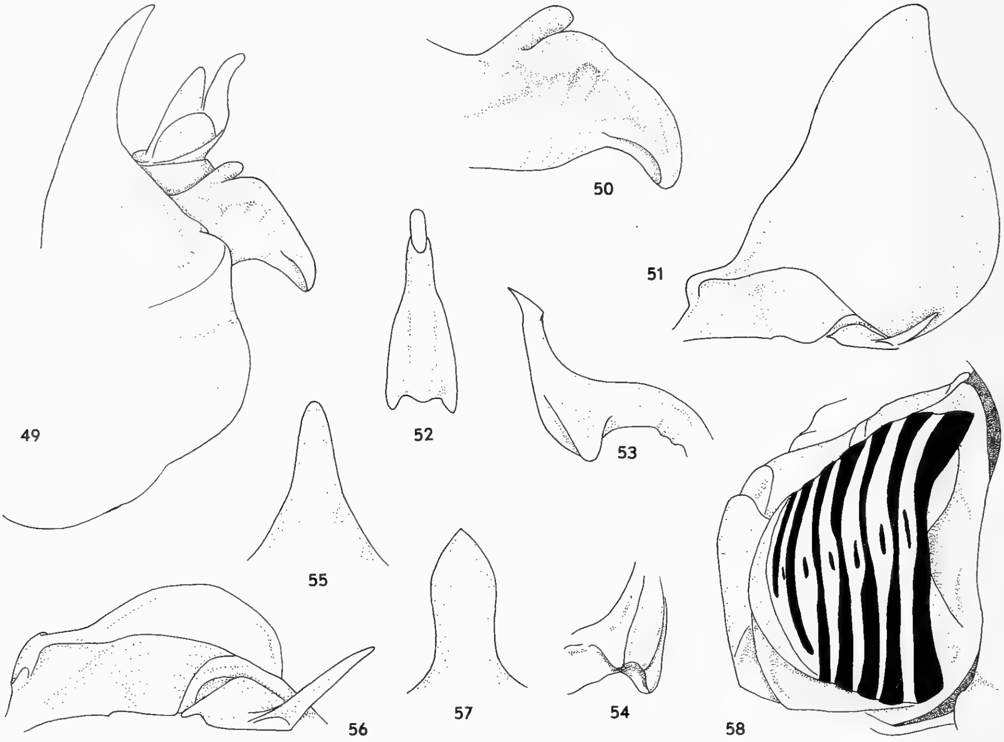
Other material. – PAPUA: NEW GUINEA (NE): Feramin, 150-120 m, 1-6.vi.1959, W.W. Brandt, 2♀, BPBM.

Of this species only one male is available, it resembles *B. silveri* in colour patterns of body and tegmina, and in clasper shape. However, *B. pigrami* is much larger, has very large triangular opercula, and an angularly swollen postclypeus. Two females, with similar colour patterns and from the same area, probably belong to this species.

Description

Body of male dark reddish brown, with very distinct light middorsal band on head and thorax. This band much broader in females, and continuing over abdomen. Male abdomen strongly inflated and 1.5× as long as head and thorax of females 1.0×. Tegmina of male 1.2× as long as total body length, of females 1.4-1.5×.

Head: Light brown with dark stains on vertex lobes, mainly between lateral ocelli and eyes. Vertex and postclypeus with long setae, more densely set than in foregoing speces. Postclypeus unstained, light ochraceous in females, slightly brown suffused in male. Male postclypeus 1.2× as broad as long, in females 1.5 and 2.2×. Postclypeus angularly swollen, almost conical in lateral view (as in fig. 4). Vertex in male very narrow, with ocelli close together. Head narrower than anterior part of pronotum. Male head 1.2× as long as distance between the eyes, in female 0.9×. Distance between lateral ocelli in male 0.7× distance between eye and lateral ocellus, in females 1.1-1.2×.



Figs. 49-58. *Baeturia pigrami* sp. n. – 49, pygofer in lateral view; 50, clasper; 51, male operculum; 52, aedeagus from behind; 53, aedeagus in lateral view; 54, detail crest between lateral lobes of aedeagus; 55, male caudodorsal beak in dorsal view; 56, female operculum; 57, female caudodorsal beak in dorsal view; 58, tymbal.

Thorax: Pronotum dark brown with light ochraceous middorsal band, narrow and sharply defined in male, much broader and more diffuse in females. Pronotal collar slightly reddish and, especially in male, stained with brown. Male mesonotum dark brown, but light ochraceous in triangle-shaped area in front of reddish brown cruciform elevation. Female mesonotum with continuous broad ochraceous middorsal band. Two black spots in front of cruciform elevation in male and female.

Tegmina and wings (fig. 59): Hyaline, though tegmina with irregular brown markings, predominantly along veins, venation reddish brown. Eight apical area short and broad, especially in females. Tegmen and wing with very narrow hyaline border along hind margin.

Tymbal (fig. 58): Five transverse sclerotized ridges spanning the tymbal from dorsal to ventral tymbal margin. A 6th ridge almost reaching ventral tymbal margin, and a 7th, most proximal, ridge running from dorsal margin to only about half the tymbal width. Six intercalary ridges seem to form a band across tymbal. Traces of red between tymbal ridges.

Opercula: Male operculum (fig. 51) very large, reddish ochraceous with dark stains. Basal part of operculum with greatest length at ¼ its width, slightly tapering towards lateal margin, more strongly tapering to base of meracanthus. Distal part triangle-shaped and slightly domed, narrowing towards narrowly rounded, almost pointed apex and reaching to half-length 3rd abdominal segment. Lateral margin of male operculum convex near base, concave at half-length, and weakly convex towards apex. Distomedial margin concave near apex and convex to short and straight medial margin. Opercula close together medially, separated by narrow and weakly elevated 1st sternite. Meracanthus very short, reaching to about ⅙ the operculum length. Female operculum (fig. 56) sickle-shaped, slightly angular at distal margin, and erect. Base of operculum forming narrow rim around base of meracanthus.

Abdomen: Male abdomen brown, dark brown stained dorsally and on sides of 7th and 8th segments, though lighter and reddish tinged, in very narrow

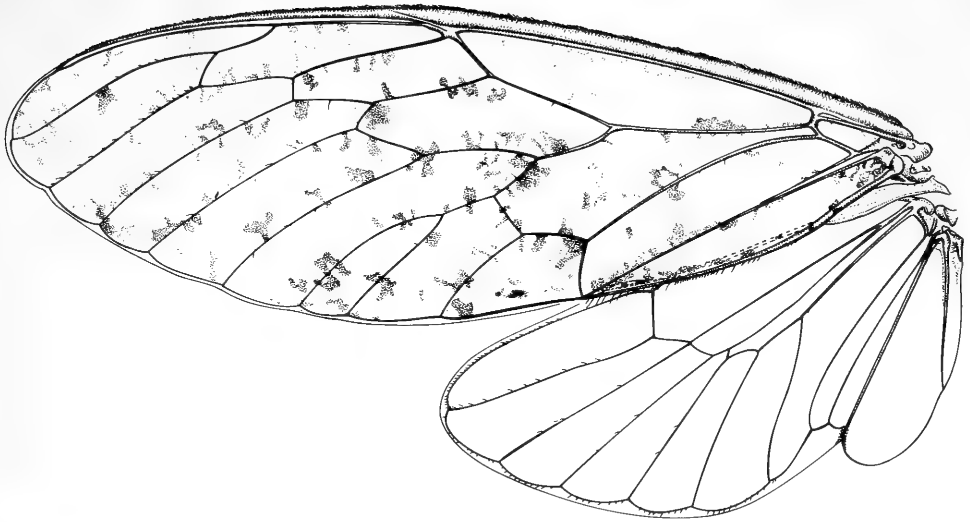


Fig. 59. *Baeturia pigrami* n. sp., female tegmen and wing.

middorsal band. A latero-ventral row of slightly darkened patches, hardly conspicuous. Segmental hind margins slightly red. Anterior margin of 2nd tergite convex middorsally. Lateral parts of 2nd tergite, with auditory capsules, and anterolateral part of 3rd tergite, weakly incurving towards ventral corner of tymbal. Tergites 4-7 with sharp latero-ventral fold. Female abdomen ochraceous, densely stained with irregular brown spots laterally and ventrally, but with broad and immaculate middorsal band. Female caudodorsal beak very characteristic in dorsal view (fig. 57), with greatest width at about ⅔ its length and sharply pointed at apex.

Male genitalia: Pygofer in lateral view (fig. 49). Dorsal margin of pygofer bending gradually into erect caudodorsal beak. Distal margin straight, angularly bending into margin of beak. Lateral lobes of pygofer strongly curving inwards, with well-developed, bluntly rounded protuberances. Ventral margin angularly convex, but strongly concave to base of pygofer. Caudodorsal beak in dorsal view (fig. 55) very slender, narrowly rounded, almost pointed at apex. Clasper (fig. 50) closely resembling that of *B. silveri*, not forming a clasper heel and slightly bent down to apex. Dorsal margin of clasper strongly bent upwards from clasper base, forming a long finger-shaped, slightly incurved protuberance. This protuberance distinctly longer than in *B. silveri*. Clasper strongly bent outwards distally of this protuberance, and forming a broadly rounded dorsal crest. Clasper hollow longer than in *B. silveri*. Aedeagus in lateral view (fig. 53) slightly concave along margin of pore, with narrow and elongate lateral lobes. Aedeagus with distinct crest at base of S-curvation, between lateral lobes (fig. 54). Aedeagus pore broad and short, oval-shaped (fig. 52).

Measurements: Body length ♂: 27.0 mm, ♀: 20.9 and 22.4 mm; tegmen length ♂: 32.0 mm, ♀: 31.3 and 31.8 mm; head length ♂: 2.6 mm, ♀: 2.1 and 2.3 mm; pronotum length ♂: 2.9 mm, ♀: 3.5 and 3.6 mm; mesonotum length ♂: 6.1 mm, ♀: 6.1 and 6.6 mm; head width ♂: 5.4 mm, ♀: 5.4 and 5.7 mm; width of pronotal collar ♂: 7.7 mm, ♀: 7.8 and 8.4 mm.

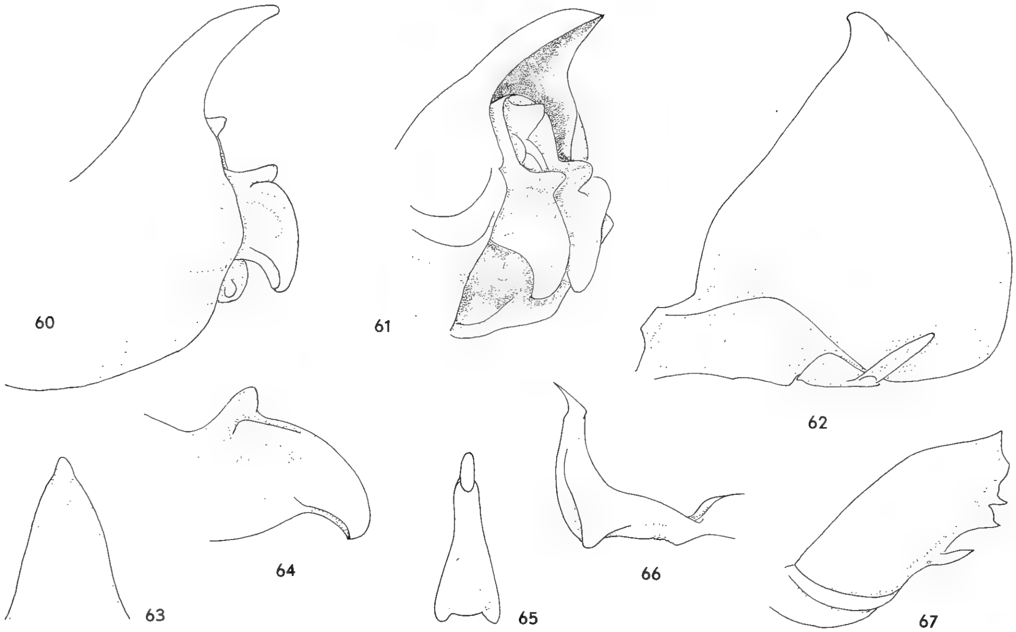
Distribution (fig. 2). – The only male known of this species comes from Sibil, Star Range, in the central mountain ranges of New Guinea. Two females, that probably belong to this species, come from nearby Feramin.

Etymology. – The species is named in honour of the geologist C. J. Pigram.

Baeturia daviesi sp. n.
(figs. 2, 60-66)

Type material. – Holotype ♂: 'Papua, Mt Lamington, G. H. Muray, 1924' (written); 'W. W. Froggatt Collection' (print); 'CANB' (print), CSIRO.

Of this species only one male is available. *B. daviesi* is very similar to *B. pigrami* in the shapes of the male operculum and genitalia, but *B. daviesi* is distinguished by a distinctly smaller size, immaculate tegmina and the absence of distinct colour markings, characteristic to *B. pigrami* and most other species of



Figs. 60-67. – 60-66, *Baeturia daviesi* n. sp., 60, pygofer in lateral view; 61, pygofer from aslant; 62, operculum; 63, caudodorsal beak in dorsal view; 64, clasper; 65, aedeagus from behind; 66, aedeagus in lateral view. – 67, *Baeturia hartonoi* sp. n., fore femur.

the *B. loriae* group, though its abdomen is densely brown speckled, as in *B. wegeneri.*

Description

Body dull grey-brown with vaguely lighter coloured middorsal band, slightly more distinct on pronotum. Abdomen 1.4× as long as head and thorax. Tegmina 1.1× as long as body length.

Head: Greyish brown, with vaguely darkened spots between eyes and lateral ocelli. Postclypeus triangularly protruding, 1.5× as wide as long. Postclypeus angularly swollen ventrally, almost conically protruding in lateral view (as in fig. 4) Head narrower than anterior part of pronotum. Vertex very narrow, with ocelli close together; distance between lateral ocelli about as wide as frontal ocellus and 0.8× the distance between eye and lateral ocellus.

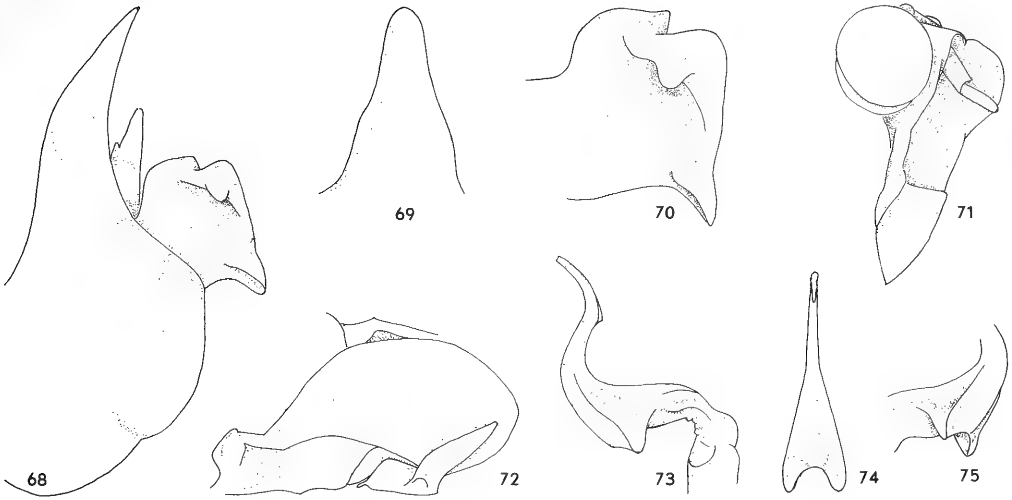
Thorax: Pronotum greyish brown with vaguely lighter coloured, middorsal band, most conspicuous over proximal half. Mesonotum brown with a greenish tinge, without special colour markings, apart from two dark spots in front of slightly reddish cruciform elevation.

Legs: Proximal spine of fore femur rather short, about as long as distance to middle spine.

Tegmina and wings: Hyaline and immaculate, veins ochraceous. Tegmina with fairly short, square, 8th apical area, and very narrow hyaline border along hind margins. This border is slightly broader in wing.

Tymbal organ: Tymbal not curved inwards towards distal margin; connecting bar between tymbal and abdomen almost parallel to body axis. Six transverse sclerotized ridges spanning the tymbal from dorsal to ventral tymbal margin. Most proximal ridge narrowing considerably towards the ventral tymbal margin and only just reaching it. Six short intercalary ridges seem to form a band across the tymbal. Traces of bright red between the ridges, especially on dorsal half of tymbal.

Operculum (fig. 62): Very similar to that of *B. pigrami,* but smaller, with dark stains near apex. Basal part of operculum somewhat quintangular, with its greatest length at base of lateral margin of distal part, weakly tapering to distolateral corner and more strongly tapering to base of meracanthus. Distal part large, triangle-shaped and slightly domed, curved to abdomen near its almost pointed apex, and reaching to about half-lenght abdominal segment 3. Proximal ⅓ of lateral margin slightly convex, distal ⅔ almost straight to apex. Distomedial margin concave near



Figs. 68-75. *Baeturia hartonoi* sp. n. – 68, pygofer in lateral view; 69, caudodorsal beak in dorsal view; 70, clasper; 71, postclypeus in lateral view; 72, operculum; 73, aedeagus in lateral view; 74, aedeagus from behind; 75, detail crest between lateral lobes of aedeagus.

apex and convex to almost rectangular medial corner. Medial margin short and straight. Opercula close together medially, separated by narrow and distally lobate 1st sternite. Meracanthus very short, reaching to about ⅙ the operculum length.

Abdomen: Light brown with brown speckling, darker brown dorsally and lateroventrally, with a slightly lighter coloured narrow middorsal line, though without a distinct row of latero-ventral spots. Segmental hind margins bright red. First tergite only slightly shorter than 2nd. Anterior margin of 2nd tergite weakly convex middorsally. Ventrolateral part of 2nd tergite, auditory capsules, and anterolateral corners of 3rd tergite, curved inwards towards ventral corner of tymbal. Anterolateral part of 2nd tergite adjacent to tymbal.

Genitalia: Pygofer in lateral view (fig. 60) slender. Dorsal margin straight, continuous with straight, slender and erect caudodorsal beak. Distal margin of pygofer straight, angularly bending into margin of beak. Lateral lobes of pygofer bent inwards, with small, bluntly rounded protuberances. Caudodorsal beak very short, pointed at apex (fig. 63). Ventral margin convex, but weakly concave to base of pygofer; ventral margins converging to sharp angle at base of pygofer opening (fig. 61). Clasper (fig. 64) much resembling that of *B. pigrami*, without clasper heel, but with dorsal margin strongly bent upwards from clasper base, forming a long finger-shaped, slightly incurved protuberance. Dorsal margin strongly bent outwards distad to protuberance, forming a broad and distinctly laterally protruding crest. Clasper slightly bending down to rounded apex. Apical part of clasper with small clasper hollow. Aedeagus in lateral view (fig. 66) slightly concave along margin of pore, with narrow and elongate lateral lobes. Aedeagus with distinct crest at base of S-curvation, between lateral lobes. Aedeagus pore broad and short, oval-shaped (fig. 65).

Measurements: Body length: 23.9 mm; tegmen length: 25.6 mm; head length: 2.0 mm; pronotum length: 2.8 mm; mesonotum length: 5.1 mm; head width: 4.8 mm; width of pronotal collar: 6.5 mm.

Distribution (fig. 2). – The only specimen available comes from Mt. Lamington on the Papuan Peninsula.

Etymology. – The species is named in honour of the geologist H.L. Davies.

Baeturia hartonoi sp. n.
(figs. 1, 67-75)

Type material. – Holotype ♂: 'PNG: NEW GUINEA: SE: S Highlands Distr.: Kutubu: Tugiri, 1000 m, 7-9.ii.1978' (print); 'J. L. Gressitt Collector BISHOP Museum' (print), BPBM.

Of this species only one male specimen is available. *B. hartonoi* is a small species, that can be recognized by an elongate apical part of aedeagus and a lateral protuberance on the clasper.

Description

Body ochraceous brown, head and thorax slightly reddish. Abdomen with conspicuous dark dorsal and midlateral bands, and slightly inflated. Abdomen 1.3× as long as head and thorax. Tegmina 1.3× as long as body length.

Head: Brown, slightly darkened around ocelli, but not as distinctly marked as in some other species of the *B. loriae* group. Postclypeus distinctly protruding beyond vertex lobes, broadly rounded at anterior margin, and 1.8× as broad as long. Postclypeus only very slightly swollen ventrally, anterior margin (lateral view) weakly convex (fig. 71). Head narrower than anterior part of pronotum. Distance between lateral ocelli about 1.5× the width of frontal ocellus and 1.2× the distance between eye and lateral ocellus.

Thorax: Pronotum, plain brown with no special markings. Mesonotum almost plain grey-brown, cruciform elevation slightly lighter ochraceous. Two vaguely darkened spots in front of elevation hardly visible.

Legs: Proximal spine of fore femur strongly bent, almost adjacent to femur, and shorter than distance to middle spine (fig. 67).

Tegmina and wings: Hyaline and immaculate, venation ochraceous. Tegmen with narrow hyaline border along hind margin, wing with fairly broad border.

Tymbal organ: Tymbal not curved inwards towards distal margin; connecting bar between tymbal and abdomen almost parallel to body axis. Six sclerotized transverse ridges spanning the tymbal from dorsal to ventral tymbal margin. A 7th, most proximal, ridge almost reaching ventral tymbal margin. Seven short intercalary ridges seem to form a midlateral band across tymbal.

Operculum (fig. 72): Short and oblong shaped as in *B. silveri.* Basal part of operculum oblong; equally long at lateral and medial margins. Distal part broader than long, flat against the body. Operculum directed mesiad, so that connecting bar between tymbal and abdomen becomes partly visible in ventral view. Lateral margin very short, bending gradually into slightly convex distal margin. Distomedial corner angular. Medial margin almost straight. Medial part of operculum reaching beyond margin of abdominal segment 2. Opercula widely separated medially, by broad and rounded 1st sternite. Meracanthus reaching to about 3/4 the operculum length.

Abdomen: Ochraceous, greenish tinged, darkened in dorsal and lateral bands, though less intensely in narrow middorsal line. Latero-ventral row of dark spots most clear on segments 3-5 on right side, and on segments 3-4 on left side of body, but faded in successive segments. First tergite very short medially. Anterior margin of 2nd tergite weakly convex medially. Lateral parts of 2nd tergite not incurved.

Genitalia: Pygofer in lateral view (fig. 68). Dorsal margin straight and angularly bending into slender and erect caudodorsal beak. Distal margin broadly rounded into margin of beak. Lateral lobes of pygofer strongly bent inwards, with small and bluntly rounded protuberances. Ventral margin weakly convex, but distinctly concave towards base of pygofer. Caudodorsal beak in dorsal view (fig. 69) slender and pointed at apex. Clasper very broad, squarely rounded in lateral view (fig. 70), abruptly broadening dorsally, distally of clasper base, so that no clasper heel is formed. Dorsal margin angularly bending down at about half-lenght, forming a small and slightly incurving dorsal protrusion on clasper. This protrusion seems to function as a support or lock for the aedeagus, since it curves inwards, around aedeagus. This in contrast with the dorsal protrusions on the claspers of the three foregoing species, which lie proximally of the aedeagus. Dorsal margin of clasper bending into almost straight distal margin, at rounded, slightly inwards curved, distodorsal corner. Claspers slightly diverging towards pointed apices. Apical part of clasper directed downwards, with narrow clasper hollow. Lateral side of clasper forming a small and angular, laminiform lateral protrusion, unique for this species. Aedeagus elongate in apical part of its S-curvation (fig. 71), with narrowly elongate lateral lobes and truncate apex. Aedeagus with distinct crest between lateral lobes (fig. 75), crest very low mid-between basal lobes, and strongly concave (seen from behind (fig. 74). Aedeagus pore narrow and sharply incised, truncate at aedeagus apex.

Measurements: Body length: 19.0 mm; tegmen length: 24.5 mm; head length: 1.8 mm; pronotum length: 2.5 mm; mesonotum length: 4.3 mm; head width: 4.3 mm; width of pronotal collar: 5.8 mm.

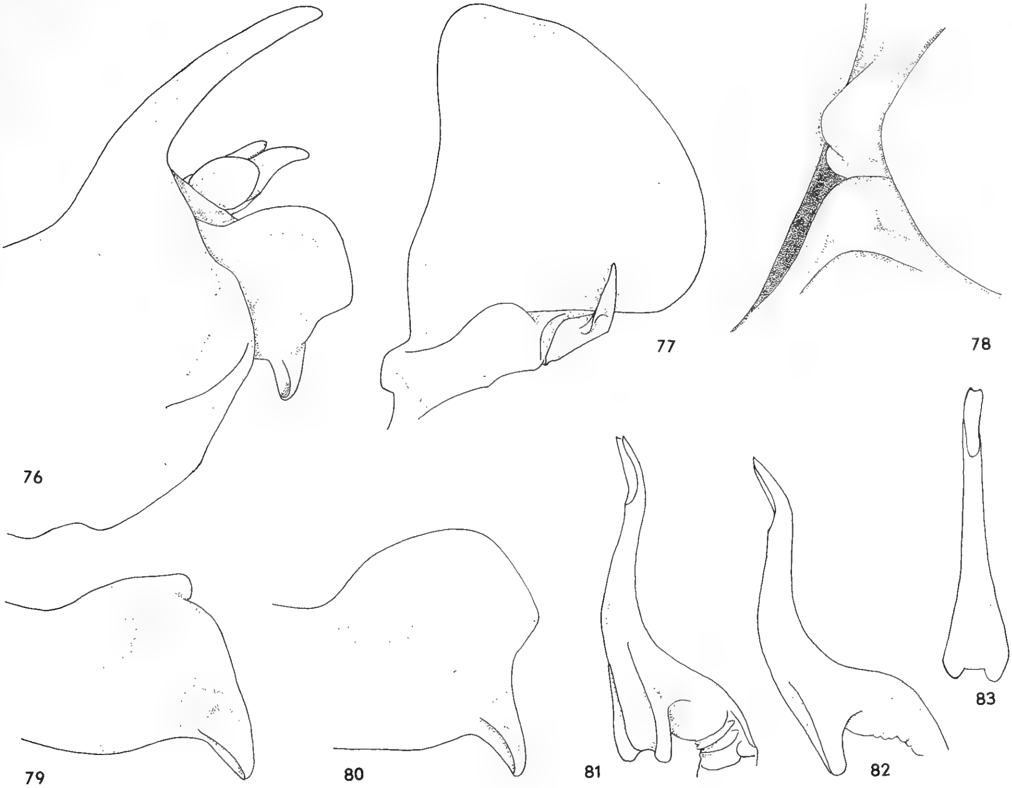
Distribution (fig. 1). – The only specimen known comes from Lake Kutubu, in central Papua New Guinea, just south of the central mountain ranges.

Etymology. – The species is named in honour of the geologist H.M.S. Hartono.

Baeturia fortuini sp. n.
(figs. 2, 76-87)

Type material. – Holotype ♂: 'Coll R.I. Sc. N.B. Papua New Guinea Morobe pr.: Anguaia, 1800 m, 21.v.1988 (st. 050) J. van Stalle, I.G. no.: 27363' (print, orange label), KBIN. – Paratypes: PAPUA: NEW GUINEA (NE): Bulldog rd., 60 km S Wau, 2070 m, 22-31.v.1964, J. Sedlacek, 1♂, BPBM; Dowalo, W Zenag, 2000 m, 4.ii.1971, J.L. Gressitt, 2♀, BPBM; Vagau, Herzog Mts., 4000 ft, 4-17.i.1965, M.E. Bacchus, 1♂, BMNH; U. Watut SW, 1500 m, 3.v.1968, J.L. Gressitt, 1♂, BPBM; same data but 1100-1600 m, 30.iv.1968, 1♂, BPBM.

Other material. – Mt Missim, 2100 m, 15.iii.1968, P.



Figs. 76-83. *Baeturia fortuini* sp. n. – 76, pygofer in lateral view; 77, male operculum; 78, first sternite; 79, clasper, Mt. Missim; 80, idem, holotype; 81, aedeagus from aslant; 82, aedeagus in lateral view; 83, aedeagus from behind.

Colman, 1♂, 1♀, BPBM; Wau, ix,1965, J. Sedlacek, 1♀, BPBM; Wau, Morobe Dist, 1200-1300 m, 14-17.i.1963, J. Sedlacek, 1♀, BPBM; Wau, Morobe Dist., Mt. Missim, 2000 m, 1.v.1966, O. R. Wilkes, 1♂, BPBM.

The most striking character of this species is the row of bronzed triangular spots along the hind margins of the tegmina. This characer is also found in *B. loriae*, described next. *B. fortuini* is very similar to *B. loriae*, but can be separated from that species by its larger and triangle-shaped male operculum.

Description

Body of males light brown or greenish tinged, with dark markings, forming dorsal and lateral bands on abdomen, and with narrow and light middorsal band over whole length of body. Females provided with irregular dark patches, and a narrow and light middorsal band. Male abdomen 1.4-1.7× as long as head and thorax, of females 0.9-1.0×. Tegmina of males 1.2-1.4× as long as total body length, of females 1.4-1.7×.

Head: Greenish or brown. Vertex and postclypeus with very long setae, as in *B. pigrami*. Dark spots on vertex lobes, between eyes and ocelli, and on lateral parts of postclypeus. Postclypeus triangularly protruding and 1.4-2.2× as wide as long. Postclypeus angularly swollen ventrally (as in fig. 4). Head narrower than anterior part of pronotum. Distance between lateral ocelli 1.1-1.4× as long as distance between eye and lateral ocellus.

Thorax: Greenish, with light brown streaks, partly along oblique fissures, and with two pairs of paramedian black spots, at both ends of a broad, greenish tinged, and immaculate middorsal band. Long setae, predominantly on these black areas and on pronotal collar. Colour pattern on mesonotum very variable. Cruciform elevation and small triangle-shaped area in front of elevation light brown or bright green, lateral parts of mesonotum either completely, or only the distal half, dark brown to castaneous.

Legs: Ochraceous, fore femora with dark brown streaks. Proximal spine of fore femur shorter than distance to middle spine.

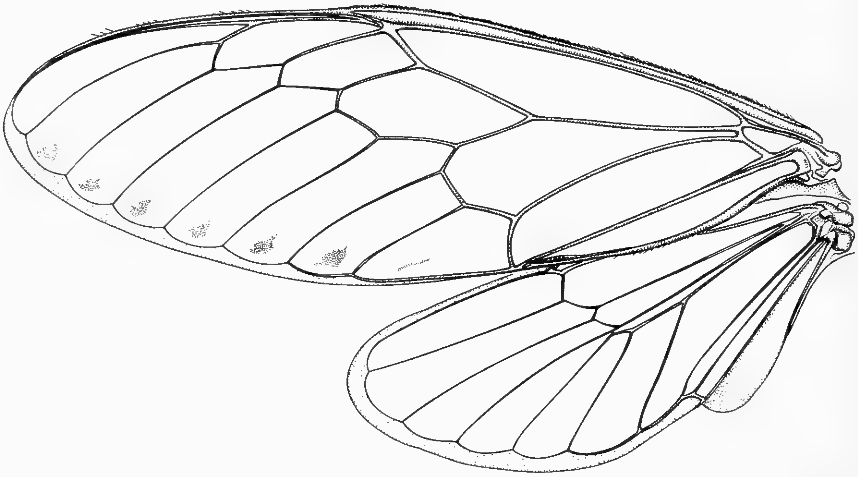


Fig. 84. *Baeturia fortuini* sp. n., male tegmen and wing.

Tegmina and wings (fig. 84): Hyaline, though tegmen with a regular row of seven triangular dark spots, close to hind margin, with one spot in each apical area from apical area 2 to 8. The 8th apical area of tegmen generally broad and almost square-shaped. Venation red. Tegmina and wings with fairly broad hyaline border along hind margins.

Tymbal organ: Tymbal somewhat incurved ventrally, connecting bar between abdomen and tymbal directed inwards. Six transverse sclerotized ridges spanning the tymbal, from dorsal to ventral tymbal margin. Most proximal ridge narrowing considerably towards ventral margin and only just reaching it. Some specimens with a 7th ridge, hardly separated from proximal tymbal margin, running from dorsal margin to about half-width of tymbal. Six short intercalary ridges seem to form a midlateral band across tymbal.

Opercula: Male operculum (fig. 77) ochraceous with longitudinal dark streaks on distal part. Basal part of operculum almost oblong, slightly elongate at half-width and slightly tapering towards medial margin. Distal part very large, triangular, and slightly domed, narrowing towards narrowly rounded and almost pointed apex, and reaching to about half-length of abdominal segment 3. Lateral margin of operculum convex near operculum base, concave at half-length and convex again near apex. Operculum strongly curved to body along distomedial margin. Distomedial margin weakly convex. Medial margin short and straight. Opercula close together medially, separated by globularly protruding 1st sternite (fig. 78). Meracanthus very short, reaching to about ⅙ the operculum length. Female operculum (fig. 85) sickle-shaped and erect, with weak crest along its distal margin. Basal part of female operculum forming a narrow rim around base of meracanthus.

Abdomen: Male abdomen light brown or greenish. Dark brown markings forming two dorsal bands, separated by a narrow and lighter coloured middorsal line, and lateral bands over abdomen. These bands are interrupted by lighter, often reddish coloured, segmental hind margins. Latero-ventral row of dark spots on segments 3-7 very clear. Ventral side of male abdomen immaculate, with bright red segmental hind margins. First tergite quite long and weakly curved. Anterior margin of 2nd tergite medially straight. Lateral parts of 2nd tergite hardly inflated, forming a weak crest along anterolateral margin, auditory capsules somewhat removed from ventral corner of tymbal. Female abdomen more intensely and irregularly dark stained. Dark lateral bands less conspicuous than in males. Light middorsal line often very clear, broader than in males. Segmental hind margins ochraceous or reddened. Ventral side of female abdomen dark brown stained. Female caudodorsal beak (fig. 86) light ochraceous, long and slender, pointed at apex.

Male genitalia: Pygofer in lateral view (fig. 76) rather stout, with very long and slender caudodorsal beak. Dorsal margin concave, gradually bending into convexly bent beak. Distal margin straight, almost forming right angle with margin of beak. Lateral lobes of pygofer strongly curving inwards towards distal margin, with well-developed, angularly rounded, protuberances. Ventral margin weakly convex, distinctly concave near base of pygofer. Caudodorsal beak in dorsal view (fig. 87) long and slender, pointed at apex. Clasper in lateral view (fig. 80) square-shaped as in *B. hartonoi*, dorsally abruptly broadening, distally of clasper base, so that no clasper heel is formed. Dorsal part of clasper forming a broad and laminiform protrusion, broadly rounded at its proximal corner, and rectangular at its distal corner. Claspers very narrow and directed downwards towards weakly diverging apices, and with a narrow and rounded clasper hollow. Both specimens from Mt. Missim with quite different clasper (fig. 79), more resembling those of *B. silveri* and *B. loriae*, with broad and laminiform, but less angular, dorsal protrusion and forming a very small, slightly inwards curved, protrusion at its rectangular distal corner. Aedeagus in lateral view (fig. 82) very long and slender, with extremely long and slender lateral lobes, and a very distinct ridge between these lobes (fig. 81). Aedeagus pore slightly larger than in foregoing species. Margin of aedeagus pore distinctly concave at aedeagus apex (fig. 83).

Measurements: Body length ♂: 22.3-24.5 mm ($\bar{x}$ 23.4 mm ± 0.9), ♀: 21.6-22.8 mm ($\bar{x}$ 22.2 mm ± 0.4); tegmen length ♂: 27.0-31.3 mm ($\bar{x}$ 29.8 mm ± 1.5), ♀: 31.4-36.6 mm ($\bar{x}$ 34.6 mm ± 1.7); head length ♂: 1.7-2.0 mm ($\bar{x}$ 1.9 mm), ♀: 2.1-2.3 mm ($\bar{x}$ 2.2 mm); pronotum length ♂: 2.5-3.0 mm ($\bar{x}$ 2.8 mm), ♀: 3.2-3.5 mm ($\bar{x}$ 3.4 mm); mesonotum length ♂: 4.5-5.4 mm ($\bar{x}$ 4.9 mm), ♀: 5.7-6.4 mm ($\bar{x}$ 6.1 mm); head width ♂: 4.6-5.2 mm ($\bar{x}$ 5.0 mm), ♀: 5.5-5.9 mm ($\bar{x}$ 5.7 mm); width of pronotal collar ♂: 6.2-7.4 mm ($\bar{x}$ 6.8 mm), ♀: 7.6-8.2 mm ($\bar{x}$ 7.9 mm).

Distribution (fig. 2). – *B. fortuini* seems restricted to a small area in Papua New Guinea, just south and west of the Huon Gulf.

Etymology. – The species is named in honour of the geologist A. R. Fortuin.

Baeturia loriae Distant, 1897 stat. n.

(figs. 2, 88-93)

Baeturia loriae Distant, 1897: 382.
Gymnotympana loriae; Distant 1906: 158; Metcalf 1963: 153.

Identification of types: In his description Distant (1897) indicates that the type series of this species contains at least one male and one female, originating from Moroka and Paumomu river, and collected by Loria. Two males from Moroka could be traced: one with a type label was found in the BMNH, the other, with identification label: '*Baeturia loriae* Dist.', was located in the MSNG. Females, or material from Paumomu river, that could possibly belong to the type series, were not found. The specimen from the BMNH is hereby designated lectotype, the other specimen belongs to a different species, possibly *Baeturia bicolorata* Distant. The lectotype bears the following labels: 'Type' (round label, red margin); '*loriae* Dist' (written); 'New Guinea SE Moroka, 1300 m, Loria, vii-xi.93' (print); 'Distant coll. 1911. 383' (print).

Classification. – The reasons for the re-allocation of this species in the genus *Baeturia* are given in the paragraph on phylogeny of the *B. loriae* group

Only one male of this species is known. *B. loriae* closely resembles *B. fortuini* in body markings, and shares the triangular dark spots in apical areas of tegmina with that species. *B. loriae* can be separated from *B. fortuini* by its flat and broader, almost rectangular, operculum.

Description

Head and thorax brown, abdomen olive green. Dark, almost black, markings forming regular dorsal and lateral bands on abdomen. A narrow and immaculate middorsal band over whole length of body. Abdomen 1.5× as long as head and thorax. Tegmen 1.2× as long as total body length.

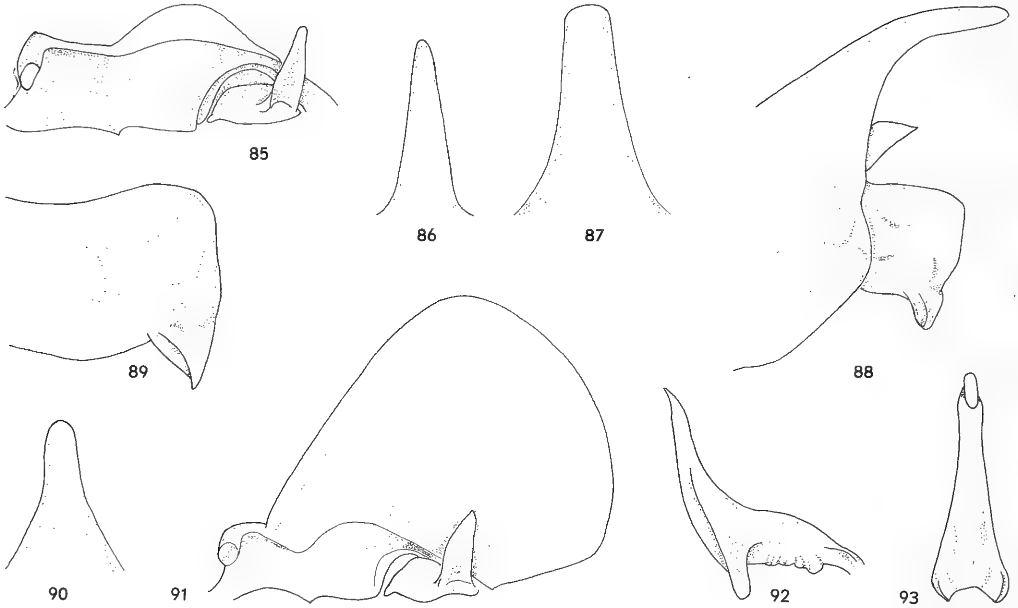
Head: Grey-brown, with dark brown spots on vertex lobes and lateral parts of postclypeus. Postclypeus broadly protruding, 1.8× as wide as long, anterior margin broadly rounded. Postclypeus distinctly swollen and ventrally conically protruding, anterior margin (lateral view) broadly rounded. Head narrower than anterior part of pronotum. Distance between lateral ocelli 1. 4× distance between eye and lateral ocellus.

Thorax: Pronotum ochraceous, with brown streaks in and along oblique fissures and two pairs of dark brown spots at both ends of immaculate and lighter coloured middorsal band. Mesonotum with two large and triangle-shaped dark spots, in front of cruciform elevation, and two brown straeks laterad of elevation.

Tegmina and wings: Hyaline, veins ochraceous. Tegmina, as in *B. fortuini*. with a regular row of seven triangular dark spots, close to hind margin, one spot in each apical area from area 2 to 8. The 8th apical area of tegmen short, almost square-shaped. Tegmina and wings with a fairly broad hyaline border along hind margin.

Tymbal organ: Six transverse sclerotized ridges spanning the tymbal, from dorsal to ventral margin. Most proximal ridge narrowing considerably towards ventral tymbal margin and only just reaching it. A 7th ridge, hardly separated from proximal tymbal margin, running from dorsal margin to about half width of tymbal. Six short intercalary ridges seem to form a midlateral band across tymbal.

Operculum (fig. 91): Ochraceous. Basal part of operculum oblong. Distal part very large and angular, flat against body. Lateral margin straight, bending into convex medial margin, at almost rectangular distal corner. Medial margin bending angularly back to base of meracanthus, at medial corner. Meracanthus



Figs. 85-93. – 85-87, *Baeturia fortuini* sp. n., 85, female operculum; 86, female caudodorsal beak in dorsal view; 87, male caudodorsal beak in dorsal view. – 88-93, *Baeturia loriae*, 88, pygofer in lateral view; 89, clasper; 90, caudodorsal beak in dorsal view; 91, operculum; 92, aedeagus in lateral view; 93, aedeagus from behind.

very short, reaching to about ¼ the operculum length.

Abdomen: Greenish brown. Dark brown markings forming two dorsal bands, separated by a lighter narrow middorsal line, and lateral bands over abdomen. These bands are interrupted by lighter, often reddish coloured, segmental hind margins. Latero-ventral row of dark spots on segments 3-7 very clear. Ventral side of male abdomen immaculate, with bright red segmental hind margins. Anterior margin of 2nd tergite straight medially. Lateral parts of 2nd tergite hardly inflated, forming a weak crest along anterolateral margin, auditory capsules somewhat removed from ventral corner of tymbal.

Genitalia: Pygofer in lateral view (fig. 88) slender, with long and slender, slightly bent, caudodorsal beak. Dorsal margin of pygofer straight, angularly bending into beak. Distal margin straight and broadly rounded into margin of beak. Lateral lobes of pygofer strongly bent inwards, with bluntly rounded protuberances. Ventral margin weakly convex, distinctly concave near base of pygofer. Margins of caudodorsal beak in dorsal view (fig. 90) converging from base, but parallel in apical part of beak. Caudodorsal beak rounded at apex. Clasper in lateral view (fig. 89) angular, square-shaped, as in the Mt. Missim specimens of *B. fortuini*. Dorsal margin of clasper very slightly bending upwards, distally of clasper base, so that no clasper heel is formed. Straight dorsal margin bending almost rectangularly into straight distal margin. Distal margin concavely incurved, just before reaching downwards directed apical part of clasper. Clasper hollow small and narrowly rounded at clasper apex. Aedeagus in lateral view (fig. 92) very long and slender, with extremely long and slender lateral lobes, and a very distinct ridge between lobes. Aedeagus pore oval (fig. 93).

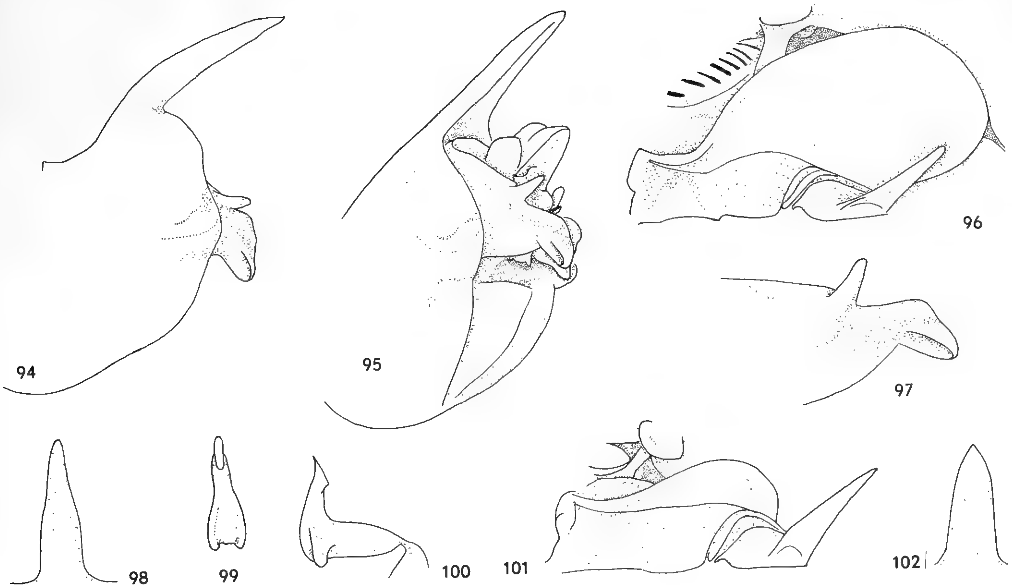
Measurements: Body length: 24.1 mm; tegmen length: 30.0 mm; head length: 1.9 mm; pronotum length: 2.9 mm; mesonotum length: 5.0 mm; head width: 5.2 mm; width of pronotal collar: 6.9 mm.

Distribution (fig. 2). – The only specimen available comes from Moroka on the Papuan Peninsula.

Baeturia tenuispina Blöte, 1960
(figs. 1, 94-102)

Baeturia tenuispina Blöte, 1960: 72, figs. 22-23. – Duffels & Van der Laan 1985: 254.

Material examined. – PAPUA: NEW GUINEA (NE): Gewak, Salawaket Range, 1530 m, 6.ix.1956, E.J. Ford Jr., 1♂, BPBM; Gurakor, 7.vii.1965, H. Pyka, 1♂, 7♀, SMN; Kokoda, 1200 ft, viii.1933, L.E. Cheesman, 1♂ holotype *Baeturia tenuispina* Blöte, 3♂, BMNH; same data, 1♂ paratype, RMNH; same



Figs. 94-102. *Baeturia tenuispina* Blöte. – 94, pygofer in lateral view; 95, pygofer from aslant; 96, male operculum; 97, clasper; 98, male caudodorsal beak in dorsal view; 99, aedeagus from behind; 100, aedeagus in lateral view; 101, female operculum; 102, female caudodorsal beak in dorsal view.

data but vi-x.1933, 9♂, 65♀, BMNH; Kokoda, xi.1957, 2♀, BMNH; Kokoda, 400 m, 15-20.xi.1965, J. and M. Sedlacek, 1♂, BPBM; Kokoda-Pitoki, 400 m, 25.iii.1956, J.L. Gressitt, 1♂, BPBM; Sangeman Village nr Busu R., NE of Lae, 25 m, 30.viii.1957, D. Elmo Hardy, 3♂, BPBM; Wau, Morobe Dist., 1200 m, 29-30.ix.1963, J. Sedlacek, 1♂, 1♀, BPBM; PAPUA: NEW GUINEA (SE): Bori nr Sasambota, Popondetta Subdist., 31.x.1963, D.K. McAlpine, 1♂, AMS; Mt Lamington Dist., Northern Division, 1925, C.T. McNamara, 1♀, AMS; same data but vii.1927, 2♀; i-ii.1929, 2♂, 1♀, all AMS; Popondetta, 25 m, v.1966, Shanahan-Lippert, 1♂, BPBM; same data but vi.1966, 2♂, BPBM; D'ENTRECASTAUX ISLANDS: GOODENOUGH: Goodenough Id., x.1943, F/D, C. Ralph, 1♂, MVM.

Males of *B. tenuispina* are easily recognized by the long spine-shaped caudodorsal beak and a small finger-shaped protrusion on the clasper heel. This protrusion forms the only indication that the species might be related to the *B. loriae* group.

Description

Body ochraceous to castaneous brown, covered with brown speckling. Females on average shorter than males, but with equally large head and thorax. Abdomen of males 1.3-1.5× as long as head and thorax, of females 1.0-1.2×. Tegmen of males 1.1-1.2× as long as body length, of females 1.3-1.4×.

Head: Ochraceous, dark brown or blackish speckled. Postclypeus angularly protruding, 1.7-2.3× as wide as long, anterior margin convex. Postclypeus slightly swollen ventrally, anterior margin (lateral view) weakly convex.

Thorax: Pronotum ochraceous brown speckled medially, between medial pair of oblique fissures. Mesonotum greyish brown, densely brown speckled but without any distinct black spots in front of cruciform elevation.

Tegmina and wings: Hyaline, venation ochraceous or reddish, often quite densely set with short setae. Tegmen with 8 apical areas, the 8th apical area longer than in most species of the *B. loriae* group. No sexual dimorphism in wings. Tegmen with narrow hyaline border along hind margin, this border distinctly broader in wing.

Tymbal organs: Tymbal not curved inwards towards distal margin; connecting bar between tymbal and abdomen almost parallel to body axis. Seven sclerotized transverse parallel ridges spanning the tymbal from dorsal to ventral margin and an 8th, most proximal ridge nearly reaching ventral margin. Seven short intercalary ridges seem to form a midlateral band across tymbal. Tymbal reddish coloured at dorsal margin and dorsally between ridges.

Opercula: Male operculum (fig. 96) quite large and almost completely covering tymbal cavity in ventral view. Distal part of male operculum broad, angularly rounded, oblong and curved towards body. Lateral margin short, convexly bending into long weakly convex distal margin. Distomedial and medial margins weakly convex. Medial corners rounded. Meracanthus reaching to about ½ operculum length. Female operculum (fig. 101) with very short, sickle-shaped and erect distal part. Medial margin short and straight

Abdomen: Male abdomen light brown or ochraceous, densely brown speckled dorsally; ventral part, and sometimes lateral parts of segments 4-5, unspeckled. Latero-ventral row of darkened spots generally very distinct on segments 3-4, but often only vaguely visible on segments 5-7. Segmental hind margins bright red. First tergite quite short. Anterior margin of 2nd tergite medially convex. Lateral parts of 2nd tergite distinctly swollen adjacent to tymbal. Female abdomen greyish brown and densely speckled, latero-ventral row of spots less distinct. Segmental hind margins often ochraceous. Ovipositor sheaths just reaching apex of caudodorsal beak. Female caudodorsal beak in dorsal view (fig. 102) very long and slender, triangle-shaped and sharply pointed at apex.

Male genitalia: Pygofer (figs. 94-95) very characteristic, with broadly rounded lateral lobes and long, slender and erect caudodorsal beak. Dorsal margin concave to base, but convexly bent into caudodorsal beak. Distal margin angularly convex, forming a narrowly rounded angle with straight margin of beak. Ventral margin convex. Lateral lobe of pygofer weakly curving inwards towards end of distal margin, forming a weakly swollen elongate and bluntly rounded protuberance. Caudodorsal beak in dorsal view (fig. 98) extremely long and slender, its parallel margins converge at about half-length of beak, towards pointed apex. Claspers conspicuous by slender finger-shaped protuberance on corner of clasper heel (fig. 97). Dorsal crest very stout and strongly outcurving, abruptly ending at distolateral corner of clasper. Apical part of clasper slightly curved down and with small clasper hollow. Aedeagus (fig. 100) very small with narrow lateral lobes, in lateral view weakly concave along its pore. Aedeagus pore oval (fig. 99).

Measurements: Body length ♂: 18.3-23.3 mm ($\bar{x}$ 20.3 mm ± 1.4), ♀: 16.7-20.0 mm ($\bar{x}$ 18.5 mm ± 1.2); tegmen length ♂: 20.0-24.9 mm ($\bar{x}$ 22.7 mm ± 1.2), ♀: 23.6-26.5 mm ($\bar{x}$ 24.9 mm ± 1.2); head length ♂: 1.6-2.0 mm ($\bar{x}$ 1.8 mm), ♀: 1.6-1.9 mm ($\bar{x}$ 1.8 mm); pronotum length ♂: 2.3-3.2 mm ($\bar{x}$ 2.7 mm), ♀: 2.7-3.0 mm ($\bar{x}$ 2.9 mm); mesonotum length ♂: 4.2-5.4 mm ($\bar{x}$ 4.6 mm), ♀: 4.2-4.9 mm ($\bar{x}$ 4.6 mm); head width ♂: 4.4-5.2 mm ($\bar{x}$ 4.8 mm), ♀: 4.5-5.0 mm ($\bar{x}$ 4.8 mm); width of pronotal collar ♂: 5.5-7.1 mm ($\bar{x}$ 6.3 mm), ♀: 6.2-6.9 mm ($\bar{x}$ 6.6 mm).

Distribution (fig. 1). – *B. tenuispina* is distributed in the eastern parts of Papua New Guinea and is also recorded from Goodenough Island of the D'Entrecasteaux islands.

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DIE PUPPEN DER SPANNER MITTELEUROPAS (LEPIDOPTERA, GEOMETRIDAE): CHARAKTERISTIK UND BESTIMMUNGSTABELLE DER GATTUNGEN

Patočka, J., 1994. Die Puppen der Spanner Mitteleuropas (Lepidoptera, Geometridae): Charakteristik und Bestimmungstabelle der Gattungen. – Tijdschrift voor Entomologie, 137: 27-56, figs. 1-227. [ISSN 0040-7496]. Published 15 July 1994.

Characteristics of the pupae of the family Geometridae (Lepidoptera) and an identification key for its 161 Central European genera are given. The present system of this family is discussed from the view of pupal characters. The species examined are listed in an appendix.

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Key words. – Geometridae; Pupae; Taxonomy; Key for genera.

Die Familie der Spanner, Geometridae (Lepidoptera) ist eine der größten und wichtigsten Schmetterlingsfamilien. Viele ihrer Vertreter sind ernste Schädlinge in Land- und Forstwirtschaft, einige sind sogar Vorratsschädlinge. Die Mehrzahl der Arten ist wegen ihrer Gebundenheit an spezifische Standorte auch vom ökologischen Gesichtspunkt wichtig und kommt als Indikatoren der bedrohten Umwelt in Betracht. Die Kenntnis ihrer jüngeren Entwicklugsstadien ist für viele Fragen unbedingt notwendig; z. B. für das Studium der Schädlinge, der Prädatoren und Parasitoide, der Bioindikatoren, Bodenfauna, verschiedener Synusien usw. Die bisherige Kenntnis der Puppen der mitteleuropäischen Geometridae ist lückenhaft. Speziell die Puppen dieser Familie behandelt Khotko (1977) und erwähnt 25 Gattungen. In der vorliegenden Arbeit werden zum Vergleich 161 mitteleuropäische Gattungen, also mehr als 90 % ihres Bestandes berücksichtigt. An Khotko's Arbeit knüpfen die Veröffentlichungen des Verfassers an, die zahlreiche weitere Arten der Unterfamilie Larentiinae (Patočka 1980-1994) und mehrere Gruppen der Ennominae (Patočka 1978, 1985, 1986 a, b, 1992, 1993) behandeln. Auf diese Weise ist zwar die Mehrzahl der Arten dieser beiden Unterfamilien eingehend bearbeitet, es fehlt jedoch eine zusammenfassende Bestimmungstabelle der Gattungen. Diese Lücke soll die vorliegende Arbeit ausfüllen. Eingehendere Angaben über viele Geometridenpuppen finden sich bei Ljungdahl (1919) und Nordström et al. (1941), über die Arten an Obstbäumen Speyer (1958), an Tannen Patočka et al. (1960), an Eichen Patočka (1980) und über die Puppen in der Bodenstreu in Kiefernwäldern Koehler (1937). Einzelbeschreibungen von Geometridenpuppen sind in weiteren Literaturquellen verstreut. Die Handbücher über die Schmetterlinge Mitteleuropas, wie Forster & Wohlfahrt (1981) geben nur kurze und für eine Bestimmung nicht ausreichende Puppenbeschreibungen. Die Puppen der kanadischen Geometridae wurden im Rahmen einer Monographie dieser Familie von McGuffin (1967-1981) bearbeitet.

Das hier benützte System und die Nomenklatur folgen grundsätzlich Leraut (1980) und Gustafsson (1987), die morphologische Terminologie richtet sich nach Mosher (1916) und McGuffin (1967-1981). Das untersuchte Material (die hier berücksichtigten Gattungen und Arten sind im Anhang aufgelistet) stammt großenteils aus der Sammlung des Verfassers, zu welcher viele Fachkollegen durch Überlassung von Puppen und Puppenexuvien beigetragen haben, wofür ihnen auch an dieser Stelle herzlich gedankt sei. Viele Arten konnte sich der Verfasser von Museen ausleihen, insbesondere von dem Museum für Naturkunde der Humboldt-Universität in Berlin (Dr. W. Mey), von dem Naturhistorischen Museum Wien (Dr. M. Lödl), von dem Zoologischen Museum Kopenhagen (O. Karsholt), von der Zoologischen Staatssammlung München (Dr. W. Dierl) und aus der Entomologischen Abteilung des Nationalmuseums in Prag (Dr. F. Krampl). Den genannten Institutionen und Herren dankt der Verfasser verbindlichst, ebenso wie auch der Alexander von Humboldt-Stiftung Bonn für die Erteilung eines Stipendiums, welches ihm das Studium des Materials in München, sowie der Hanskarl-Göttling-Stiftung der Bayerischen forstlichen Versuchs- und Forschungsanstalt, welche einen Aufenthalt in Berlin ermöglichten.

Die Puppen und ihre Exuvien wurden mit Hilfe eines Stereomikroskopes und z. T. eines Abbeschen Zeichenapparates untersucht und gezeichnet.

CHARAKTERISTIK DER FAMILIE GEOMETRIDAE

Eine Übersicht der Puppenmorphologie dieser Familie geben die Abb. 1-6. Die Puppen der mitteleuropäischen Geometridae sind kleine bis mittelgroße (etwa 5-25 mm lang) Pupae obtectae. Sie sind schlank (Abb. 86) bis gedrungen (Abb. 94), meistens in der Mitte am breitesten, vorne abgerundet und hinten mehr zugespitzt (Abb. 1, 2, 88, 94). Manche Formen (z.B. *Cyclophora*, Abb. 130) sind vorne durch einen Höcker an der Basis der Vorderflügel breiter und sehen in Ventralansicht eher keilartig aus. Die Mehrzahl der Puppen ist einfarbig gelb-, rot-, oder schwarzbraun bis fast schwarz gefärbt und ± glänzend. Es handelt sich hierbei um Arten die sich im Boden oder in der Bodenstreu, in einem Erdkokon bzw. einer Erdhöhle verpuppen. Die übrigen Puppen sind grün, gelblich oder sandfarben, ± glanzlos und oft mit dunklen Zeichnungen versehen. Das sind Arten, die sich oberirdisch bzw. am Boden in einem leichten Gespinst, oder nur mit Einzelfäden befestigt verpuppen. Eine Gattung (*Abraxas*) ist glänzend schwarz mit satt gelben Querstreifen am Abdomen, die sich ebenfalls oberirdisch verpuppt.

Die Oberfläche der Puppen ist fein bis grob skulpturiert. Meist ist der Kopf und Thorax ± gerunzelt oder gefurcht und das Abdomen (manchmal auch der Thorax, insbesondere das Metanotum) mit kleinen punktförmigen Grübchen, den sog. Punktgrübchen (Abb. 210) besetzt. Selten entspringen von diesen Microbörstchen (*Apeira*, Abb. 74). Bei wenigen Puppen (z. B. bei der Gattung *Geometra*, Abb. 78) kommt eine Stachelskulptur vor. Die Körperborsten sind kaum sichtbar bis relativ groß und stark (Abb. 31). Der Vertex wächst entweder mit der Frons ohne eine Epicranialnaht zusammen (Vertreter der Unterfamilie Ennominae und einige andere, Abb. 4), oder er ist durch eine deutliche Epicranialnaht abgetrennt (Mehrzahl der übrigen Unterfamilien, Abb. 3). Beim Schlüpfen löst sich der Vertex bei dieser Gruppe von der Frons ab. Die Frons ist in wenigen Fällen mit einem Paar Höcker (Abb. 8, 9, 86, 125) versehen, oder kegelförmig vorgezogen (Abb. 43), ansonst meist abgerundet. Zwei Paare von Frontal- (Abb. 4) und ein Paar von Clypealborsten (Abb. 116) sind meist deutlich und groß ausgebildet. Von der Frontoclypealnaht sind nur Teile nahe der Antennen deutlich erkennbar. Die Komplexaugen sind groß und bestehen aus einem ± glatten, ventralen Streifen und einem oft mehr rauhen Dorsalteil (Abb. 95, 96). Die Mandibeln sind meist kaum differenziert (Abb. 112, 116), bei *Theria* jedoch stark hervortretend (Abb. 22). Das Labrum erscheint meist halbkreis- (Abb. 46), schaufel- (Abb. 117) oder trapezförmig (Abb. 47), gemeinsam mit dem schwach abgegrenzten Postclypeus oft fünfeckig (Abb. 116). Das Labium ist entweder ganz verdeckt (Abb. 87) oder klein (Abb. 209) bis groß (Abb. 101), als eine drei- oder fünfeckige Platte sichtbar. Die Maxillar- und Labialpalpen sind stets verdeckt. Die Genae grenzen an die Vorderbeine; diese Grenze immer kürzer als die Grenze zwischen Auge und Vorderbein. Die Grenzen zwischen Vorderbeine und Antennen kurz oder lang (Abb. 19, 21). Bei den sonst ähnlichen Puppen der Herminiinae, Noctuidae, grenzen die Vorderbeine nicht an die Antennen, weil die Mittelbeine die Augen berühren. Die Vorder- und Mittelbeine sind meist relativ lang, die Vorderbeine zuweilen (Abb. 16), die Mittelbeine meistens ungefähr so lang wie die Antennen und Vorderflügel. Die Enden der Hinterbeine sind oft sichtbar. Die Vorderschenkel sind sichtbar, groß (Abb. 1, 125) oder klein, schmal (Abb. 94, 77, 165), oft aber ganz verdeckt (Abb. 16, 94a). Die Proboscis ist meist so lang oder wenig kürzer als die Vorderflügel, selten stark verkürzt und deutlich kürzer als die Mittelbeine, bzw. auch als die Vorderbeine, (Abb. 16, 98, 99). In wenigen Fällen überragt die Proboscis (Abb. 9, 12, 94a, 123) und noch seltener überragen auch die Mittelbeine und Antennen (Abb. 13) die Spitzen der Vorderflügel und den Kaudalrand des 4. Abdominalsegmentes. Bei *Rhodometra* (Abb. 123) verschiebt die vergrößerte Proboscis das Labrum bis nahe am Frontalende des Kopfes, was oft auch bei Sphingidae mit langer Proboscis vorkommt. Die Antennen sind meist ungefähr so lang wie die Vorderflügel (Abb. 1). Die Vorderflügel überragen den Kaudalrand des 4. Abdominalsegmentes nicht, sind voneinander getrennt (Ausnahme: *Apeira*, Abb. 76) und zeichnen sich zuweilen durch hervorstehende (Abb. 94) oder dunkel gestreifte bzw. helle Adern aus. Selten liegt an ihren Wurzeln je ein Höcker (Abb. 123, 125, 130). Die Hinterflügel säumen die Vorderflügel meist zu ¼ bis ⅔ des 4. Abdominalsegmentes, nicht aber bis zu deren Spitzen, wie es bei der Familie Drepanidae, die den Geometridae sonst ähnlich ist, vorkommt. Eine Ausnahme ist die Gattung *Archiearis*.

Die thorakalen Spiracula sind klein und spaltförmig. Oft bildet sich kaudal von ihnen am Mesonotum, ein auffälliger, tomentöser (Abb. 31, 91), rauh skulpturierter (Abb. 54) oder 'ohrartig' hervortretender, kantiger Höcker (Abb. 33, 35). Das Metanotum besitzt frontal in der Mitte meist einen mitteltiefen und abgerundeten Ausschnitt. Die Frontolaterale Lappen des Metanotums sind meist abgerundet (Abb. 102, 103), zuweilen spitz oder winkelig (Abb. 153), insbesondere bei den Vertretern der Unterfamilie Sterrhinae. Die Vorderecken des 1. Abdominalsegmentes sind meist abgerundet, Ihre Seiten ± parallel. Die Spiracula sind am 2.-3. Abdominalsegment sichtbar oder ± verdeckt. Die abdominalen Spiracula sind klein bis mittelgroß, meist schmal elliptisch, oft mit breiten elliptischen Höfen und nicht selten ± erhaben. Die 5.-7. Abdominalsegmente sind beweglich. An der Basis des 5. Segmentes frontal des Spiraculums finden sich oft Leisten, Gruben und verdichtete Punktgrübchen (Abb. 34, 38, 40, 45, 49-55, 138, 140-142), die gute Unterscheidungsmerkmale bieten. An der intakten Puppe sind sie jedoch durch den Kaudalrand des 4. Abdominalsegmentes oft verdeckt; dieser sollte deshalb, um eine Untersuchung zu ermöglichen, mit einer Nadel beseitigt werden. An der Puppenexuvie sind diese Gebilde auch ohne diesen Eingriff meist gut sichtbar. Bei der Gattung *Rheumaptera* gibt es Querleisten und Rinnen an der Basis der Dorsalseite des 5. Abdominalsegmentes (Abb. 139). Zwischen dem 9. und 10. Segment besitzt die Mehrzahl der Spannerpuppen einen ± tiefen, rinnenartigen Quereinschnitt, die sog. Dorsalrinne, welche an ihrer Kaudalseite meist einen oder mehrere Ausläufer aufweist, deren Ränder oft verdunkelt und ± tomentös sind. Seltener bildet die Dorsalrinne auch einen oder einige Ausläufer frontalwärts (Frontalausläufer, Abb. 6). An den Seiten entspringt von dieser Rinne oft noch ein dorso-kaudalwärts gerichteter Lateraleinschnitt (Abb. 5).

Dorsalseite des 10. Abdominalsegmentes ist verschieden lang (Abb. 70, 71), seine Ventralseite oft ± breit mit gewölbten Seiten, abgeflacht, und der manchmal erhabene frontolaterale Teil durch flache Furchen abgegrenzt. Die Analnaht ist meist lang, ihre oft erhabenen Seiten wallartig, manchmal auch mit Längs-, seltener Querrunzelung. Das sog. Analfeld groß und auffällig. Die Genitalnaht und ihr Genitalfeld, besonders bei den Männchen sind oft groß. Der Absturz zur Basis des Kremasters verläuft steil bis schräg (Abb. 137, 182). Der Kaudalausläufer des 10. Segmentes, der Kremaster, welcher bei der Puppe eine Haft- und Stützfunktion besitzt (Patočka 1978), ist bei den Puppen der Geometridae immer vorhanden und ± groß, seltener klein (Abb. 17) und mehr oder weniger scharf von dem 10. Abdominalsegment abgegrenzt bzw. abgesetzt. In der Dorsalsicht ist er oft haufen- (Abb. 119) oder zungenförmig (Abb. 80), dreieckig (Abb. 178), seltener trapez- (Abb. 18, 164) oder ankerförmig (Abb. 7). Ventral an seiner Basis gibt es oft ein Paar Basalhöcker, dazwischen eine Vertiefung bzw. Mulde. Bei der Unterfamilie Geometrinae ist der Kremaster ventral charakteristisch radial gefurcht (Abb. 75, 79), ansonst ist er ± glatt oder verschiedenartig skulpturiert (gerunzelt, gefurcht, gerippt; Abb. 120, 122). Der Kremaster trägt meist 4, seltener 1-3 oder 5-7 (bei *Apeira* eine Anzahl) Paare von Borsten, die oft am Ende hakenartig gekrümmt sind. Die Bezeichnung von 4 Paaren von Primärborsten am Kremaster (nach McGuffin 1967-1981) zeigen die Abb. 5-6. Bei vielen Geometriden-Puppen wachsen die starken Borsten D_2 zu einem Stiel zusammen und nur ihre Spitzen bleiben als eine Gabelspitze frei (Abb. 32), die manchmal auch vermehrt sind (Abb. 28). Während bei vielen Vertretern der Unterfamilie Larentiinae die übrigen Borsten noch erhalten bleiben (Abb. 177, 178) verschwinden sie bei zahlreichen Ennominae vollständig (Abb. 71). Bei *Bupalus* bleibt nur eine einfache, stumpfe Spitze übrig (Abb. 42).

Die Puppen der Spanner findet man z. T. an der Nahrungspflanze, durch die Häkchen am Kremaster und einen Gürtelfaden befestigt (z.B. bei *Cyclophora*) oder in einem lockeren Gespinst (*Abraxas*, *Ennomos*, bei den Comibaenini in dem Sack der Raupe) direkt an der Nahrungspflanze oder auch am Boden. Die Mehrzahl der Puppen ruht jedoch in einem ± festen Erdkokon oder einer Erdhöhle in der Bodenstreu oder im Boden selbst. Die Puppen variieren in der Größe insbesondere nach Geschlecht, Generation oder relativer Abundanz. Die Raupen leben an verschiedenen Gruppen von Pflanzen, sogar an Sporenpflanzen bzw. an Detritus. Es gibt ebenso polyphage, wie relativ streng oligophage, an spezielle Pflanzengattungen gebundene Arten (z. B. *Clematis*, *Actaea*, *Berberis*, *Rhamnus*, *Hypericum*, *Veratrum*). Manche Gruppen (Eupitheciini, Perizomini) bevorzugen Blüten und Früchte. Viele Arten leben an Laubhölzern, an denen sie oft auch schädlich werden, aber auch an Nadelhölzern, und eine zahlreiche Gruppe von *Larentiinae* lebt an *Galium*.

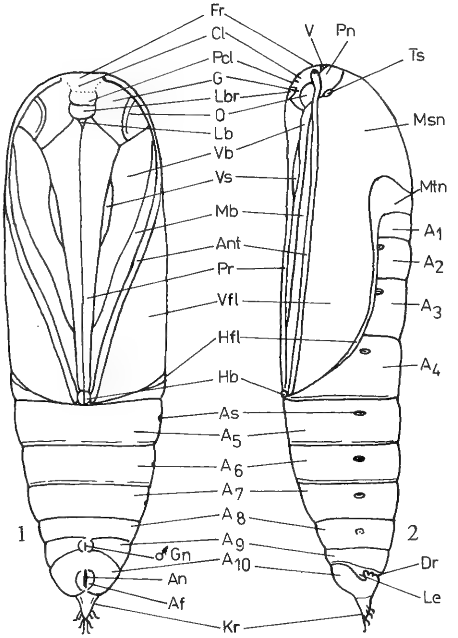
Die Spanner bewohnen verschiedenartige Biotope, sehr viele Wälder und steppenartige, mehrere auch ruderale Standorte, Sümpfe bzw. Torfmoore, Felsen und Alpenwiesen im Hochgebirge. Viele Arten sind für bestimmte Biotope recht charakteristisch.

BESTIMMUNGSTABELLE DER GATTUNGEN

Einige Gattungen, wie *Orthostixis* Hübner, 1822, *Costaconvexa* Agenjo, 1949, *Coenocalpe* Hübner, 1825, *Bichroma* Gumppenberg, 1887, *Eilicrinia* Hübner, 1825, *Mannia* Prout, 1915, konnten infolge Materialmangels nicht berücksichtigt werden.

1 Kaudalhälfte des Kremasters in Dorsalsicht einfach zugespitzt (selten mit zwei Börstchen am Ende) (Abb. 42) .... *Bupalus* Leach

– Kaudalhälfte des Kremasters in Dorsalsicht mit 2-4 Dornen oder Zähnen, jedoch ohne Börstchen oder Häkchen (Abb. 7, 14, 20). Die Dornen oft gestielt (Abb. 32, 52), zuweilen auch verzweigt (Abb. 28) 2



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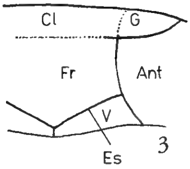

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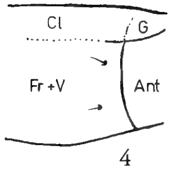

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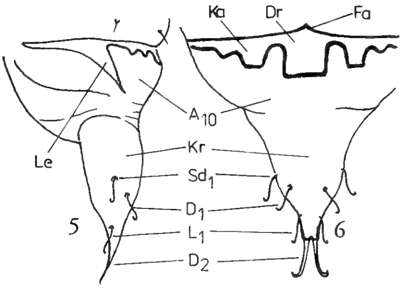

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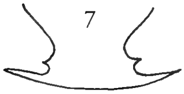

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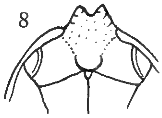

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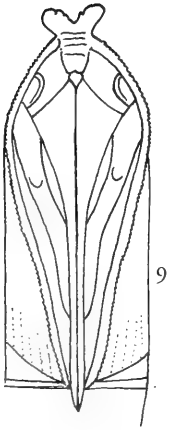

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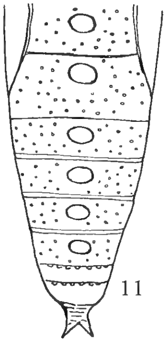

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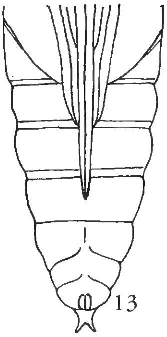

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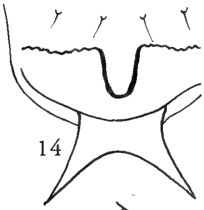

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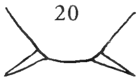

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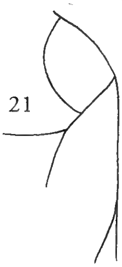

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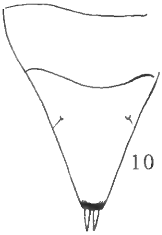

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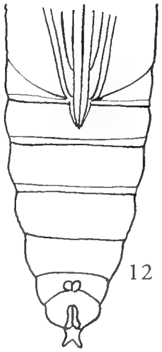

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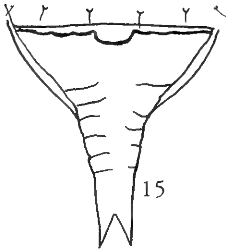

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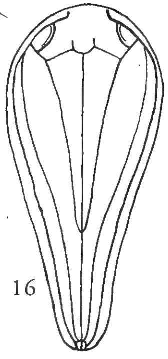

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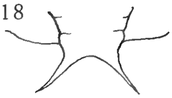

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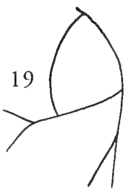

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– Kaudalhälfte des Kremasters mit 2-8 (seltener mehr) Häkchen oder Borsten (Abb. 6, 72, 80, 89, 136). Die Endborsten (D_2) zuweilen ± dornartig umgebildet (Abb. 89, 143, 218). 55

2 (1) Frons mit einem Paar kräftiger Höcker (Abb. 8, 9) 3

– Frons ohne ein Höckerpaar, selten kegelförmig vorgezogen (Abb. 43), sonst abgerundet (Abb. 16) 4

3 (2) Proboscis überragt deutlich den Kaudalrand des 4. Abdominalsegmentes (Abb. 9) .... *Siona* Duponchel

– Proboscis überragt den Kaudalrand des 4. Abdominalsegmentes nicht (vgl. Abb. 1) .... *Aethalura* McDunnough

4 (2) Einzelne Abdominalsegmente dorsal mit großen, elliptischen, dunkel umrandeten Gruben (Abb. 11) 5

– Abdominalsegmente ohne solche Gruben (vgl. Abb. 2) 6

5 (4) Am 5.-7. Abdominalsegment dorsal fehlen die Gruben .... *Lithostege* Hübner

– Auch am 5.-7. Abdominalsegment gibt es dunkel umrandete Gruben (Abb. 11) .... *Chesias* Treitschke

6 (4) Proboscis überragt den Kaudalrand des 4. Abdominalsegmentes (Abb. 12, 13) 7

– Proboscis überragt nicht den Kaudalrand des 4. Abdominalsegmentes (Abb. 1) 9

7 (6) Sowohl die Antennen wie auch Mittelbeine überragen den Kaudalrand des 4. Abdominalsegmentes 8

– Nur die Antennen, nicht jedoch die Mittelbeine überragen den Kaudalrand des 4. Abdominalsegmentes .... *Odezia* Boisduval

– Weder Antennen noch Mittelbeine überragen den Kaudalrand des 4. Abdominalsegmentes (Abb. 12) .... *Schistostege* Hübner

8 (7) Kremaster länger als basal breit (Abb. 15) .... *Carsia* Hübner

– Kremaster kürzer als basal breit (Abb. 13, 14) .... *Aplocera* Stephens

9 (6) Kremaster ankerartig, stumpf abgerundet, an seinen Seiten je ein größerer und oft auch kleinerer Zahn (Abb. 7). Puppe schlank .... *Archiearis* Hübner

– Kremaster am Ende mit gabelartigen, schräg kaudalwärts gerichteten Dornen (Abb. 25, 32, 52), diese zuweilen weiter verzweigt (Abb. 28). Wenn die Dornen ± gegeneinander stehen (Abb. 17, 20), nur in einem Paar und die Puppe ist gedrungen 10

10 (9) Weder Labium, noch Vorderschenkel sichtbar (Abb. 16, 39) 11

– Labium, Vorderschenkel, oder beides sichtbar (vgl. Abb. 1) 23

11 (10) 8. Abdominalsegment dorsal mit einem Paar spitzer Höcker .... *Nychiodes* Lederer

– 8. Abdominalsegment dorsal ohne Höcker 12

12 (11) Kremaster mit zwei Paaren schlanker, wenig divergierender Dornen, außerdem in seinem Basalteil noch ein Paar Höcker (Abb. 23) .... *Artiora* Meyrick

– Kremaster mit 1 Paar Dornen, die zuweilen noch verzweigt sein können, außerdem höchstens mit kurzen Zähnen an den Seiten (Abb. 17, 20, 25, 26, 28) 13

13 (12) Kremaster klein, kurz, seine Dornen stark divergierend (Abb. 17, 18, 20) 14

– Kremaster groß, am Ende mit langen Dornen oder mit einer gestielten Gabel (Abb. 25, 27, 30) 16

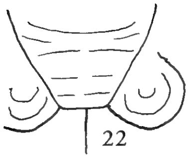
14 (13) Proboscis kürzer als die Vorderbeine (Abb. 16) .... *Operophtera* Hübner

– Proboscis länger als die Vorderbeine (Abb. 1) 15

15 (14) Grenzen zwischen Vorderbeine und Antennen etwa 2× so lang wie die Grenzen zwischen Vorderbeine und Augen (Abb. 21). Mandibeln erhaben .... *Theria* Hübner

– Grenzen zwischen Vorderbeine und Antennen höchstens wenig länger (oft kürzer) als die Grenze mit den Augen (Abb. 19). Mandibeln nicht erhaben .... *Alsophila* Hübner

Abb. 1-21. – 1,2,3,5,6, *Horisme vitalbata*; 4, *Synopsia sociaria*; 7, *Archiearis notha*; 8, *Aethalura punctulata*; 9, 10, *Siona lineata*; 11, *Chesias legatella*; 12, *Schistostege treitschkei*; 13, 14, *Aplocera praeformata*; 15, *Carsia sororiata*; 16, 17, *Operophthera brumata*; 18, 19, *Alsophila quadripunctaria*; 20, 21, *Theria rupicapraria*.
1, Habitusbild der Puppe, Ventral; 2, Dorsalsicht; 3, 4, Frons und Umgebung; 5, Abdominalende in Lateralsicht; 6, idem, in Dorsalsicht; 7, Kremaster in Dorsalsicht; 8, Kopf in Ventralsicht; 9, Frontalhälfte der Puppe in Ventralsicht; 10, 14, 15, 17, 18, 20, Abdominalende in Dorsalsicht; 11, Abdominalhälfte der Puppe in Dorsalsicht; 12, 13, idem in Ventralsicht; 16, Kopf und Beine in Ventralsicht; 19, 21, Augen und Umgebung.
A_1-A_{10} = 1.-10. Abdominalsegment, Af = Analfeld, An = Analnaht, Ant = Antennen, As = abdominale Spiracula, Cl = Clypeus, D_1, D_2 = Dorsalborsten 1,2, Dr = Dorsalrinne, Es = Epicranialnaht, Fa = Frontalausläufer der Dorsalrinne, Fr = Frons, G = Genae, Gn = Genitalnaht, Hb = Hinterbeine, Hfl = Hinterflügel, Ka = Kaudalausläufer der Dorsalrinne, Kr = Kremaster, L_1 = Lateralborste 1, Lb = Labium, Lbr = Labrum, Le = Lateraleinschnitt, Mb = Mittelbeine, Msn = Mesonotum, Mtn = Metanotum, O = Auge, Pcl = Postclypeus, Pn = Pronotum, Pr = Proboscis, Sd_1 = Subdorsalborste 1, Ts = thorakales Spiraculum, V = Vertex, Vb = Vorderbeine, Vfl = Vorderflügel, Vs = Vorderschenkel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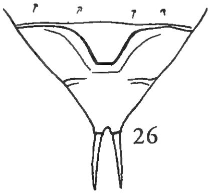
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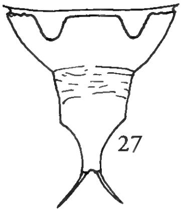
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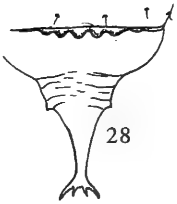
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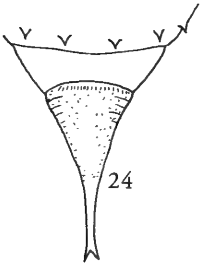
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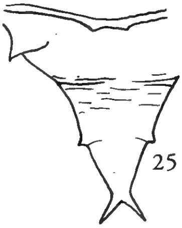
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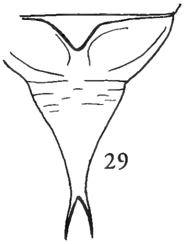
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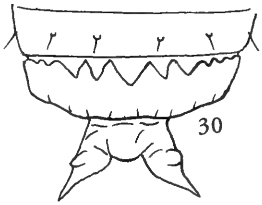
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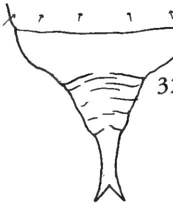
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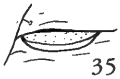
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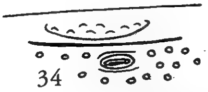
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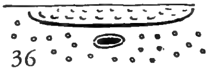
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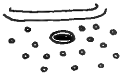
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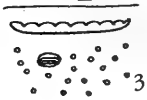
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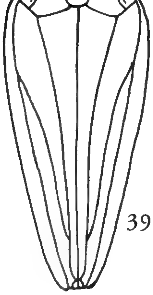
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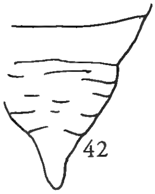
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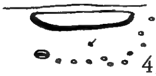
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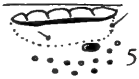
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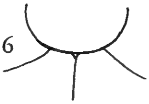
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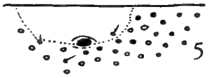
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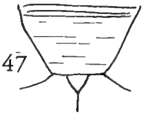
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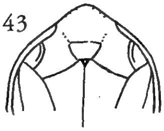
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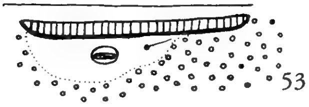
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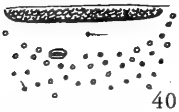
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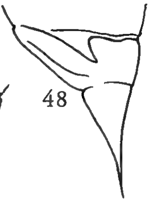
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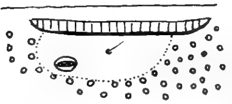
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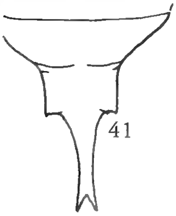
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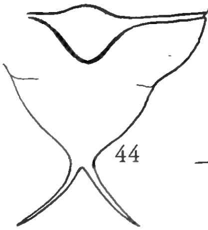
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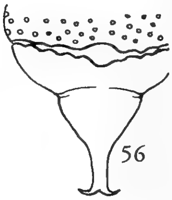
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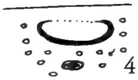
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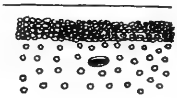
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16 (13) 9. Abdominalsegment mit einer Querreihe von Dornen (Abb. 24).. *Eurrhanthis* Hübner

– 9. Abdominalsegment ohne Dornen (Abb. 32).. 17

17 (16) 10. Abdominalsegment mit je einem spitzen lateralen Fortsatz (manchmal ein weiterer an der Mitte des Kremasters, Abb. 25) .... *Lycia* Hübner

– 10. Abdominalsegment ohne, Kremaster oft mit einem Paar von laterale Fortsätze (Abb. 28, 32).. 18

18 (17) Dorsalrinne vorhanden, Kaudalausläufer ± tomentös, Lateraleinschnitt deutlich (Abb. 26, 27, 28).. 19

– Dorsalrinne und Lateraleinschnitt nicht vorhanden (Abb. 32) 21

19 (18) Erhebung kaudal des thorakalen Spiraculums flach, länglich elliptisch, stark tomentös (Abb. 31). Puppe 12-15 mm lang................ .... *Erannis* Hübner

– Erhebung kaudal des thorakalen Spiraculums 'ohrartig', kantig (Abb. 33, 35). Puppe über 17 mm lang... 20

20 (19) Leiste frontal des Spiraculums am 5. Abdominalsegment doppelt (Abb. 34). Erhebung kaudal des thorakalen Spiraculums steiler frontal- als kaudalwärts (Abb. 33). Puppe 17 mm lang........................ *Apocheima* Hübner

– Leiste frontal des Spiraculums am 5. Abdominalsegment einfach (Abb. 36). Erhebung kaudal des thorakalen Spiraculums weniger steil frontal- als kaudalwärts. (Abb. 35) Puppe 20-26 mm lang.................... *Biston* Leach

21 (18) Puppe 17-21 mm lang.. *Phigalia* Duponchel

– Puppe 10-15 mm lang................................ 22

22 (21) Kremaster mit deutlichen lateralen Fortsätzen (Abb. 41). Vertiefung frontal des Spiraculums am 5. Abdominalsegment mit zahlreichen Punktgrübchen frontal der Querleiste (Abb. 40)....... *Selidosema* Hübner

– Kremaster ohne, bzw. nur mit angedeuteten lateralen Fortsätzen (Abb. 32). Vertiefung am 5. Abdominalsegment frontal des Spiraculums mit Querleisten, ohne Punktgrübchen (Abb. 37, 38) .... *Agriopis* Hübner

23 (10) Dorsalrinne mit 1-2 großen Kaudalausläufern (Abb. 26, 27, 29)............................ 24

– Dorsalrinne mit mehreren Kaudalausläufern, oder nicht vorhanden (Abb. 56, 62, 70) .. 28

24 (23) Vorderschenkel nicht sichtbar (vgl. Abb. 82) 25

– Vorderschenkel sichtbar (vgl. Abb. 1) 26

25 (24) Dorsalrinne mit nur einem großen Kaudalausläufer. Kremaster ohne laterale Fortsätze (Abb. 26) .... *Chondrosoma* Anker

– Dorsalrinne mit zwei großen Kaudalausläufern (Abb. 27)................ *Lignyoptera* Lederer

26 (24) Frons breit kegelförmig vorgezogen (Abb. 43). Dorsalrinne auch an der Frontalseite ausgebuchtet (Abb. 44) .... *Pelurga* Hübner

– Frons nicht vorgezogen. Dorsalrinne nur an der Kaudalseite mit einem großen, spitzen Vorsprung (Abb. 29) 27

27 (26) Puppe mehr gedrungen, schwärzlich, Exuvie schwarzbraun. Puppenlänge 6-8 mm .... *Phibalapteryx* Stephens

– Puppe schlanker, bräunlich, Exuvie gelbbraun. Puppenlänge 9-10 mm .... *Cataclysme* Hübner

28 (23) Dornen am Kremaster voneinander entfernt entspringend (Abb. 30)........................... 29

– Dornen am Kremaster gabelartig, gestielt (Abb. 28, 67, 202, 206).......................... 30

29 (28) Kremaster an der Dorsalseite fein skulpturiert. Puppe nur 6-8 mm lang...................... .... *Pygmaena* Boisduval

– Kremaster an der Dorsalseite grob skulpturiert. Puppe über 10 mm lang...................... .... *Gnophos* Treitschke s. lat.

30 (28) Proboscis wesentlich kürzer als die Mittelbeine. Labium sehr klein. Puppe 7-9 mm lang................................ *Tephronia* Hübner

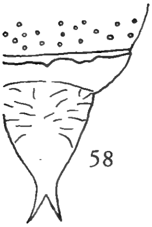
– Proboscis nicht oder wenig kürzer als die Mittelbeine (im Zweifelsfall Labium Mittelgroß) 31

31 (30) Dornen am Kremaster ± länger als ihr Stiel (Abb. 102, 206). Puppen nur 6-8 lang... 152

– Dornen am Kremaster ± kürzer als ihr Stiel (Abb. 52, 62, 67). Meist größere Puppen 32

32 (30) Dorsalrinne entwickelt (Abb. 56, 58, 61-63) 33

Abb. 22-57. – 22, 39, *Theria rupicapraria*; 23, *Artiora evonymaria*; 24, *Eurranthis plumistaria*; 25, *Lycia zonaria*; 26, *Chondrosoma fiduciaria*; 27, *Lignyoptera thaumastaria*; 28, 31, *Erannis defoliara*; 29, *Phibalapteryx virgata*; 30, *Gnophos obfuscatus*; 32, 38, *Agriopis aurantiaria*; 33, 34, *Apocheima hispidaria*; 35, 36, *Biston strataria*; 37, *Agriopis bajaria*; 40, 41, *Selidosema plumaria*; 42, *Bupalus piniarius*; 43, 44, *Pelurga comitata*; 45, 46, *Ectropis crepuscularia*; 47-49, *Calospilos sylvata*; 50, *Cleora cinctaria*; 51, *Fagivorina arenaria*; 52-54, *Serraca punctinalis*; 55, *Ematurga atomaria*; 56, 57, *Chiasmia clathrata*. 22, Labrum, Mandibulae; 23-30, 32, 41, 42, 44, 52, 56, Abdominalende in Dorsalsicht; 31, 33, 35, Erhebung kaudal des thorakalen Spiraculums; 34, 36, 38, Basis des 5. Abdominalsegmentes, Lateralsicht; 29, Kopf und Beine in Ventralsicht; 40, 45, 49-51, 53, 57, Basis des 5. Abdominalsegmentes, Lateralsicht; 43, Kopf in Ventralsicht; 46, 47, Labrum, Labium; 48, Abdominalende in Lateralsicht; 54, Erhebung kaudal des thorakalen Spiraculums.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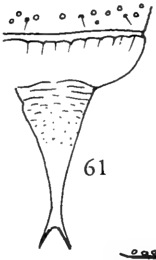
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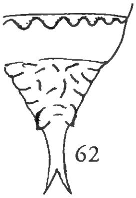
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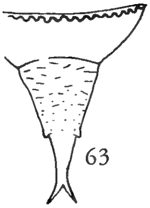
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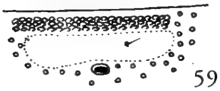
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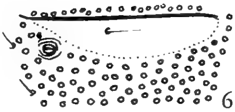
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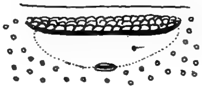

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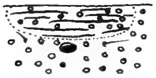
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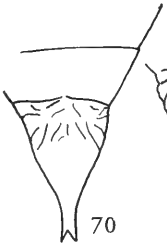
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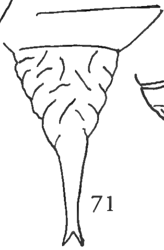
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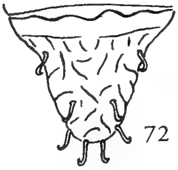
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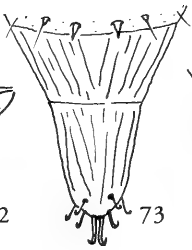
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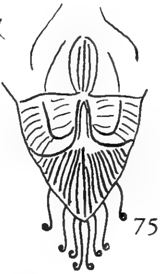
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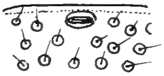
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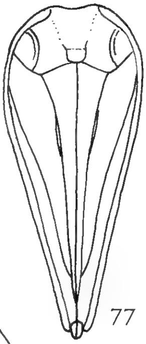
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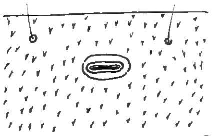
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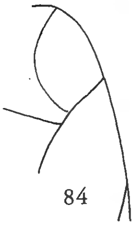
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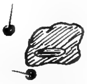
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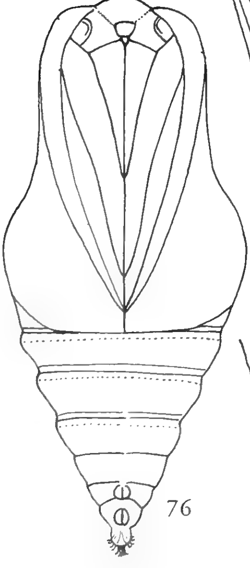
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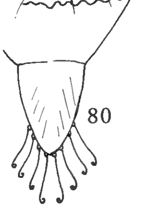
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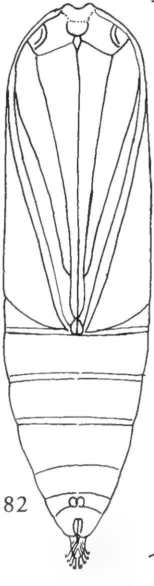
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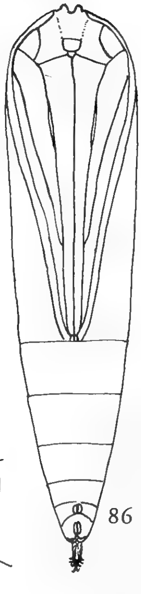
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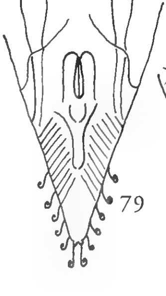
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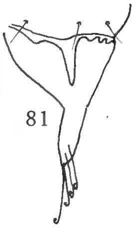
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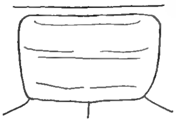


– Dorsalrinne nicht entwickelt (Abb. 70, 71) 47

33 (32) Kaudal des thorakalen Spiraculums je eine relativ große, breite, sehr rauhe, erhöhte Fläche (Abb. 54). An der Basis des 5. Abdominalsegmentes lateral zwischen zwei dunklen Querleisten wenigstens 12 Zellen in einer Reihe (Abb. 53, 55) 34

– Kaudal des thorakalen Spiraculums eine kleine, längliche oder eine unauffällige Erhebung (vgl. Abb. 106, 111). Wenn diese jedoch größer und rauher ist (Abb. 227) und auch sonst, gibt es an der Basis des 5. Abdominalsegmentes lateral anders aussehende Bildungen (Abb. 51, 57, 65, 68, 69) oder nur etwa 5 Zellen (Abb. 50) 36

34 (33) Mesonotum ohne Punktgrübchen .... *Hypomecis* Hübner

– Mesonotum mit Punktgrübchen 35

35 (34) Spiraculum am 5. Abdominalsegment liegt in der Nähe der 10.-15. Zelle (von der Ventralseite gezählt, Abb. 53). Puppe meist über 14 mm lang, eher glänzend ... *Serraca* Moore

– Spiraculum am 5. Abdominalsegment liegt in der Nähe der 2.-6. Zelle (Abb. 55). Puppe meist matter, unter 13 mm lang .... *Ematurga* Lederer

36 (33) Abdomen ohne Punktgrübchen (vgl. Abb. 92) .... *Lomaspilis* Hübner

– Abdomen mit Punktgrübchen (vgl. Abb. 51) 37

37 (36) Am 5. Abdominalsegment frontal des Spiraculum eine länglich ovale, von einer dunklen Leiste umgebene Fläche (Abb. 45) 38

– Am 5. Abdominalsegment vor dem Spiraculum andere Bildungen: Zellen (Abb. 50), Leisten (Abb. 65, 68, 69) oder nur Punktgrübchen (Abb. 57) bzw. eine glatte Fläche (Abb. 51) 39

38 (37) Labium ganz klein (Abb. 46) bzw. fehlend. Vorderschenkel gut sichtbar (vgl. Abb. 1). Lateraleinschnitt undeutlich .... *Ectropis* Hübner

– Labium (Abb. 47) und Lateraleinschnitt (Abb. 48) deutlich. Vorderschenkel verdeckt (vgl. Abb. 39) .... *Calospilos* Hübner

39 (37) Frontal des Spiraculums am 5. Abdominalsegment nur eine glatte Fläche, weder mit Leisten, noch Punktgrübchen (Abb. 51) .... *Fagivorina* Wehrli

– Frontal des Spiraculums am 5. Abdominalsegment eine dunkle Leiste und vor ihr etwa fünf Zellen (Abb. 50) .... *Ascotis* Hübner

– Frontal des Spiraculums am 5. Abdominalsegment Leisten und Punktgrübchen (Abb. 65, 69), oder nur Leisten (Abb. 68) oder Punktgrübchen (Abb. 57) 40

40 (39) 9. Abdominalsegment mit Punktgrübchen (Abb. 56, 61) 41

– 9. Abdominalsegment ohne Punktgrübchen (Abb. 62, 63) 43

41 (40) Frontal des Spiraculums am 5. Abdominalsegment keine glatte Fläche, nur Punktgrübchen (Abb. 57) .... *Chiasmia* Hübner

– Frontal bzw. frontodorsal des Spiraculums am 5. Abdominalsegment eine glatte Fläche und davor liegen Punktgrübchen bzw. eine Querleiste (Abb. 59, 60) 42

42 (41) An der Basis des 5. Abdominalsegmentes lateral nur Punktgrübchen ohne eine dunkle Querleiste (Abb. 59). Stiel am Kremaster relativ kurz (Abb. 58) .... *Parectropis* Sato

– An der Basis des 5. Abdominalsegmentes lateral eine dunkle Querleiste mit einer Reihe von dicht gedrängten Punktgrübchen (Abb. 60). Stiel des Kremasters lang (Abb. 61) .... *Tephrina* Gueneé

43 (40) Dorsalrinne ohne Kaudalausläufer .... *Euconista* Lederer

– Dorsalrinne mit Kaudalausläufern 44

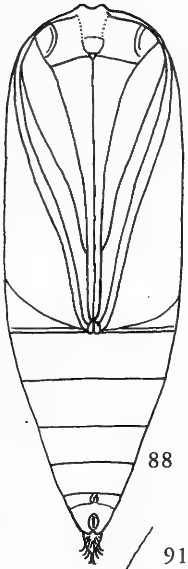
44 (43) Frontal des Spiraculums am 5. Abdominalsegment liegen nur Punktgrübchen (Abb. 57) 45

– Frontal des Spiraculum am 5. Abdominalsegment liegt eine glatte Fläche, dann Punktgrübchen (Abb. 59) 46

– Frontal des Spiraculums am 5. Abdominalsegment liegt zuerst eine glatte Fläche, dann eine dicke Leiste und eine Vertiefung mit Leisten und Punktgrübchen (Abb. 226). .... *Odontognophos* Wehrli

45 (44) Kaudal des thorakalen Spiraculums eine längliche tomentöse Erhebung (vgl. Abb. 31) .... *Isturgia* Hübner

Abb. 58-87. – 58, 59, *Parectropis similaria*; 60, 61 *Tephrina arenacearia*; 62, *Deileptenia ribeata*; 63, *Arichanna melanaria*; 64, *Stegania dilectaria*; 65, *Peribatodes rhomboidaria*; 66, *Semiothisa signaria*; 67, 68, *Itame brunneata*; 69, 71, *Diastictis artesiaria*; 70, *Narraga fasciolaria*; 72, *Abraxas grossulariata*; 73, *Ennomos autumnaria*; 74, 76, *Apeira syringaria*; 75, 77, 78, *Hemistola biliosata*; 79, *Jodis putata*; 80, 81, *Pseudoterpna pruinata*; 82-84, *Thalera fimbrialis*; 85, *Chlorissa cloraria*; 86, *Hemithea aestivaria*; 87, *Epirrita christyi*.
58, 61-63, 66, 67, 70-73, 80, Abdominalende in Dorsalsicht; 59, 60, 64, 65, 68, 69, 75, 78, 89, Basis des 5. Abdominalsegmentes in Lateralsicht; 75, 79, Abdominalende in Ventralsicht; 76, 82, 86, Habitusbild in Ventralsicht; 77, Kopf und Beine in Ventralsicht; 81, Abdominalende in Lateralsicht; 84, 85, Augen und Umgebung.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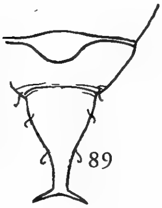
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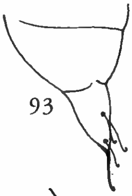
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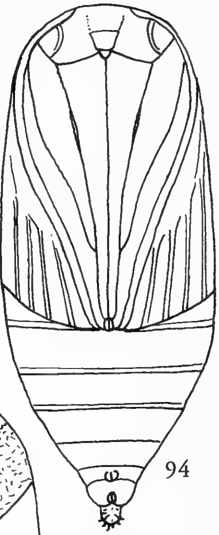
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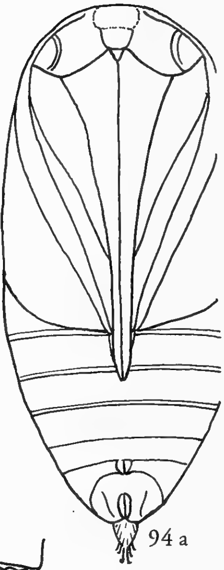
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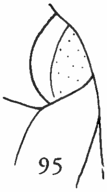
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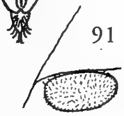
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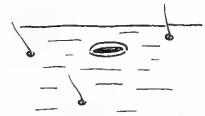
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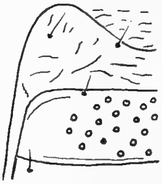
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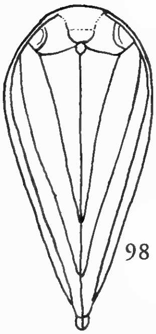
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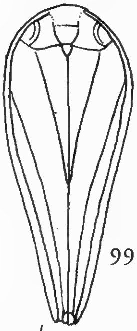
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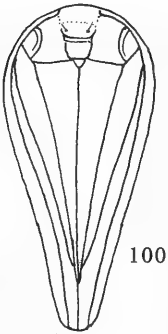
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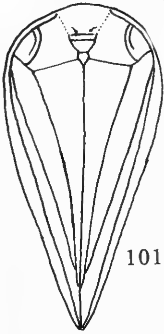
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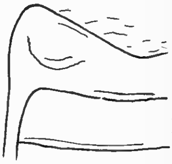
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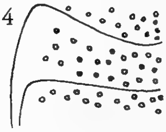
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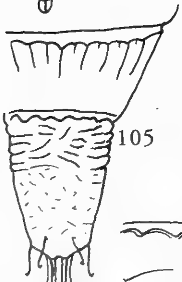
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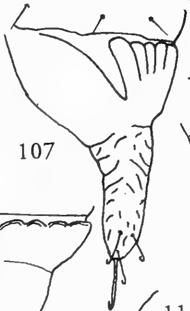
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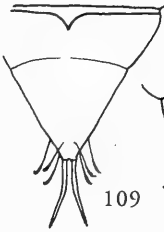
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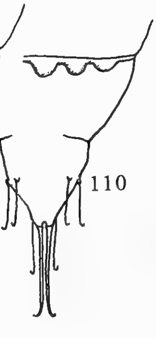
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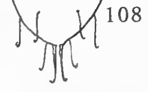
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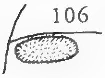
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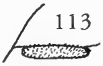
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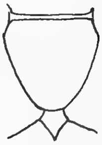
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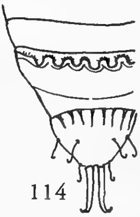
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– Kaudal des thorakalen Spiraculums keine tomentöse Erhebung, nur grobe Runzeln.. *Lobophora* Curtis

46 (44) Dorsalrinne mit 8-9 mittelgroßen kaudalen Ausbuchtungen (Abb. 62). Lateraleinschnitt ohne Runzeln um die Spitze. Ventralseite des Kremasters mit großen Basalhöckern.. *Deileptenia* Hübner

– Dorsalrinne mit etwa 20 kleinen Ausbuchtungen (Abb. 63). Lateraleinschnitt mit starken Runzeln um die Spitze. Basalhöcker an der Ventralseite des Kremasters schwach oder fehlend............................ *Arichanna* Moore

47 (32) 5. Abdominalsegment frontal des Spiraculums mit einer schlank ovalen Leiste. Auch der Kaudalrand des 4. Segmentes dort verdickt (Abb. 64).. 48

– 5. Abdominalsegment frontal des Spiraculums mit etwa fünf Zellen, die kaudal durch eine dicke Querleiste begrenzt sind (Abb. 50) .... *Cleora* Curtis

– 5. Abdominalsegment frontal des Spiraculums mit Punktgrübchen und/oder Leisten (Abb. 57, 60, 65, 68, 69)......................... 49

48 (47) Puppe 6-8 × 2,5 mm........ *Stegania* Guneeé

– Puppe 9-10 × 3 mm............ *Lygdia* Guneeé

49 (47) Frontal des Spiraculums am 5. Abdominalsegment eine fast skulpturlose, glatte Fläche und vor ihr Punktgrübchen bzw. Leisten (Abb. 59, 65).. 50

– Frontal des Spiraculums am 5. Abdominalsegment Punktgrübchen und/oder Leisten, ohne eine glatte Fläche dazwischen (Abb. 57, 68, 69).. 52

50 (49) 9. Abdominalsegment mit Punktgrübchen (vgl. Abb. 61)............................ *Alcis* Curtis

– 9. Abdominalsegment ohne Punktgrübchen (vgl. Abb. 71)... 51

51 (50) Lateral an der Basis des 5. Abdominalsegmentes eine dicke Querleiste und vor ihr dichte Punktgrübchen (Abb. 65).. *Peribatodes* Wehrli

– Lateral an der Basis des 5. Abdominalsegmentes nur Punktgrübchen, keine Querleiste (Abb. 59)........................ *Paradarsia* Warren

52 (49) An der Basis des 5. Abdominalsegmentes lateral nur Punktgrübchen (Abb. 57).......... 53

– An der Basis des 5. Abdominalsegmentes lateral Leisten und dazwischen manchmal Punktgrübchen (Abb. 68, 69).................. 54

53 (52) Stiel des Kremasters lang (Abb. 66). Ventralseite des Kremasters ohne deutliche Basalhöcker. Metanotum ohne Punktgrübchen (vgl. Abb. 102)............... *Semiothisa* Hübner

– Stiel des Kremasters kurz (Abb. 70). Ventralseite des Kremasters mit deutlichen Basalhöckern. Metanotum mit Punktgrübchen (vgl. Abb. 210).................. *Narraga* Walker

54 (52) Stiel des Kremasters lang und schlank (Abb. 71)................................. *Diastictis* Hübner

– Stiel des Kremasters kurz und dick (Abb. 67) .... *Itame* Hübner

55 (1) Puppe glänzend braunschwarz, Kaudalstreifen des 5.-8. Abdominalsegmentes leuchtend gelb. Häkchen am Kremaster gleich groß, dick, zerstreut, Sd_1 entspringt nahe der Basis des Kremasters (Abb. 72)....... *Abraxas* Leach

– Puppe nicht glänzend schwärzlich mit gelben Seitenstreifen. Wenn die Häkchen am Kremaster gleich groß und dick sind, entspringt Sd_1 nicht nahe der Basis des Kremasters.. 56

56 (55) Mittelteil der Puppe stark verbreitert (Abb. 76) Thorax und Abdomen dorsal mit dichten winzigen Börstchen besetzt (Abb. 74)... *Apeira* Gistl

– Puppe nicht verbreitert, ohne Börstchen....... 57

57 (56) Am 9. Abdominalsegment an Stelle der Borsten D_1 (und manchmal auch D_2) zahnartige Spitzen. 9. Abdominalsegment dorsal stark längsgefurcht (Abb. 73). Puppen etwa 15-22 mm lang, matt.... *Ennomos* Treitschke

– Am 9. Abdominalsegment D^1 borstenartig oder rückgebildet. Puppe oft kleiner und/oder glänzend.. 58

58 (57) Kremaster ventral stark radial gefurcht, und/oder seine Borsten, auch D_1, entspringen fächerartig von den Seiten der Spitze, sind ± gleich groß (D_2 manchmal etwas stärker) und am Ende stark spiralig eingerollt (Abb. 75, 79, 80). Vorderschenkel nicht sichtbar oder klein (Abb. 82, 86, 88). Puppen bunt, oft grün gefärbt und/oder mit Zeichnungen.......

Abb. 88-114. – 88, *Chlorissa cloraria*; 89, *Epirrita christyi*; 90, *Larentia clavaria*; 91, *Selenia dentaria*; 92, *Hypoxystis pluviaria*; 93, *Plagodis pulveraria*; 94, *Opisthograptis luteolata*; 94a, *Therapis flavicaria*; 95, 100, *Angerona prunaria*; 96, 101, *Crocallis elinguaria*; 97, *Epione parallelaria*; 98, *Synopsia sociaria*; 99, *Aspilates gilvaria*; 102, *Epione repandaria*; 103, 105-107, *Dyscia conspersaria*; 104, 108, *Pseudopanthera macularia*; 109, *Petrophora chlorosata*; 110-112, *Epirrhanthis diversata*; 113, *Hylaea fasciaria*; 114, *Odontopera bidentata*.

88, 94, 94a, Habitusbild in Ventralsicht; 89, 90, 105, 108, 109, 110, 114, Abdominalende in Dorsalsicht; 91, 106, 111, 113, Erhebung kaudal von dem thorakalen Spiraculum; 92, Basis des 5. Abdominalsegmentes in Lateralsicht; 93, 107, Abdominalende in Lateralsicht; 95, 96, Augen und Umgebung; 97, Lateraleinschnitt und Dorsalrinne in Lateralsicht; 98-101, Kopf und Beine in Ventralsicht; 102-104, Metanotum, 1. Abdominalsegment; 112, Labrum, Labium.

.... 59

– Kremaster anders gestaltet, ventral meist nicht regelmäßig radial gefurcht. D_1 wenn vorhanden, entspringt von seiner Dorsalseite. Borsten oft ungleich groß oder lang. Im Zweifelsfall Vorderschenkel groß (Abb. 1), Puppen oft zeichnungslos und ± glänzend 67

59 (58) Proboscis so lang wie die Mittelbeine (Abb. 82, 86). Abdomen ohne stachelige Skulptur 63

– Proboscis kürzer als die Mittelbeine, doch länger als die Hälfte dieser (Abb. 77). Wenigstens die mittleren Abdominalsegmente mit stacheliger Skulptur (Abb. 78) 60

– Proboscis kürzer als die Hälfte der Mittelbeine. Abdominalsegmente ohne stachelige Skulptur .... *Aplasta* Hübner

60 (59) Puppe einfarbig grün, Exuvie weißlich grüngelb .... *Hemistola* Warren

– Puppe mit Zeichnungen und dunklen Pinnacula der Borsten 61

61 (60) Puppe grün, am Rücken z. T. rotbraun, 15-20 mm lang. Hinterbeine meist nicht sichtbar .... *Geometra* Linnaeus

– Puppe nicht grün gefärbt, 11-14 mm lang. Spitze der Hinterbeine sichtbar, groß 62

62 (61) Flügeladerung deutlich schwarz abgesetzt, Grundfärbung weißgräulich......................... .... *Thetidia* Boisduval

– Flügeladern kaum dunkler, Grundfärbung hell rostbraun .... *Comibaena* Hübner

63 (59) Kremaster mittellang mit 4 Paaren von Häkchen (Abb. 80) 64

– Kremaster sehr lang mit 5-7 Paaren von Häkchen (Abb. 79) .... *Jodis* Hübner

64 (63) Dorsalrinne und Lateraleinschnitt vorhanden, deutlich (Abb. 80, 81) .... *Pseudoterpna* Hübner

– Dorsalrinne und Lateraleinschnitt nicht vorhanden (vgl. Abb. 93) 65

65 (64) Puppe recht schlank, mehr als 4 mal so lang wie breit. Frontalhöcker relativ groß (Abb. 86). Puppe eintönig sandfarben oder grünlich, nur der Rückenstreifen am 1.-8. Abdominalsegment dunkel. Spiracula hell .... *Hemithea* Duponchel

– Puppe ± gedrungen, Frontalhöcker klein (Abb. 82, 88). Puppe meist bunter gezeichnet, auch am Kopf und Thorax. Spiracula dunkel gefleckt (Abb. 83) 66

66 (65) Grenze zwischen Vorderbein und Antenne etwa 2× so lang wie die Grenze zwischen Vorderbein und Gena (Abb. 84). Kopf und Thorax ventral, auch die Adern der Vorderflügel sehr kontrastreich dunkel gezeichnet. Puppe relativ schlanker, 13-15 mm lang....... .... *Thalera* Hübner

– Grenze zwischen Vorderbein und Antenne etwa 3× so lang wie die Grenze zwischen Vorderbein und Gena (Abb. 85). Kopf und Thorax ventral oft weniger kontrastreich gezeichnet. Puppe mehr gedrungen, 9-11 mm lang .... *Chlorissa* Stephens

67 (58) Vorderschenkel nicht sichtbar (Abb. 99, 101) 68

– Vorderschenkel sichtbar (Abb. 1, 165, 166) 98

68 (67) D_2 am Kremaster ± parallel, Spitze hakenförmig, wenn divergierend, dann erst im Kaudalteil (Abb. 109) oder Kremaster kurz und stumpf abgerundet (Abb. 119) 72

– D_2 am Kremaster stark divergierend, Spitze oft mehr dorn- als hakenförmig, manchmal ± gestielt. Kremaster länger und/oder spitz (Abb. 89, 167, 168, 174)......................... 69

69 (68) Mittlerer Kaudalausläufer der Dorsalrinne vergrößert, tief (Abb. 89, 174) 70

– Mittlerer Kaudalausläufer der Dorsalrinne klein oder flach (Abb. 167, 168, 171) bzw. Dorsalrinne nicht entwickelt (Abb. 93) ... 73

70 (69) Labium nicht sichtbar (Abb. 87). Kremaster lang vorgezogen, D_2 einen Winkel von fast 180° bildend (Abb. 89) ...... *Epirrita* Hübner

– Labium groß (vgl. Abb. 135), Stiel des Kremasters kürzer, D_2 einen spitzen Winkel bildend 71

71 (70) Sd_1 vorhanden, entspringt nahe der Basis des Kremasters, Kaudalausläufer der Dorsalrinne spitz (Abb. 90) .... *Larentia* Treitschke

– Sd_1 am Kremaster fehlt. Kaudalausläufer der Dorsalrinne stumpf abgerundet (Abb. 174) 131

72 (68) Proboscis überragt deutlich den Kaudalrand des 4. Abdominalsegmentes (Abb. 94 a) .... *Therapis* Hübner

– Proboscis überragt den Kaudalrand des 4. Abdominalsegmentes nicht (Abb. 94)...... 73

73 (72) Dorsalrinne nicht entwickelt (Abb. 93) ... 74

– Dorsalrinne entwickelt, mindestens stärker und tiefer als der Dorsaleinschnitt zwischen dem 8. und 9. Abdominalsegment (Abb. 105, 109, 110)....................................... 75

74 (73) Punktgrübchen am Abdomen fehlen (Abb. 92). Proboscis kürzer als die Vorderbeine (vgl. Abb. 98) .... *Hypoxystis* Prout

– Punktgrübchen am Abdomen vorhanden (vgl. Abb. 102). Proboscis länger als die Vorderbeine (vgl. Abb. 94)....... *Plagodis* Hübner

75 (73) Kremaster mit 4 Paaren von Häkchen (Abb. 105, 114). D_2 ± größer als die übrigen Borsten... 76

– Kremaster mit 2 Paaren von Häkchen. D_2 lang, schlank. Puppe 10-11 mm lang .... *Pachycnemia* Stephens

– Kremaster mit 2 Paaren von Häkchen. D_2 kürzer, relativ dick (Abb. 164). Puppe 16-18 mm lang .... *Colotois* Hübner

76 (75) Adern der Vorderflügel stark hervortretend. Vorderschenkel meist etwas sichtbar (Abb. 94). Puppe sandfarben .... *Opisthograptis* Hübner

– Adern der Vorderflügel nicht oder kaum hervortretend 77

77 (76) Vorderbeine grenzen aneinander (Abb. 98, 99) 78

– Vorderbeine grenzen nicht aneinander (Abb. 94, 100) 79

78 (77) Mittelbeine grenzen aneinander (Abb. 98). Kremaster wenig länger als basal breit .... *Synopsia* Hübner

– Mittelbeine grenzen nicht aneinander (Abb. 99). Kremaster länger als basal breit (Abb. 105) .... *Aspilates* Treitschke

79 (77) Mittelbeine grenzen aneinander (Abb. 100, 101) 80

– Mittelbeine grenzen nicht aneinander (vgl. Abb. 94) 82

80 (79) Kremaster in Lateralsicht stumpf. Dorsalrinne mit flachen, breiten Ausläufern. Puppe unter 13 mm lang .... *Cleorodes* Warren

– Kremaster in Lateralsicht eher spitz. Dorsalrinne mit tieferen Kaudalausläufern. Puppe über 15 mm lang 81

81 (80) Puppe fein skulpturiert, am Rücken glänzend, Augen glatt (Abb. 95). Antennen und Mittelbeine kaudal stumpf, abgerundet (Abb. 100) .... *Angerona* Duponchel

– Puppe grob skulpturiert, am Rücken kaum glänzend. Augen dorsal grob skulpturiert (Abb. 96). Antennen und Mittelbeine kaudal spitz, keilförmig (Abb. 101) .... *Crocallis* Treitschke

82 (79) Kremaster (in Dorsalsicht, ohne Häkchen) fast zweimal so lang als basal breit (Abb. 105, 107). Kaudal der thorakalen Spiracula je eine relativ große tomentöse Erhebung (Abb. 91, 106) 83

– Kremaster kaum länger oder kürzer als basal breit. Im Zweifelsfall der Höcker kaudal des thorakalen Spiraculum klein, unauffällig, kaum tomentös 85

83 (82) Dorsalrinne mit starken, abgerundeten Kaudalausläufern (vgl. Abb. 114) .... *Charaspilates* Wehrli

– Dorsalrinne mit undeutlichen, kleinen bzw. mehr spitzen Kaudalausläufern (Abb. 105) 84

84 (83) 1. Abdominalsegment ohne Punktgrübchen (Abb. 103). Lateraleinschnitt groß, tief (Abb. 107) .... *Dyscia* Hübner

– 1. Abdominalsegment mit starken Punktgrübchen (Abb. 102). Lateraleinschnitt schwach entwickelt oder klein (Abb. 97) .... *Epione* Duponchel

85 (82) Metanotum mit Punktgrübchen (Abb. 104) 86

– Metanotum ohne Punktgrübchen (Abb. 102, 103) 87

86 (85) Pro- und Mesonotum mit Punktgrübchen (Abb. 104). D_2 am Kremaster hakenförmig (Abb. 108) .... *Pseudopanthera* Hübner

– Pro- und Mesonotum ohne Punktgrübchen (vgl. Abb. 210). D_2 am Kremaster schlank dornförmig, in der kaudalen Hälfte voneinander divergierend (Abb. 109) .... *Petrophora* Hübner

87 (85) Thorakale Spiracula kaudal mit je einem großen, elliptischen, tomentösen Höcker (Abb. 91) .... *Selenia* Hübner

– Thorakale Spiracula kaudal ohne oder nur mit kleinen und schmalen, bzw. nicht tomentösen Höckern (Abb. 111, 113) 88

88 (87) 1-2. Abdominalsegment ohne Punktgrübchen (vgl. Abb. 103). D_2 am Kremaster meist ± weit voneinander entfernt (Abb. 120-122) 96

– 1-2. Abdominalsegment mit Punktgrübchen (vgl. Abb. 102). D_2 am Kremaster entspringen nahe beieinander (Abb. 110, 114, 119) 89

89 (88) D_2 am Kremaster in Dorsalsicht deutlich länger als der Kremaster selbst, parallel (Abb. 110). Labrum auffallend lang , abgerundet (Abb. 112) .... *Epirrhanthis* Hübner

– D_2 am Kremaster nicht länger als der Kremaster selbst oder distal stark divergierend (Abb. 114, 115, 119). Labrum meist kurz und breit (Abb. 116, 117) 90

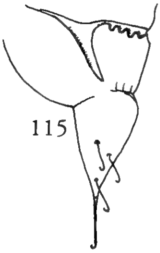
90 (89) 10. Abdominalsegment (ohne Kremaster) in Dorsalsicht fast 2 mal länger als das 9. Abdominalsegment, mit einer gebogenen, feinen Querfurche (Abb. 114). Puppe 17-20 mm lang .... *Odontopera* Stephens

– 10. Abdominalsegment (ohne Kremaster) nicht oder wenig länger als das 9. Abdominalsegment, ohne durchgehende Querfurche. Puppen oft kürzer als 15 mm 91

91 (90) Lateraleinschnitt groß, wenigstens bis zur Mitte des 10. Abdominalsegmentes reichend (Abb. 115) 92

– Lateraleinschnitt klein und kurz (Abb. 118) 95

92 (91) Kaudal des thorakalen Spiraculums je eine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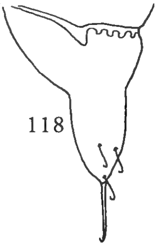
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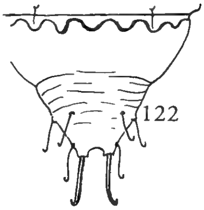
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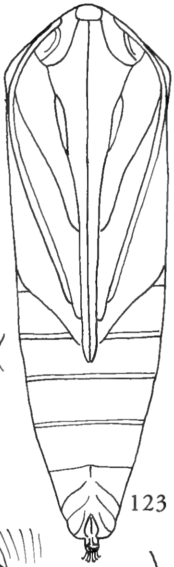
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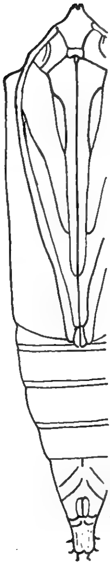
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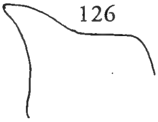
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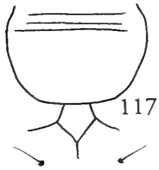
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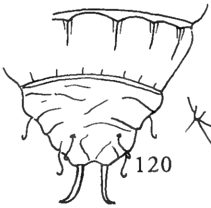
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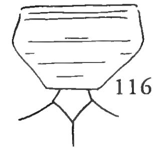
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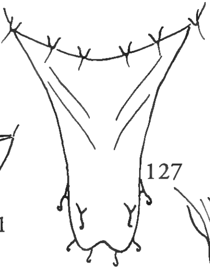
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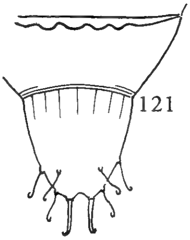
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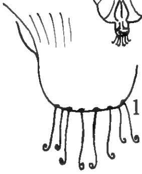
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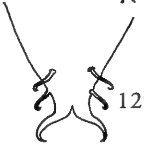
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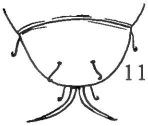
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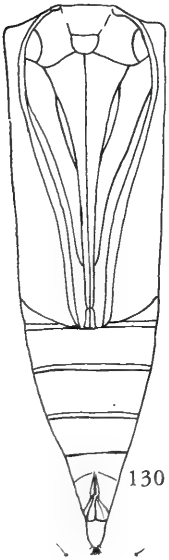
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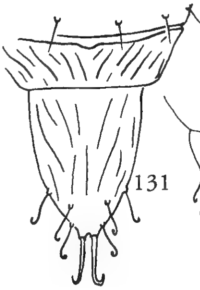
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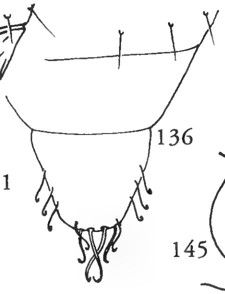
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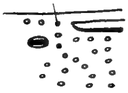
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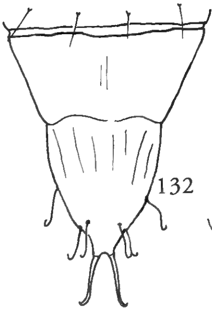
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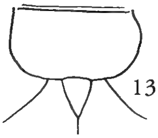
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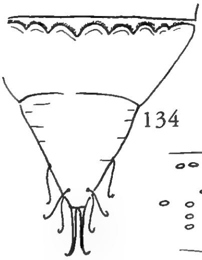
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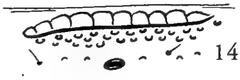
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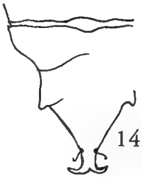
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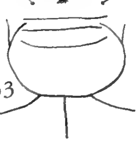
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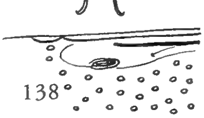
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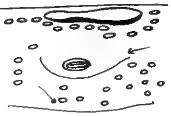
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längliche, stark tomentöse Erhebung (Abb. 113). Lateraleinschnitt distal schmal. Kremaster auch im distalen Bereich dorsal skulpturiert, Sd_1 entspringen etwa in seiner Mitte .... *Hylaea* Hübner

– Kaudal des thorakalen Spiraculums ebenfalls je eine längliche tomentöse Erhebung. Lateraleinschnitt distal ± breit. Kremaster dorsal auch im distalen Bereich skulpturiert, Sd_1 entspringt nahe seiner Basis .... *Menophra* Moore

– Kaudal des thorakalen Spiraculum liegt keine oder eine ganz unauffällige und kaum tomentöse Erhebung (Abb. 111). Kremaster im distalen Bereich ± glatt. Sd_1 entspringt meist nicht so nahe der Kremasterbasis 93

93 (92) Labrum mit wenig konvergierenden Seiten (Abb. 117). Puppen fein skulpturiert, relativ stark glänzend. Kremaster im Basalteil schwach gerunzelt ... *Puengeleria* Rougemont

– Labrum trapezförmig mit stark konvergierenden Seiten (Abb. 116). Puppe nur mäßig glänzend, ± gröber skulpturiert. Kremaster dorsal an der Basis stark gerunzelt 94

94 (93) Puppe 12-20 mm lang. 8. Abdominalsegment ohne Punktgrübchen .... *Campaea* Lamarck

– Puppe 8-11 mm lang. 8. Abdominalsegment mit starken Punktgrübchen .... *Cepphis* Hübner

95 (91) Sd_1 entspringen nahe der Basis des Kremasters, dieser kurz, stumpf, abgerundet, D_2 groß (Abb. 119) .... *Lomographa* Hübner

– Sd_1 entspringen etwa von der Mitte des Kremasters, dieser relativ lang, spitz (Abb. 118) .... *Cabera* Treitschke

96 (88) Sd_1 entspringen am Kremaster auf der Höhe von D_1, in der Mitte des Kremasters oder distal davon (Abb. 121, 122). Lateraleinschnitt schmal 97

– Sd_1 entspringen am Kremaster mehr frontal als D_1, nahe der Basis (Abb. 120). Lateraleinschnitt kurz, breit, stumpf abgerundet .... *Sciadia* Hübner

97 (96) D_2 mehr als halb so lang wie der Kremaster, dieser kürzer als basal breit. Dorsalrinne mit 2-3 Kaudalausläufern (Abb. 224). Labium sehr groß (Abb. 225) *Perconia* Hübner

– D_2 mehr als halb so lang wie der Kremaster, dieser kürzer als basal breit. Dorsalrinne mit mehreren Kaudalausläufern (Abb. 122). Labium groß .... *Gnophos* Treitschke s. lat.

– D_2 weniger als halb so lang wie der Kremaster, dieser länger als basal breit. Dorsalrinne mit mehreren Kaudalausläufern (Abb. 121). Labium groß *Crocota* Hübner

98 (67) An der Basis der Vorderflügel je ein starker Höcker (Abb. 123, 125, 130) 99

– An der Basis der Vorderflügel kein Höcker (Abb. 1, 2) 101

99 (98) Proboscis überragt den Kaudalrand des 4. Abdominalsegmentes (Abb. 123). Kremaster mit relativ langen Borsten (Abb. 124) .... *Rhodometra* Meyrick

– Proboscis überragt den Kaudalrand des 4. Abdominalsegmentes nicht (Abb. 125, 130). Kremaster mit kurzen Borsten (Abb. 127, 128) 100

100 (99) Frons mit langem, zweispitzigem Fortsatz (Abb. 125). Die Borsten am Ende des Kremasters einzeln (Abb. 127) .... *Timandra* Duponchel

– Frons ohne Fortsatz (Abb. 130). Die Borsten am Ende des Kremasters in einer Gruppe (Abb. 128) .... *Cyclophora* Hübner

101 (98) Puppe ± matt, grün oder leder- bzw. sandfarben, dann mit dunkler Sprenkelung oder anderer Zeichnung bzw. schwarzen Spiracula. Exuvie grünweiß, gelbweiß oder trüb bräunlichgelb 102

– Puppe ± glänzend, gelb-, rot- bis schwarzbraun, zeichnungslos......................... 113

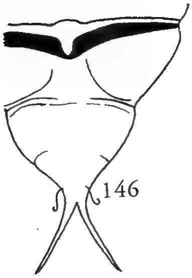
102 (101) Frontolaterale Lappen des Metanotums spitz (Abb. 153) 128

– Frontolaterale Lappen des Metanotums abgerundet (Abb. 195) 165

103 (165) Adern der Vorderflügel stark hervortretend 76

– Adern der Vorderflügel nicht stark hervortretend 104

Abb. 115-145. – 115, 117, *Puengeleria capreolaria*; 116, *Campaea honoraria*; 118, *Cabera pusaria*; 119, *Lomographa temerata*; 120, *Sciadia tenebraria*; 121, *Crocota niveari*a; 122, *Gnophos dilucidaria*; 123, 124, *Rhodometra sacraria*; 125-127, *Timandra griseata*; 128, 130, *Cyclophora linearia*; 129, *Ourapteryx sambucaria*; 131, *Eulithis populata*; 132, 133, *Ecliptopera silaceata*; 134, *Electrophaes corylata*; 135, *Dysstroma truncata*; 136, *Cidaria fulvata*; 137, *Thera variata*; 138, *Rheumaptera cervinalis*; 139, 140, *R. undulata*; 141, *Philereme transversata*; 142, *Triphosa dubitata*; 143, *Pterapherapteryx sexalata*; 144, *Xanthorhoe designata*; 145, *Epirrhoe alternata*.
115-118, 137, Abdominalende in Lateralsicht; 116, 117, 133, 135, Labrum, Labium; 119-122, 124, 127-129, 131, 132, 134, 136, 143, Abdominalende in Dorsalsicht; 123, 125, 130, Habitusbild in Ventralsicht; 126, Kopffortsatz in Lateralsicht (Umriss); 138, 140, 141, 142, Basis des 5. Abdominalsegmentes in Lateralsicht; 139, Basis des 5. Abdominalsegmentes, Dorsalsicht; 144, 145, Auge und Umgebung.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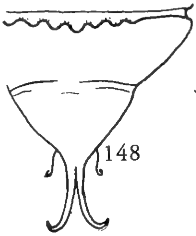
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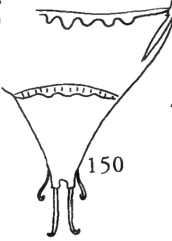
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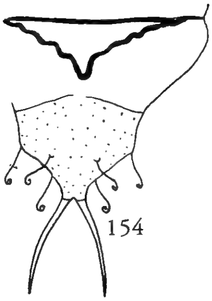
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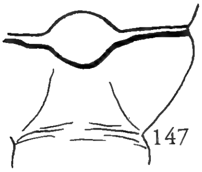
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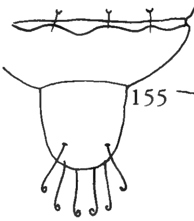
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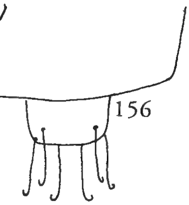
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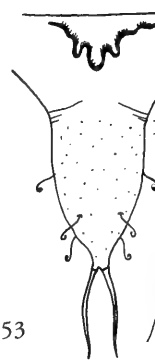
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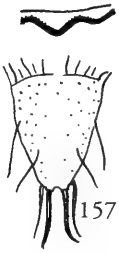
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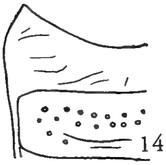
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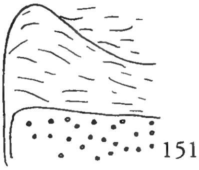
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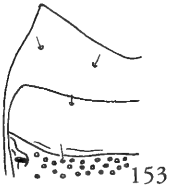
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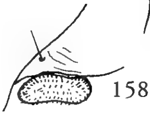
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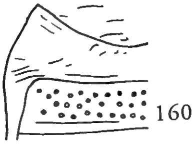
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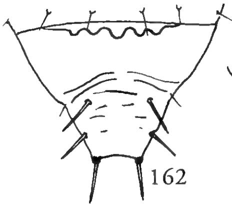
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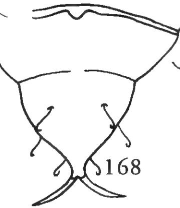
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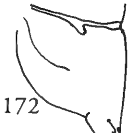
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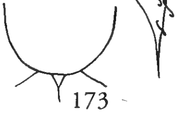
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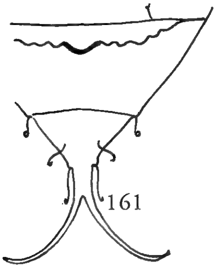
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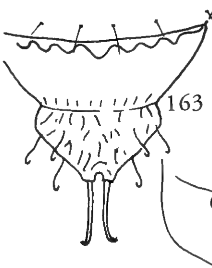
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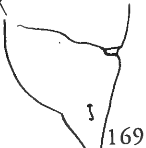
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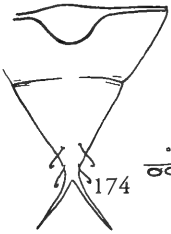
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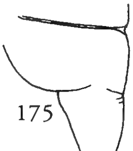
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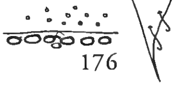
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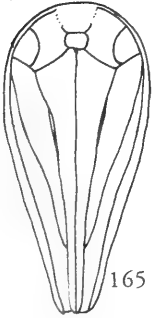
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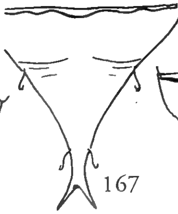
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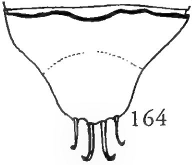
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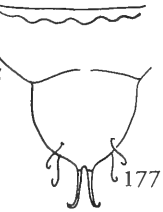
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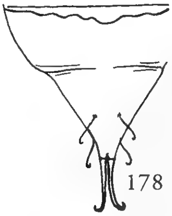
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104 (103) D_2 am Kremaster an einem kurzen Stiel, eine Winkel von fast 90° bildend (Abb. 129). Puppe über 18 mm lang .... *Ourapteryx* Leach

– D_2 am Kremaster nicht oder kaum gestielt. Puppe unter 16 mm lang 105

105 (104) Kremaster mit 4 Paaren von Borsten (Abb. 131, 132) 106

– Kremaster mit 6 Paaren von Borsten (Abb. 136, 137) 111

106 (105) 10. Abdominalsegment dorsal stark verkürzt und ± längsgefurcht oder längsgerippt (Abb. 131). Puppen über 12, oft über 13 mm lang .... *Eulithis* Hübner

– 10. Abdominalsegment stark verkürzt, jedoch nicht längsgefurcht. Puppenlänge unter 12 mm .... *Xanthorhoe* Hübner p.p (*X. munitata* (Hübner))

– 10. Abdominalsegment nicht stark verkürzt, kaum längsgefurcht (Abb. 132) 107

107 (106) Labium nicht sichtbar oder ganz klein (Abb. 133, 209) 108

– Labium relativ groß (Abb. 135) 110

108 (107) Dorsalrinne ohne Kaudalausläufer (Abb. 132) .... *Ecliptopera* Warren

– Dorsalrinne mit Kaudalausläufern, wenigstens der mittlere gut sichtbar (Abb. 134, 208) 109

109 (108) Dorsalrinne mit deutlichen spitzen tomentösen Ausläufern (Abb. 134). Puppe deutlich dunkel gefleckt ...... *Electrophaes* Prout

– Dorsalrinne mit undeutlichen Ausläufern, nur der mittlere etwas mehr ausgeprägt (Abb. 208). Puppe undeutlich oder nicht gefleckt 156

110 (107) Puppe dünnschalig, nicht gesprenkelt, nicht bereift, Exuvie matt gelblich .... *Dysstroma* Hübner

– Puppe dickschalig, dunkel gesprenkelt, deutlich bereift, Exuvie hellbraun .... *Chloroclysta* Hübner

– Puppe dickschalig, braun mit Zeichnungen, insbesondere an den Adern der Vorderflügel, nicht bereift, nur 7-8 mm lang 150

111 (105) Dorsalrinne und Lateraleinschnitt nicht sichtbar (Abb. 136) ..... *Cidaria* Treitschke

– Dorsalrinne und Lateraleinschnitt ± sichtbar (Abb. 137) 112

112 (111) Borsten am Kremaster satt braunrot, Exuvie weißlichgelb. Dorsalrinne schwach, meist nur mit einzelnen, kleinen Kaudalausläufern .... *Plemyria* Hübner

– Borsten am Kremaster bräunlich. Exuvie bräunlich weiß oder gelb. Dorsalrinne mit mehreren meist deutlichen Kaudalausläufern (Abb. 137) .... *Thera* Stephens

113 (101) An der Basis des 5. Abdominalsegmentes, dorsal oder lateral, dunkle Leisten, die Querrinnen oder -vertiefungen begrenzen (Abb. 138-142) 114

– An der Basis des 5. Abdominalsegmentes keine Leisten, Querrinnen oder -vertiefungen, höchstens dichte Punktgrübchen (Abb. 221) 116

114 (113) An der Dorsalseite der Basis des 5. Abdominalsegmentes Querleisten und dazwischen eine Querrinne. Sie laufen lateral ± in die Nähe der Spiracula herab (Abb. 138-140) .... *Rheumaptera* Hübner

– Nur lateral an der Basis des 5. Abdominalsegmentes Querleisten und Vertiefungen (Abb. 141, 142) 115

115 (114) 1-2 laterale Vertiefungen am 5. Abdominalsegment ungeteilt (Abb 141) .... *Phileremе* Hübner

– Laterale Vertiefung an der Basis des 5. Abdominalsegmentes in mehrere Zellen unterteilt (Abb. 142) .... *Triphosa* Stephens

116 (113) Am Kremaster - außer den Borsten D_2, die starke Endhäkchen, Enddornen bzw. eine gestielte Endgabel bilden - gibt es nur ein Paar kleiner Borsten (L_1 oder D_1) (Abb. 143, 146, 150) 117

– Am Kremaster, außer D_2 noch 2-3 Paaren von Borsten (Abb. 167, 183, 201, 218) 123

117 (116) Kremaster mit einem Paar von lateralen Höckern. D_2 zusammen gestielt, stark divergierend (Abb. 143) .... *Pterapherapteryx* Curtis

Abb. 146-178. – 146, *Catarhoe cucullata*; 147, *C. rubidata*; 148, *Epirrhoe alternata*; 149, 150, *Nycterosea obstipata*; 151, 152, *Camptogramma bilineata*; 153, 154, *Scopula marginepunctata*; 155, *Idaea aureolaria*; 156, *I. rufaria*; 157, *I. deversaria*; 158, 159, *Rhodostrophia vibicaria*; 160, 161, *Baptria tibiale*; 162, *Glacies alticolaria*; 163, *Gnophos unicoloraria*; 164, *Colotois pennaria*; 165, 167, *Nothacasis sertata*; 166, 171-173, *Anticollix sparsata*; 168, *Acasis appensata*; 169, *Trichopteryx polycommata*; 170, *T. carpinata*; 174-176, *Anticles badiata*; 177, *Discoloxia blomeri*; 178, *Venusia cambrica*.
146, 148, 150, 152, 154, 157, 159, 161-164, 167, 168, 171, 172, 174, 177, 178, Abdominalende in Dorsalsicht; 147, Dorsalrinne; 149, 151, 153, Pronotum, 1. Abdominalsegment; 158, Erhebung kaudal von dem thorakalen Spiraculum; 160, Metanotum, 1. Abdominalsegment; 165, Kopf und Beine in Ventralsicht; 166, Vorderschenkel; 169, 170, 175, Abdominalende in Lateralsicht; 176, Punktgrübchen an der Basis des 2. Abdominalsegmentes.

– Kremaster ohne Lateralhöcker. Enddornen schlanker, nicht so lang gestielt, weniger divergierend (Abb. 146, 150) 118

118 (117) Grenzen zwischen Vorderbeine und Antennen viel länger als die Grenzen zwischen Vorderbeine und Augen. Grenzen zwischen Antennen und Augen kaum länger als die zwischen Antennen und Vorderbeine (Abb. 144) 119

– Grenzen zwischen Vorderbeine und Antennen nicht oder wenig länger als die Grenzen zwischen Vorderbeine und Augen. Grenzen zwischen Antennen und Augen deutlich länger als die zwischen Antennen und Vorderbeine (Abb. 145) 120

119 (118) Am Kremaster außer D_2 noch L_1 vorhanden, nahe bei D_2 (vgl. Abb. 148) .... *Xanthorhoe* Hübner

– Am Kremaster außer D_2 noch D_1, von D_2 entfernt 120

120 (118) Dorsalrinne nur mit einem großen Kaudal- und Frontalausläufer in der Mitte (Abb. 146, 147) .... *Catarhoe* Herbulot

– Dorsalrinne mit mehreren Kaudalausläufern (Abb. 148, 150, 152) 121

121 (120) D_2 so lang wie oder länger als der Kremaster (Abb. 148) .... *Epirrhoe* Hübner

– D_2 kürzer als der Kremaster, dieser ± länger als basal breit (Abb. 150, 152) 122

122 (121) Frontolaterale Lappen des Metanotums spitz (Abb. 149). Dorsalrinne im Mittelteil wenig verbreitert (Abb. 150) .... *Nycterosea* Hulst

– Frontolaterale Lappen des Metanotums abgerundet. Dorsalrinne im Mittelteil stark verbreitert (Abb. 152) .... *Camptogramma* Stephens

123 (116) Frontolaterale Lappen des Metanotums spitzwinkelig (Abb. 153, 160). (Wenn jedoch das 1. Abdominalsegment mit deutlichen Punktgrübchen versehen und die Skulptur relativ grob ist, suche weiter unter 143) 124

– Frontolaterale Lappen des Metanotums stumpf, abgerundet (Abb. 151, 181).. 129

124 (123) D_2 gleichlang und selten stärker als die übrigen Borsten des Kremasters (Abb. 155-157) 125

– D_2 deutlich länger als die übrigen Borsten des Kremasters (Abb. 154, 159, 161) 126

125 (124) Dorsalrinne nur mit einem mittelgroßen Vorsprung in der Mitte. Labium klein (Abb. 193). Lateraleinschnitt kurz, abgerundet 149

– Dorsalrinne mit kleinen Vorsprüngen, der mittlere aber sehr lang, bis nahe zur Basis des Kremasters reichend. (Labium an der untersuchten Puppe nicht vorhanden) .... *Glossotrophia* Prout

– Dorsalrinne mit mehreren Vorsprüngen, keiner von ihnen nähert sich der Basis des Kremasters (Abb. 155, 157). Wenn nur einer dorsal in der Mitte oder gar keiner vorhanden ist, dann fehlt das Labium und/-oder der Lateraleinschnitt sehr groß .... *Idaea* Treitschke

126 (124) Kremaster rauh skulpturiert, D_2 entspringen weit voneinander entfernt. Vorderschenkel klein 97

– Kremaster ± fein skulpturiert. D_2 entspringen nahe beieinander, Vorderschenkel groß 127

127 (126) Sd_1 entspringen nahe der Basis des Kremasters (Abb. 161). Labium klein (vgl. Abb. 192) .... *Baptria* Hübner

– Sd_1 (wenn vorhanden) entspringen weit von der Basis des Kremasters entfernt (Abb. 154, 159). Labium meist groß (vgl. Abb. 135) 128

128 (127) Kaudal des thorakalen Spiraculums je eine große, elliptische, stark tomentöse Erhebung (Abb. 158). Puppe sandfarben oder grün .... *Rhodostrophia* Hübner

– Kaudal des thorakalen Spiraculums eine längliche, weniger auffällige Erhebung (vgl. Abb. 113). Puppe rotbraun, glänzend .... *Scopula* Schrank

129 (123) Kremaster mit 4 Paaren steifer, gleich großer Borsten, am Ende nicht hakenartig. D_2 entspringen weit voneinander entfernt (Abb. 162). Punktgrübchen fehlen........... .... *Glacies* Milliere, 1874

– Wenigstens ein Teil der Borsten am Kremaster hakenartig. Punktgrübchen am Abdomen ± vorhanden 130

130 (129) Vorderschenkel klein, oft recht schmal. Labium klein oder fehlend (Abb. 165). D_2 am Kremaster länger und stärker als die übrigen Borsten, ± divergierend (Abb. 167, 168, 171, 174) 131

– Vorderschenkel, Labium, oder beide mittelgroß bis groß (Abb. 1), sonst D_2 am Kremaster nicht viel länger oder stärker als die übrigen Borsten. (Abb. 193) 135

131 (130) Dorsalrinne in der Mitte beiderseits, insbesondere kaudalwärts, mit abgerundeten Ausschnitt. Borsten am Enddrittel des Kremasters konzentriert (Abb. 174). Punktgrübchen an der Basis des 1.-3. Abdominalsegmentes stark vergrößert (Abb.

176) .... *Anticlea* Stephens p.p. (*A. badiata* Denis et Schiffermüller)

– Dorsalrinne mit einem oder mehreren flachen Kaudalen Ausschnitten. Borsten auch an der Basalhälfte des Kremasters (Abb. 167, 168, 171). Punktgrübchen an der Basis des 1. -3. Abdominalsegmentes nicht vergrößert 132

132 (131) Metanotum mit Punktgrübchen (Abb, 181, 210) 133

– Metanotum ohne Punktgrübchen (Abb. 151) 134

133 (132) Kremaster in Dorsalsicht länger als basal breit. Borsten Sd_1 entspringen nahe der Basis des Kremasters (Abb. 167) .... *Nothacasis* Prout

– Kremaster in Dorsalsicht kürzer als basal breit. Sd_1 entspringen etwa in der Mitte des Kremasters (Abb. 168) .... *Acasis* Duponchel

134 (132) Puppe ohne oder mit sehr kleinem Labium. Lateraleinschnitt undeutlich oder in der Form eines Grübchens (Abb. 169, 170) .... *Trichopteryx* Hübner

– Puppe mit deutlicherem mittelkleinem Labium. Lateraleinschnitt rinnenförmig, mit einem kurzen Kaudalausläufer (Abb. 172) .... *Anticollix* Prout

135 (130) Kremaster kürzer als basal breit, sehr grob skulpturiert (gefurcht, gerippt). D_2 hakenförmig, kaum divergierend, stärker und länger als die übrigen Borsten, basal ± voneinander entfernt, der Kremaster dazwischen ± konkav (Abb. 163). Epicranialnaht zwischen Vertex und Frons nicht sichtbar (Abb. 4). Puppen über 11 mm lang 97

– Kremaster kürzer als breit, stumpf, grob skulpturiert. D_2 stärker als die übrigen Borsten, basal nahe beieinander, ohne Einschnitt dazwischen, ziemlich parallel laufend. Epicranialnaht sichtbar. Puppenlänge 10-12 mm .... *Epilobophora* Inoue

– Kremaster oft länger als breit, nur schwach oder mäßig skulpturiert. D_2 entspringen entweder nahe beieinander und divergieren, oder sind nicht größer als die übrigen Borsten des Kremasters. Puppen manchmal auch kürzer als 10 mm. Epicranialnaht relativ deutlich (Abb. 3) 136

136 (135) Kremaster mit 3 Paar Borsten (Abb. 178-180) 137

– Kremaster mit 4 Paar Borsten (Abb. 190, 207, 213, 218) 144

137 (136) Lateraleinschnitt nicht entwickelt, oder als einfache Rinne ohne einen größeren Kaudalausläufer (Abb. 175, 182) 138

– Lateraleinschnitt deutlich entwickelt, mit einem starken Kaudalausläufer (Abb. 184) 142

138 (137) Borsten am Kremaster gleich groß (Abb. 179) .... *Gymnoscelis* Mabille

– D_2 viel größer als die übrigen Borsten am Kremaster (Abb. 180) 139

139 (138) Punktgrübchen an der Basis des 1.-4. Abdominalsegment stark vergrößert und vertieft (Abb. 176) 140

– Punktgrübchen an der Basis des 1-4. Abdominalsegmentes nicht vergrößert (Abb. 151) 141

140 (139) Kremaster am Ende abgerundet, schaufelförmig (Abb. 177). Puppe 7-8 mm lang.... .... *Discoloxia* Warren

– Kremaster am Ende spitz (Abb. 178). Puppe 8-9 mm lang........... *Venusia* Curtis

141 (139) Metanotum ohne Punktgrübchen (vgl. Abb. 194) .... *Euchoeca* Hübner

– Metanotum mit Punktgrübchen (Abb. 181) .... *Hydrelia* Hübner

142 (137) Kremaster in Dorsalsicht nicht länger als basal breit (Abb. 183)..... *Euphyia* Hübner

– Kremaster in Dorsalsicht länger als basal breit (Abb. 185) 143

143 (142) Dorsalrinne nur mit drei Kaudalausläufern (Abb. 185) .... *Mesoleuca* Hübner

– Dorsalrinne mit mehreren Kaudalausläufern (Abb. 186) 146

144 (136) Puppenlänge über 11 mm. Punktgrübchen fehlen am Metanotum und meist auch am 1. Abdominalsegment (Abb. 187, 219); falls vorhanden, dann Kremaster recht lang und die Borsten am 9. Abdominalsegment deutlich (Abb. 186) 145

– Metanotum oder wenigstens das 1. Abdominalsegment mit deutlichen Punktgrübchen, oder Puppen unter 10 mm lang....... 148

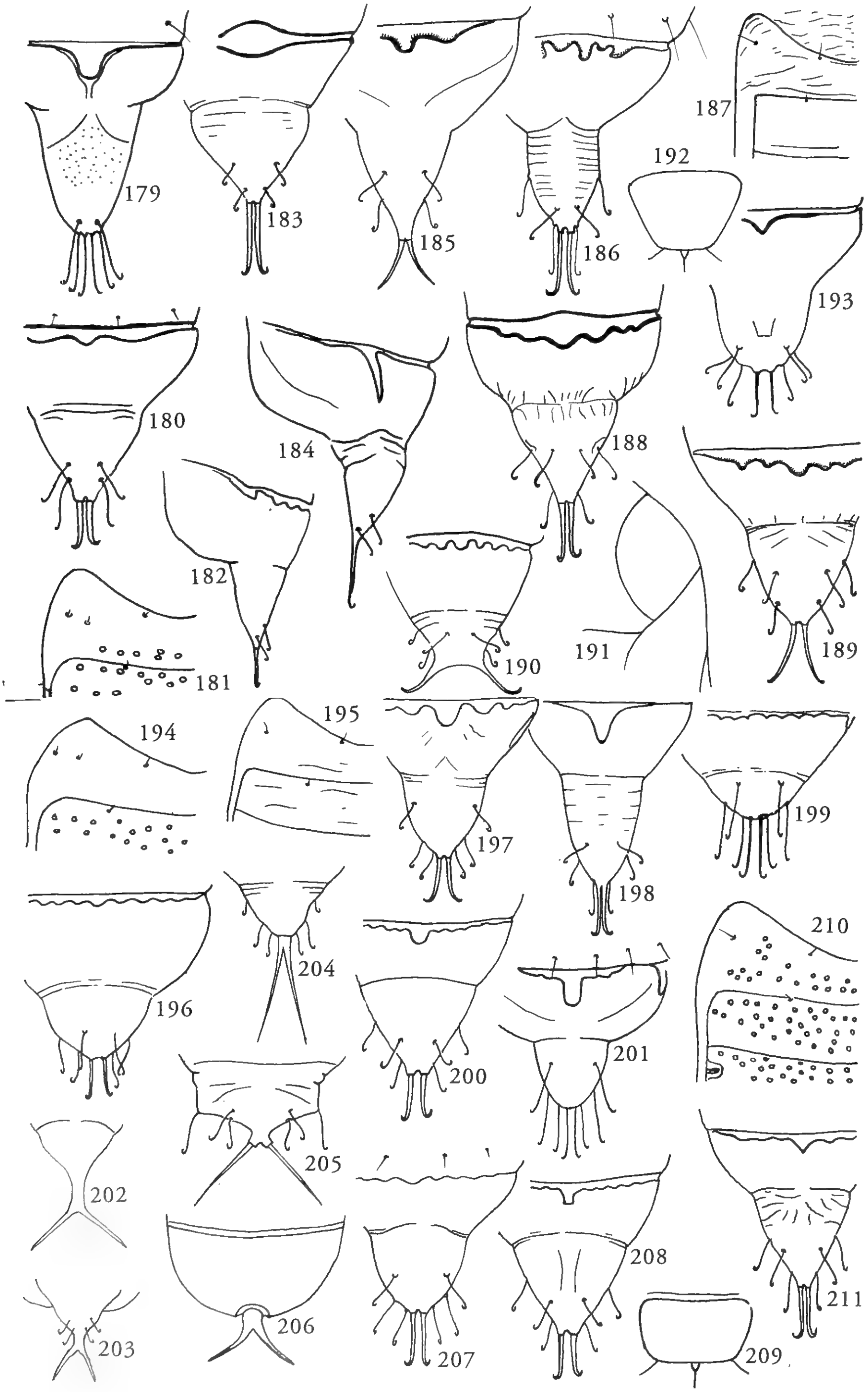
145 (144) D_1 am Kremaster entspringt weit ventral von Sd_1 (Abb. 186, 220) 146

– D_1 entspringt etwa auf derselben Höhe wie Sd_1 (Abb. 188, 189) 147

146 (145) Kremaster lang zungenförmig (Abb. 186). Borsten am 9. Abdominalsegment relativ kräftig (Abb. 186) ...... *Scotopteryx* Hübner

– Kremaster in Dorsalsicht dreieckig, nicht länger als basal breit (Abb. 220) .... *Pareulype* Herbulot

147 (145) Grenzen zwischen Vorderbeinen und Antennen viel länger als zwischen Vorderbeinen und Augen; Grenzen zwischen Antennen und Augen kaum länger als zwischen Antennen und Vorderbeinen (Abb. 144) ..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.... *Xanthorhoe* Hübner p. p. (*X. montanata* (Denis et Schiffermüller), *X. incursata* (Hübner))

– Grenzen zwischen Vorderbeinen und Antennen nicht oder kaum länger als zwischen Vorderbeinen und Augen; Grenzen zwischen Antennen und Augen viel länger als zwischen Antennen und Vorderbeinen (Abb. 145) .... *Entephria* Hübner

148 (144) Grenzen zwischen Vorderbeinen und Antennen deutlich länger als zwischen Vorderbeinen und Augen (etwa gleich lang wie die Grenzen mit Augen und Genae zusammen). Grenzen zwischen Antennen und Augen etwa gleich lang wie zwischen Antennen und Vorderbeine (Abb. 144, 191). Kleine Arten, unter 9, meist unter 8 mm Länge, Skulptur oft grob, D_2 am Kremaster hakenförmig, nicht oder nur wenig divergierend. (Abb. 196-201) Lateraleinschnitt und Labium meist gut entwickelt 149

– Grenzen zwischen Vorderbeinen und Antennen nicht oder kaum länger als zwischen Vorderbeinen und Augen; Grenzen zwischen Antennen und Augen deutlich länger als zwischen Antennen und Vorderbeinen (Abb. 145). Wenn die Puppen unter 8 mm lang, fehlt oft das Labium und der Lateraleinschnitt. D_2 oft gabelartig divergierend (Abb. 203-205, 220) 151

149 (148) Labium sehr klein (Abb. 192). Dorsalrinne mit einem einzigen, kleinen Kaudalausläufer (Abb. 193). Borsten am Kremaster ± gleich groß, nur im distalen Drittel (Abb. 193). Frontolaterale Lappen des Metanotums ziemlich spitz (Abb. 194) .... *Calliclystis* Dietze

– Labium größer (Abb. 1), Dorsalrinne mit mehreren Ausläufern (Abb. 196, 199, 200), oder D_2 deutlich größer als die übrigen Borsten des Kremasters (Abb. 198). Frontolaterale Lappen des Metanotums ± abgerundet (Abb. 210) 150

150 (149) Metanotum ohne, 1. Abdominalsegment ohne oder mit schwach angedeuteten Punktgrübchen (Abb.195). Dorsalrinne mit kleinen Kaudalausläufern, Borsten am Kremaster fast gleich groß, nur in der distalen Hälfte (Abb. 196) .... *Chloroclystis* Hübner

– Skulptur ± grob, 1. Abdominalsegment und oft auch das Metanotum (bzw. ganze Thorax dorsal) mit deutlichen Punktgrübchen. Sonst meist entweder die Kaudalausläufer der Dorsalrinne groß (Abb. 201) oder D_2 länger als die übrigen Borsten des Kremasters (Abb. 197, 198, 200) bzw. Borsten auch in der Basalhälfte des Kremasters .... *Eupithecia* Curtis

151 (148) D_2 am Kremaster deutlich, weit voneinander entfernt, einem stumpfen Winkel bildend (Abb. 190). Metanotum mit Punktgrübchen (vgl. Abb. 210) .... *Anticlea* Stephens p. p. (*Anticlea erivata* (Denis et Schiffermüller))

– D_2 entspringen nahe beieinander (Abb. 216, 218) 152

152 (151) D_2 in Dorsalsicht länger als der Kremaster, dornartig, divergierend und ± lang gestielt. Oft kleinere Arten, unter 9 mm Länge (Abb. 203-205) .... *Perizoma* Hübner

– D_2 in Dorsalsicht nicht länger als der Kremaster, oft hakenartig und ± parallel laufend (Abb. 213, 216, 223), wenn divergierend (Abb. 218, 220), dann oft größere Arten, über 9 mm lang...................... 153

153 (152) Labium fehlt, oder sehr klein (vgl. Abb. 87, 209). Dorsalrinne und Lateraleinschnitt ± schwach ausgebildet. D_2 hakenartig, viel stärker als die übrigen Borsten (Abb. 207, 208, 211). Oft kleinere Arten, 6-8 mm lang..................................... 154

– Labium mittelgroß, bis groß (Abb. 1, 135). Dorsalrinne und Lateraleinschnitt meist deutlich und tief. D_2 stärker oder auch gleichstark wie die übrigen Kremasterborsten 157

154 (153) Metanotum mit Punktgrübchen (vgl. Abb. 210). Puppe nur etwa 6-7 lang........... 155

– Metanotum ohne Punktgrübchen (vgl. Abb. 195). Puppe oft länger als 7 mm 156

155 (154) D_1 am Kremaster viel näher an L_1 als an Sd_1

Abb. 179-211. – 179, *Gymnoscelis rufifasciata*; 180, 181, *Hydrelia flameolaria*; 182, *Euchoeca nebulata*; 183, *Eyphyia*; 185, *Mesaleuca albicillata*; 186, 187, *Scotopteryx moeniata*; 188, *Xanthorhoe montanata*; 189, *Entephria caesiata*; 190 *Anticlea derivata*; 191-194, *Calliclystis v-ata*; 195, 196, *Chloroclystis rectangulata*; 197, *Eupithecia absinthiata*; 198, *E. pulchellata*; 199, *E. tenuiata*; 200, *E. abietaria*; 201, *E. pusillata*; 202, *Perizoma alchemillata*; 203, *P. bifasciata*; 204, *P. didymata*; 205, *P. perallelolineata*; 206, *P. blandiata*; 207, *P. incultaria*; 208, 209, *Eustroma reticulata*; 210, 211, *Asthena albulata*.
179, 180, 183, 185, 186, 188-190, 193, 196-208, 211, Abdominalende in Dorsalsicht; 181, 187, 194, 195, 210, Metanotum, 1. bzw. 2. Abdominalsegment; 182, 184, Abdominalende in Lateralsicht; 191, Augen und Bereich; 192, 209, Labrum, Labium.

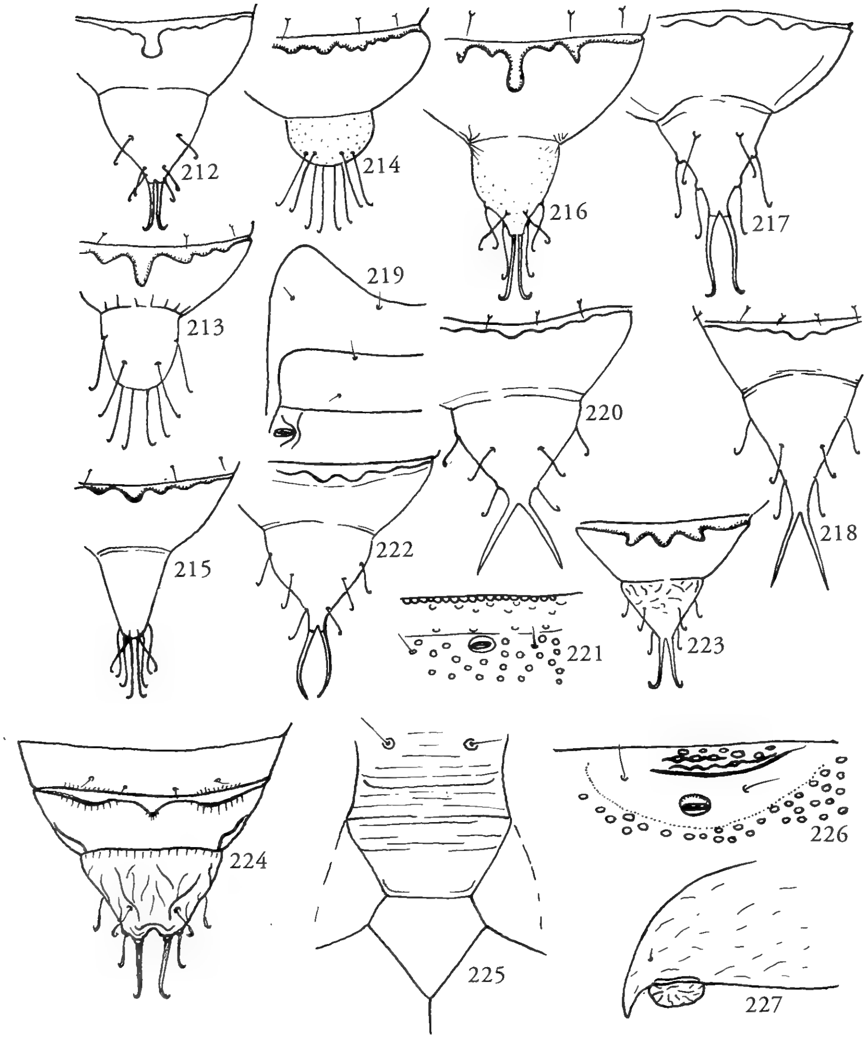

Abb. 212-225. – 212, *Minoa murinata*; 213, *Cosmorhoe ocellata*; 214, *Nebula salicata*; 215, *N. nebulata*; 216, *Colostygia aptata*; 217, *Hydriomena ruberata*; 218, *Lampropteryx otregiata*; 219-221, *Pareulype berberata*; 222, *Spargania luctuata*; 223, *Melanthia procellata*; 224, 225, *Perconia strigillaria*, 226, 227, *Odontognophos dumetata*.
212-218, 220, 222-224, Abdominalende in Dorsalsicht; 219, Metanotum, 1-2. Abdominalsegment; 221, 226, Basis der 5. Abdominalsegmentes in Lateralsicht; 225, Labrium, Labium; 227, Höcker kaudal von dem thorakalen Spiraculum.

entspringend (Abb. 212) .... *Minoa* Treitschke

– D_1 am Kremaster etwa in der Mitte zwischen Sd_1 und L_1 entspringend (Abb. 211) .... *Asthena* Hübner

156 (154) D_1 am Kremaster entspringen frontal von Sd_1 (Abb. 207) .... *Perizoma* Hübner p.p. ....(*P. incultaria* Herrich-Schäffer)

– D_1 am Kremaster entspringen kaudal von Sd_1 (Abb. 208) .... *Eustroma* Hübner

157 (153) Borsten am Kremaster fast gleich lang und gleich dick, schlank. Sd_1 entspringt nahe der Basis des Kremasters (Abb. 213) .... *Cosmorhoe* Hübner

– Borsten am Kremaster nicht gleich lang und gleich groß (D_2 deutlich größer, Abb. 216, 218). Wenn doch gleich groß, dann entspringt Sd_1 ± auf der Höhe von D_1, weit von der Basis des Kremasters entfernt (Abb. 214) 158

158 (157) D_1 entspringt am Kremaster frontal von Sd_1 (Abb. 217) .... *Hydriomena* Hübner

– D_1 entspringt ± auf der Höhe von Sd_1 (Abb. 214, 216) 159

– D_1 entspringt kaudal von Sd_1. (Abb. 220, 222, 223) 161

159 (158) D_2 nicht, oder nur wenig länger als die übrigen Borsten (Abb. 214, 216) 160

– D_2 deutlich länger und stärker als die übrigen Borsten des Kremasters...................... .... *Orthonama* Hübner

160 (159) D_2 kaum länger, manchmal etwas stärker als die übrigen Borsten am Kremaster, dieser kaudal ± stumpf (Abb. 214, 215) .... *Nebula* Bryard

– D_2 deutlich länger und stärker als die übrigen Borsten des Kremasters, dieser kaudal zugespitzt (Abb. 216) .. *Calostygia* Hübner

161 (158) Metanotum und 1. Abdominalsegment ohne Punktgrübchen (Abb. 219) 146

– Metanotum und 1. Abdominalsegment mit Punktgrübchen (Abb. 210).......... 162

162 (161) Kremaster in Dorsalsicht länger als basal breit, D_2 oft dornartig, divergierend (Abb. 218) .... *Lampropteryx* Stephens

– Kremaster in Dorsalsicht nicht länger als basal breit, D_2 hakenartig (Abb. 220, 223) 163

163 (162) Kremaster in Dorsalsicht kürzer als basal breit. D_2 hakenartig (Abb 223)................. .... *Melathia* Duponchel

– Kremaster in Dorsalsicht nicht oder kaum kürzer als basal breit, D_2 mitunter dornartig (Abb. 5, 222) 164

164 (163) Dorsalrinne mit deutlichen Kaudalausläufern, auch oft ein Frontalausläufer in der Mitte vorhanden (Abb. 6). D_2 ± hakenförmig .... *Horisme* Hübner

– Dorsalrinne mit relativ kleinen Kaudal- und keinem Frontalausläufer. D_2 am Kremaster eher dornartig, gebogen (Abb. 222) .... *Spargania* Guéneé, 1857

165 (102) Proboscis kürzer als die Vorderbeine. Vorderflügel grenzen kurz aneinander....... .... *Lythria* Hübner

– Proboscis länger als die Vorderbeine. Vorderflügel grenzen nicht aneinander...... 103

DISKUSSION

In der vorliegenden Arbeit wurde auf eine Bestimmungstabelle der in den derzeitigen Systemen üblichen Unterfamilien der Geometridae, sowie der Tribus nach Herbulot (1962-1963) verzichtet. Die bisherigen Tabellen zur Bestimmung der Unterfamilien von Khotko (1977), sowie von McGuffin (1967-1981) kann man für größere oder kleinere Zahl der Gattungen, jedoch nicht für alle erfolgreich benutzen. Die Tabelle von Khotko ist allzu kompliziert - zur Bestimmung von fünf Unterfamilien sind dort mehr als zwei Textseiten nötig. Die Tabelle von McGuffin ist einfacher, es gibt jedoch bei der Bestimmung mancher Puppen der mitteleuropäischen Fauna Schwierigkeiten, besonders was die Unterscheidung der Unterfamilien Sterrhinae und Larentiinae betrifft. Noch schwieriger ist dies bei den Tribus im Sinne von Herbulot. Nur für einen Teil von ihnen gelang es mir anhand der Puppenmerkmale eine benutzbare Diagnose aufzustellen und auch dort ist diese nicht für alle Gattungen nach dem Herbulot'schen System gültig. Unter die von puppenmorphologischer Hinsicht uneinheitlichen Tribus gehören z. B. die Pseudoterpnini (Unterfamilie Geometrinae) und die Lythriini (Unterfamilie Larentiinae). Mehrere Gattungen sollten anhand der Puppenmorphologie in andere Tribus gehören als in welche sie von Herbulot gestellt wurden, wie z. B. : *Calospilos*, *Lomaspilis*, *Lygdia* und *Stegania* (siehe Patocˇka 1986a), oder *Odontognophos*, *Cleorodes*, *Crocota*, *Synopsia* und *Menophra* (siehe Patocˇka 1993).

Die Gattungen des Herbulot'schen Systems entsprechen dagegen in der Mehrzahl auch auf Grund der Puppenmerkmale sehr gut. Auf wenige Ausnahmen soll hier aufmerksam gemacht werden: Die Art *obstipata* weicht von *vittata* stark ab, es wird für sie deshalb der Gattungsname *Nycterosea* (im Sinne von Forster-Wohlfart 1981) benützt. Ebenso wurde es mit den Gattungen *Dysstroma*, *Chiasmia*, *Diastictis* und *Phigalia* gemacht. Außerdem ist auch die Gattung *Xanthorhoe* puppenmorphologisch uneinheitlich. Insbesondere die Art *X. munitata* entspricht viel besser der gattung *Eulithis*. Die Arten *Xanthorhoe montanata* und *incursata* weichen von den übrigen stärker ab. Ähnlich ist es auch mit der Gattung *Perizoma*, wo besonders die Art *incultaria* den übrigen puppenmorphologisch unähnlich ist. Stark voneinander abweichende Arten enthält auch die Gattung *Anticlea*. Dagegen sind die größeren oder großen Gattungen *Cyclophora*, *Sterrha*, *Idaea* und *Eupithecia* hinsichtlich der Puppenmorphologie relativ einheitlich gebaut. Die Verhältnisse in der Gattung *Gnophos* s. lat. (vgl. Sauter 1990) werden in einer besonderen Arbeit (Patočka im Druck) besprochen.

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ANHANG

Übersicht der Gattungen und Arten der Familie Geometridae, deren Puppen als Unterlage für die Aufstellung dieser Gattungstabelle untersucht wurden.

Archiearis Hübner, 1823
parthenias (Linnaeus, 1761) (Slowakei, Holland)
notha (Hübner, 1803) (Slowakei)
puella (Esper, 1787) (Slowakei)

Alsophila Hübner, 1825
aescularia ([Denis & Schiffermüller], 1775) (Slowakei)
quadripunctaria (Esper, 1787) (Slowakei)

Aplasta Hübner, 1823
ononaria (Fuessly, 1783) (Deutschland)

Pseudoterpna Hübner, 1823
pruinata (Hufnagel, 1767) (Slowakei)

Geometra Linnaeus, 1758
papilionaria (Linnaeus, 1758) (Böhmen)

Comibaena Hübner, 1823
bajularia ([Denis & Schiffermüller], 1775) (Slowakei)

Thetidia Boisduval, 1840
smaragdaria (Fabricius, 1787) (Slowakei)

Hemithea Duponchel, 1829
aestivaria (Hübner, 1799) (Slowakei, Böhmen)

Chlorissa Stephens, 1831
viridata (Linnaeus, 1758) (Polen)
cloraria (Hübner, 1813) (Slowakei)
etruscaria (Zeller, 1848) (Slowakei)

Thalera Hübner, 1823
fimbrialis (Scopoli, 1763) (Österreich)

Hemistola Warren, 1893
biliosata (Villers, 1789) (Slowakei)

Jodis Hübner, 1823
lactearia (Linnaeus, 1758) (Slowakei)
putata (Linnaeus, 1758) (Böhmen, Österreich)

Cyclophora Hübner, 1822
pendularia (Clerck, 1759) (Slowakei, Böhmen)
albiocelaria (Hübner, 1789) (Slowakei)
annulata (Schulze, 1775) (Slowakei)
albipunctata (Hufnagel, 1767) (Slowakei, Böhmen)
puppillaria (Hübner, 1799) (Frankreich)
ruficiliaria (Herrich-Schäffer, 1855) (Slowakei)
porata (Linnaeus, 1767) (Österreich)
quercimontaria (Bastelberger, 1897) (Slowakei)
punctaria (Linnaeus, 1758) (Slowakei)
suppunctaria (Zeller, 1847) (Slowakei)
linearia (Hübner, 1799) (Slowakei)

Timandra Duponchel, 1829
griseata W. Petersen, 1902 (Slowakei)

Scopula Schrank, 1802
immorata (Linnaeus, 1758) (Slowakei)
umbelaria (Hübner, 1813) (Österreich)
virgulata (Denis & Schiffermüller, 175) (Slowakei)
ornata (Scopoli, 1763) (Slowakei)
rubiginata (Hufnagel, 1767) (Slowakei)
marginepunctata (Goeze, 1781) (Slowakei)
corrivalaria (Kretschmar, 1862) (Deutschland)
immutata (Linnaeus, 1758) (Slowakei)
ternata Schrank, 1802 (Slowakei)

Glossotrophia Prout, 1913
asellaria (Millière, 1868) (Italien)

Idaea Treitschke, 1825
rufaria (Hübner, 1799) (Österreich)
serpentata (Hufnagel, 1767) (Slowakei)
aureolaria (Denis & Schiffermüller, 1775) (Österreich)
extersaria (Herrich-Schäffer, 1848) (Italien)
typicata (Gueneé, 1857) (Italien)
filicata (Hübner, 1799) (Österreich)
laevigata (Hübner, 1799) (Deutschland)
obsoletaria (Rambur, 1833) (Italien)
biselata (Hufnagel, 1767) (Slowakei)
calunetaria (Staudinger, 1859) (Schweiz)
inquinata (Scopoli, 1763) (Deutschland)
dilutaria (Hübner, 1799) (Slowakei)
fuscovenosa (Goeze, 1781) (Slowakei)
humiliata (Hufnagel, 1767) (Slowakei)
seriata (Schrank, 1802) (Österreich)
subsericeata (Haworth, 1809) (Italien)
emarginata (Linnaeus, 1758) (Deutschland)
aversata (Linnaeus, 1758) (Slowakei)
degeneraria (Hübner, 1799) (Slowakei)
deversaria (Herrich-Schäffer, 1847) (Slowakei)

Rhodostrophia Hübner, 1823
vibicaria (Clerck, 1759) (Slowakei)

Rhodometra Meyrick, 1892
sacraria (Linnaeus, 1767) (Bosnien)

Lythria Hübner, 1823
purpuraria (Linnaeus, 1758) (Slowakei)
rotaria (Fabricius, 1798) (Russland)

Cataclysme Hübner, 1825
riguata (Hübner, 1813) (Slowakei)

Phibalapteryx Stephens, 1829
virgata (Hufnagel, 1767) (Slowakei)

Scotopteryx Hübner, 1825
moeniata (Scopoli, 1763) (Österreich)
coarctaria ([Denis & Schiffermüller], 1775) (Slowakei)
chenopodiata (Linnaeus, 1758) (Slowakei, Dänemark)
luridata (Hufnagel, 1767) (Slowakei)

Larentia Treitschke, 1825
clavaria (Haworth, 1809) (Polen)

Orthonama Hübner, 1825
vittata (Borkhausen, 1794) (Deutschland)

Nycterosea Hulst, 1896
obstipata (Fabricius, 1794) (Österreich)

Xanthorhoe Hübner, 1825
biriviata (Borkhausen, 1794) (Slowakei)
designata (Hufnagel, 1767) (Slowakei)
munitata (Hübner, 1809) (Schweiz)
spadicearia ([Denis & Schiffermüller], 1775) (Slowakei)
ferrugata (Clerck, 1759) (Slowakei)
quadrifasciata (Clerck, 1759) (Slowakei)
montanata ([Denis & Schiffermüller], 1775) (Slowakei)
fluctuata (Linnaeus, 1758) (Slowakei)
incursata (Hübner, 1813) (Schweiz)

Catarhoe Herbulot, 1951
rubidata ([Denis & Schiffermüller], 1775) (Slowakei)
cuculata (Hufnagel, 1767) (Slowakei)
putridata (Herrich-Schäffer, 1852) (Frankreich)

Epirrhoe Hübner, 1825
hastulata (Hübner, 1813) (Slowakei)
pupillata (Thunberg, 1788) (Deutschland)
tristata (Linnaeus, 1758) (Slowakei)
alternata (Müller, 1764) (Slowakei)
rivata (Hübner, 1813) (Dänemark)
molluginata (Hübner, 1813) (Slowakei)
galiata ([Denis & Schiffermüller], 1775) (Slowakei)

Camptogramma Stephens, 1831

bilineata (Linnaeus, 1758) (Dänemark, Slowakei)

Entephria Hübner, 1825
cyanata (Hübner, 1809) (Schweiz)
flavicinctata (Hübner, 1813) (Deutschland)
infidaria (La Harpe, 1852) (Schweiz)
caesiata (Denis & Schiffermüller, 1775) (Slowakei)

Anticlea Stephens, 1831
badiata ([Denis & Schiffermüller], 1775) (Slowakei)
derivata ([Denis & Schiffermüller], 1775) (Slowakei)

Mesoleuca Hübner, 1825
albicillata (Linnaeus, 1758) (Slowakei)

Pelurga Hübner, 1825
comitata (Linnaeus, 1758) (Slowakei)

Lampropteryx Stephens, 1831
suffumata ([Denis & Schiffermüller], 1775) (Slowakei)
otregiata (Metcalfe, 1917) (Mähren)

Cosmorhoe Hübner, 1825
ocellata (Linnaeus, 1758) (Slowakei)

Nebula Bruand, 1846
salicata (Hübner, 1799) (Slowakei)
tophaceata (Denis & Schiffermüller, 1775) (Mähren)
nebulata (Treitschke, 1828) (Österreich)
achromaria (La Harpe, 1852) (Slowakei)

Eulithis Hübner, 1821
prunata (Linnaeus, 1758) (Slowakei)
testata (Linnaeus, 1761) (Slowakei, Böhmen)
populata (Linnaeus, 1758) (Böhmen)
pyropata (Hübner, 1822) (Polen)
pyraliata ([Denis & Schiffermüller], 1775) (Slowakei)

Ecliptopera Warren, 1894
silaceata ([Denis & Schiffermüller], 1775) (Slowakei)
capitata (Herrich-Schäffer, 1839) (Slowakei)

Chloroclysta Hübner, 1825
siterata (Hufnagel, 1767) (Slowakei)
miata (Linnaeus, 1758) (Slowakei, Deutschland)

Dysstroma Hübner, 1825
citrata (Linnaeus, 1761) (Deutschland, Slowakei)
truncata (Hufnagel, 1767) (Slowakei)
infuscata (Tengström, 1869) (Schweden)

Cidaria Treitschke, 1825
fulvata (Forster, 1771) (Slowakei)

Plemyria Hübner, 1825
rubiginata ([Denis & Schiffermüller], 1775) (Slowakei)

Thera Stephens, 1831
obeliscata (Hübner, 1787) (Slowakei)
variata ([Denis & Schiffermüller], 1775) (Slowakei)
britannica (Turner, 1925) (Slowakei)
stragulata (Hübner, 1809) (Slowakei)
cognata (Thunberg, 1792) (Österreich)
juniperata (Linnaeus, 1758) (Slowakei)
cupressata (Geyer, 1831) (Frankreich)

Eustroma Hübner, 1825
reticulata (Denis & Schiffermüller, 1775) (Slowakei)

Electrophaes Prout, 1923
corylata (Thunberg, 1792) (Slowakei)

Colostygia Hübner, 1825
aptata (Hübner, 1813) (Österreich)
austriacaria (Herrich-Schäffer, 1856) (Österreich)
tempestaria (Herrich-Schäffer, 1856) (Österreich)
multistrigaria (Haworth, 1809) (Schweiz)

Hydriomena Hübner, 1825
furcata (Thunberg, 1784) (Slowakei)
impluviata ([Denis & Schiffermüller], 1775) (Slowakei)
ruberata (Freyer, 1831) (Österreich, Deutschland)

Horisme Hübner, 1825
vitalbata ([Denis & Schiffermüller], 1775) (Slowakei, Österreich)
tersata ([Denis & Schiffermüller], 1775) (Slowakei, Deutschland)
aemulata (Hübner, 1813) (Slowakei)
aquata (Hübner, 1813) (Deutschland)
corticata (Treitschke, 1835) (Österreich)
radicaria (La Harpe, 1855) (Deutschland)

Melanthia Duponchel, 1829
procellata ([Denis & Schiffermüller], 1775) (Slowakei)
alaudaria (Freyer, 1846) (Slowakei)

Pareulype Herbulot, 1951
berberata ([Denis & Schiffermüller], 1775) (Dänemark, Slowakei)

Spargania Guenee, 1857
luctuata ([Denis & Schiffermüller], 1775) (Slowakei)

Rheumaptera Hübner, 1822
hastata (Linnaeus, 1758) (Slowakei)
cervinalis (Scopoli, 1763) (Slowakei)
undulata (Linnaeus, 1758) (Slowakei, Österreich)

Triphosa Stephens, 1829
dubitata (Linnaeus, 1758) (Slowakei)
sabaudiata (Duponchel, 1830) (Österreich)

Philereme Hübner, 1825
vetulata ([Denis & Schiffermüller], 1775) (Slowakei)
transversata (Hufnagel, 1767) (Slowakei)

Euphyia Hübner, 1825
biangulata (Haworth, 1809) (Slowakei)
unangulata (Haworth, 1809) (Böhmen)
frustata (Treitschke, 1828) (Österreich)

Epirrita Hübner, 1822
dilutata ([Denis & Schiffermüller], 1775) (Slowakei)
christyi (Allen, 1906) (Slowakei)
autumnata (Borkhausen, 1794) (Slowakei)

Operophtera Hübner, 1825
brumata (Linnaeus, 1758) (Slowakei)
fagata (Scharfenberg, 1805) (Slowakei)

Perizoma Hübner, 1825
affinitata (Stephens, 1831) (Polen)
alchemillata (Linnaeus, 1758) (Slowakei)
hydrata (Treitschke, 1829) (Schweiz)
blandiata ([Denis & Schiffermüller], 1775) (Slowakei)
flavofasciata (Thunberg, 1792) (Slowakei)
didymata (Linnaeus, 1758) (Slowakei, Böhmen)
obsoletaria (Herrich-Schäffer, 1838) (Österreich, Schweiz)
sagittata (Fabricius, 1787) (Dänemark, Böhmen)
incultaria (Herrich-Schäffer, 1848) (Österreich)
parallelolineata (Retzius, 1783) (Österreich)

Baptria Hübner, 1825
tibiale (Esper, 1791) (Österreich)

Eupithecia Curtis, 1825
tenuiata (Hübner, 1813) (Slowakei)
inturbata (Hübner, 1817) (Schweiz, Deutschland)
haworthiata Doubleday, 1856 (Dänemark, Deutschland)
immundata (Lienig & Zeller, 1846) (Slowakei, Deutschland)
plumbeolata (Haworth, 1809) (Deutschland)
abietaria (Goeze, 1781) (Deutschland)
analoga Djakonov, 1926 (Deutschland, Polen, Slowakei)
linariata ([Denis & Schiffermüller], 1775) (Deutschland, Slowakei)
pulchellata Stephens, 1831 (Deutschland)
pyreneata Mabille, 1871 (Slowakei, Deutschland)
laquaearia Herrich-Schäffer, 1848 (Slowakei, Deutschland)
irriguata (Hübner, 1813) (Slowakei, Deutschland)
liguriata Millière, 1884 (Frankreich)
exiguata (Hübner, 1813) (Deutschland)
insigniata (Hübner, 1790) (Deutschland)
valerianata (Hübner, 1813) (Slowakei, Deutschland)
pygmaeata (Hübner, 1799) (Deutschland)
undata (Freyer, 1840) (Schweiz)
variostrigata Alpheraky, 1878 (Schweiz)
silenata Assman, 1849 (Böhmen, Deutschland)
carpophagata Staudinger, 1871 (Italien)
venosata (Fabricius, 1787) (Slowakei, Deutschland)
schiefereri Bohatsch, 1893 (Italien)
silenicolata Mabille, 1866 (Italien)
alliaria Staudinger, 1870 (Slowakei)
egenaria Herrich-Schäffer, 1848 (Deutschland)
extraversaria Herrich-Schäffer, 1852 (Deutschland)
centaureata ([Denis & Schiffermüller], 1775) (Slowakei, Deutschland)
queneeata Miller, 1862 (Österreich)
gratiosata Herrich-Schäffer, 1861 (Frankreich)
thalictrata (Püngeler, 1902) (Schweiz, Italien)
acteata Walderdorf, 1869 (Deutschland)
selinata Herrich-Schäffer, 1861 (Deutschland, Slowakei)
trisignaria Herrich-Schäffer, 1848 (Slowakei, Deutschland)
intricata (Zetterstedt, 1839) (Slowakei, Deutschland)
veratraria Herrich-Schäffer, 1848 (Slowakei, Deutschland)
cauchiata (Duponchel, 1830) (Deutschland)
satyrata (Hübner, 1813) (Slowakei, Deutschland)
cretaceata Packard, 1874 (Italien)
pernotata Guenée, 1857 (Schweiz)
absinthiata (Clerck, 1759) (Slowakei, Deutschland)
goossensiata Mabille, 1869 (Dänemark, Deutschland)
assimilata Doubleday, 1856 (Slowakei, Deutschland)
expallidata Doubleday, 1856 (Deutschland)
vulgata (Haworth, 1809) (Slowakei, Deutschland)
tripunctaria Herrich-Schäffer, 1852 (Slowakei, Deutschland)
denotata (Hübner, 1813) (Slowakei, Deutschland)
subfuscata (Haworth, 1809) (Slowakei, Deutschland)
icterata (Villers, 1789) (Deutschland)
succenturiata (Linnaeus, 1758) (Deutschland)
denticulata (Treitschke, 1828) (Deutschland)
impurata (Hübner, 1813) (Deutschland)
orphnata W. Petersen, 1909 (Slowakei, Deutschland)
subumbrata ([Denis & Schiffermüller], 1775) (Deutschland)
semigraphata Bruand, 1851 (Deutschland)
millefoliata Rössler, 1866 (Deutschland)
santolinata Mabille, 1871 (Frankreich)
simpliciata (Haworth, 1809) (Slowakei, Deutschland)
sinuosaria Eversmann, 1848 (Slowakei, Polen, Deutschland)
druentiata Dietze, 1902 (Frankreich)
distinctaria (Herrich-Schäffer, 1848) (Slowakei, Deutschland)
graphata (Treitschke, 1828) (Schweiz, Italien, Österreich)
pimpinellata (Hübner, 1813) (Deutschland)
pauxillaria Boisduval, 1840 (Deutschland)
gelidata (Möschler, 1860) (Böhmen, Deutschland)
nanata (Hübner, 1813) (Dänemark, Deutschland)
innotata (Hufnagel, 1767) (Deutschland)
fraxinata Grewe, 1863 (Deutschland)
unedonata Mabille, 1868 (Spanien)
virgaureata Doubleday, 1861 (Slowakei, Deutschland)
abbreviata Stephens, 1831 (Deutschland)
dodoneata Guenee, 1857 (Deutschland)
pusillata ([Denis & Schiffermüller], 1775) (Slowakei, Deutschland)
ericeata (Rambur, 1833) (Slowakei)
phoeniceata (Rambur, 1834) (Spanien)
scopariata (Rambur, 1833) (Frankreich)
oxycedrata (Rambur, 1833) (Italien)
lanceata (Hübner, 1825) (Slowakei, Deutschland)
lariciata (Freyer, 1842) (Slowakei, Deutschland)
tantillaria Boisduval, 1840 (Slowakei, Deutschland)

Gymnoscelis Mabille, 1868
rufifasciata (Haworth, 1809) (Slowakei, Deutschland)

Chloroclystis Hübner, 1825
v-ata (Haworth, 1809) (Slowakei, Deutschland)
chloerata (Mabille, 1870) (Slowakei, Deutschland, Dänemark)
rectangulata (Linnaeus, 1758) (Slowakei, Deutschland)
debiliata (Hübner, 1817) (Böhmen, Dänemark, Deutschland)

Anticollix Prout, 1938
sparsata (Treitschke, 1828) (Dänemark, Deutschland)

Chesias Treitschke, 1825
legatella ([Denis & Schiffermüller], 1775) (Mähren, Schweden)

Carsia
sororiata (Linnaeus, 1758) (Schweden)

Aplocera Stephens, 1827
plagiata (Linnaeus, 1758) (Slowakei)
efformata (Guenee, 1857) (Dänemark)
praeformata (Hübner, 1826) (Slowakei)

Odezia Boisduval, 1840
atrata (Linnaeus, 1758) (Deutschland)

Schistostege Hübner, 1825
treitschkei Kovács, 1957 (Ungarn)
decussata (Denis & Schiffermüller, 1775) (Österreich)

Lithostege Hübner, 1825
griseata ([Denis & Schiffermüller], 1775) (nach Khotko, 1977)

Disciloxia Warren, 1895
blomeri (Curtis, 1832) (Slowakei)

Venusia Curtis, 1839
cambrica (Curtis, 1839) (Slowakei)

Euchoeca Hübner, 1823
nebulata (Scopoli, 1763) (Slowakei)

Asthena Hübner, 1825
albulata (Hufnagel, 1767) (Slowakei)
anseraria (Herrich-Schäffer, 1855) (Slowakei)

Hydrelia Hübner, 1825
flammeolaria (Hufnagel, 1767) (Slowakei)

Minoa Treitschke, 1825
murinata (Scopoli, 1763) (Slowakei)

Lobophora Curtis, 1825
halterata (Hufnagel, 1767) (Slowakei)

Trichopteryx Hübner, 1825
polycommata ([Denis & Schiffermüller], 1775) (Slowakei)
carpinata (Borkhausen, 1794) (Slowakei)

Epilobophora Inoue, 1943
sabinata (Geyer, 1831) (Schweiz)

Nothocasis Prout, 1937
sertata (Hübner, 1817) (Slowakei)

Pterapherapteryx Curtis, 1825
sexalata (Retzius, 1783) (Slowakei)

Acasis Duponchel, 1845
appensata (Eversmann, 1842) (Slowakei)

Abraxas Leach, 1815
grossulariata (Linnaeus, 1758) (Slowakei)

Calospilos Hübner, 1825
sylvata (Scopoli, 1763) (Slowakei)

Lomaspilis Hübner, 1825
marginata (Linnaeus, 1758) (Slowakei)

Ligdia Guenée, 1857
adustata ([Denis & Schiffermüller], 1775) (Slowakei)

Stegania Guenée, 1857
dilectaria (Hübner, 1790) (Slowakei, Frankreich)

Semiothisa Hübner, 1818
notata (Linnaeus, 1758) (Slowakei)
alternaria (Hübner, 1809) (Slowakei)
signaria (Hübner, 1809) (Slowakei)

Chiasmia Hübner, 1823
clathrata (Linnaeus, 1758) (Slowakei)
glarearia (Brahm, 1791) (Slowakei)

Diastictis
artesiaria (Denis & Schiffermüller, 1775) (Slowakei)

Isturgia Hübner, 1823
limbaria (Fabricius, 1775) (Slowakei)

Narraga Walker, 1861
fasciolaria (Hufnagel, 1767) (Slowakei)

Itame Hübner, 1823
wauaria (Linnaeus, 1758) (Slowakei)
brunneata (Thunberg, 1784) (Böhmen, Schweden)

Tephrina Guenée, 1845
arenacearia (Denis & Schiffermüller, 1775) (Slowakei)
murinaria (Denis & Schiffermüller, 1775) (Slowakei)

Enconista Lederer, 1853
miniosata (Duponchel, 1829) (Frankreich)

Pygmaena Boisduval, 1840
fusca (Thunberg, 1792) (Schweiz)

Cepphis Hübner, 1823
advenaria (Hübner, 1799) (Polen)

Petrophora Hübner, 1811
chlorosata (Scopoli, 1763) (Slowakei, Böhmen)

Plagodis Hübner, 1823
pulveraria (Linnaeus, 1758) (Slowakei)
dolabraria (Linnaeus, 1767) (Slowakei)

Pachycnemia Stephens, 1829
hippocastanaria (Hübner, 1799) (Holland)

Opisthograptis Hübner, 1823
luteolata (Linnaeus, 1758) (Slowakei)

Epione Duponchel, 1829
repandaria (Hufnagel, 1767) (Slowakei)
paralellaria ([Denis & Schiffermüller], 1775) (Slowakei)

Pseudopanthera Hübner, 1823
macularia (Linnaeus, 1758) (Slowakei)

Hypoxystis Prout, 1915
pluviaria (Fabricius, 1787) (Slowakei)

Therapis Hübner, 1823
flavicaria (Denis & Schiffermüller, 1775) (Österreich)

Epirrhanthis Hübner, 1823
diversata (Denis & Schiffermüller, 1775) (Böhmen)

Ennomos Treitschke, 1825
autumnaria (Werneburg, 1859) (Slowakei)

quercinaria (Hufnagel, 1767) (Slowakei)
alniaria (Linnaeus, 1758) (Slowakei, Deutschland)
fuscantaria (Haworth, 1809) (Österreich, Deutschland)
erosaria ([Denis & Schiffermüller], 1775) (Slowakei)
quercaria (Hübner, 1813) (Italien)

Selenia Hübner, 1823
dentaria (Fabricius, 1775) (Slowakei)
lunularia (Hübner, 1788) (Slowakei, Böhmen)
tetralunaria (Hufnagel, 1767) (Slowakei)

Apeira Gistl, 1848
syringaria (Linnaeus, 1758) (Böhmen, Slowakei)

Artiora Meyrick, 1892
evonymaria (Denis & Schiffermüller, 1775) (Slowakei)

Odontopera Stephens, 1831
bidentata (Clerck, 1759) (Slowakei)

Crocallis Treitschke, 1825
tusciaria (Borkhausen, 1793) (Deutschland)
elinguaria (Linnaeus, 1758) (Slowakei)

Ourapteryx Leach, 1814
sambucaria (Linnaeus, 1758) (Slowakei, Böhmen)

Colotois Hübner, 1823
pennaria (Linnaeus, 1761) (Slowakei)

Angerona Duponchel, 1829
prunaria (Linnaeus, 1758) (Slowakei)

Chondrosoma
fiduciaria Anker, 1854 (Österreich)

Apocheima Hübner, 1825
hispidaria ([Denis & Schiffermüller], 1775) (Slowakei)

Phigalia Duponchel, 1829
pilosaria ([Denis & Schiffermüller], 1775) (Slowakei)

Lycia Hübner, 1825
hirtaria (Clerck, 1759) (Slowakei)
graecaria (Staudinger, 1870) (Bosnien)
isabellae (Harrison, 1914) (Böhmen)
pomonaria (Hübner, 1790) (Slowakei)
zonaria ([Denis & Schiffermüller], 1775) (Slowakei)

Biston Leach, 1815
strataria (Hufnagel, 1867) (Slowakei)
betularia (Linnaeus, 1758) (Slowakei)

Agriopis Hübner, 1825
leucophaearia ([Denis & Schiffermüller], 1775) (Slowakei)
bajaria ([Denis & Schiffermüller], 1775) (Slowakei)
aurantiaria (Hübner, 1799) (Slowakei)
marginaria (Fabricius, 1776) (Slowakei)

Erannis Hübner, 1825
defoliaria (Clerck, 1759) (Slowakei)

Nychiodes Lederer, 1853
obscuraria (De Viller, 1789) (Frankreich)

Eurranthis Hübner, 1823
plumistaria (De Viller, 1789) (Frankreich)

Peribatodes Wehrli, 1943
rhomboidaria ([Denis & Schiffermüller], 1775) (Slowakei)
umbraria (Hübner, 1809) (Italien)
secundaria ([Denis & Schiffermüller], 1775) (Slowakei)

Cleora Curtis, 1825
cinctaria ([Denis & Schiffermüller], 1775) (Slowakei)

Deileptenia Hübner, 1825
ribeata (Clerck, 1759) (Slowakei)

Alcis Curtis, 1826
repandata (Linnaeus, 1758) (Slowakei)
maculata (Staudinger, 1890) (Slowakei)

Arichanna Moore, 1868
melanaria (Linnaeus, 1758) (Slowakei, Böhmen)

Hypomecis Hübner, 1821
roboraria ([Denis & Schiffermüller], 1775) (Slowakei)
viertlii (Bohatsch, 1883) (Slowakei)

Serraca Moore, 1887
punctinalis (Scopoli, 1763) (Slowakei)

Fagivorina Wehrli, 1943
arenaria (Hufnagel, 1767) (Slowakei)

Ascotis Hübner, 1825
selenaria (Denis & Schiffermüller, 1775) (Slowakei)

Ectropis Hübner, 1825
crepuscularia ([Denis & Schiffermüller], 1775) (Slowakei)

Paradarsia Warren, 1897
consonaria (Hübner, 1799) (Slowakei)

Parectropis Sato, 1980
similaria (Hufnagel, 1767) (Slowakei)

Aethalura Mc Dunnough, 1920
punctulata ([Denis & Schiffermüller], 1775) (Slowakei)

Ematurga Lederer, 1853
atomaria (Linnaeus, 1758) (Slowakei)

Tephronia Hübner, 1825
sepiaria (Hufnagel, 1767) (Deutschland)

Odontognophos Wehrli, 1951
dumetata (Treitschke, 1827) (Slowakei)

Selidosema Hübner, 1823
brunnearia (Villers, 1789) (Böhmen)
plumaria ([Denis & Schiffermüller], 1775) (Slowakei)

Bupalus Leach, 1815
piniaria (Linnaeus, 1758) (Slowakei)

Crocota Hübner, 1823
lutearia (Fabricius, 1794) (Frankreich, Schweiz)
niveata (Scopoli, 1763) (Österreich)

Menophra Moore, 1887
nycthemeraria (Geyer, 1831) (Deutschland)

Synopsia Hübner, 1825
sociaria (Hübner, 1799) (Slowakei)

Cleorodes Warren, 1894
lichenaria (Hufnagel, 1767) (Deutschland)

Gnophos Treitschke, 1825
furvatus ([Denis & Schiffermüller], 1775) (Slowakei)
obfuscatus ([Denis & Schiffermüller], 1775) (Österreich)
ambiguatus (Duponchel, 1838) (Österreich)
pullatus ([Denis & Schiffermüller], 1775) (Österreich)
glaucinarius (Hübner, 1799) (Österreich)
variegatus (Duponchel, 1830) (Österreich, Schweiz)
intermedia Wehrli, 1917 (Slowakei)
dilucidaria ([Denis & Schiffermüller], 1775) (Österreich, Schweiz)
serotinaria ([Denis & Schiffermüller], 1775) (Österreich, Schweiz)
zelleraria (Freyer, 1836) (Österreich)
caelibaria (Herrich-Schäfer, 1852) (Österreich)
operaria (Hübner, 1813) (Österreich)

Sciadia Hübner, 1822
tenebraria (Esper, 1806) (Österreich, Schweiz)

Glacies Millière, 1874
alticolaria (Mann, 1853) (Österreich)

Siona Duponchel, 1829
lineata (Scopoli, 1763) (Slowakei)

Chariaspilates Wehrli, 1953
formosaria (Eversmann, 1837) (nach Khotko, 1977)

Aspitates Treitschke, 1825
gilvaria ([Denis & Schiffermüller], 1775) (Slowakei)

Dyscia Hübner, 1825
conspersaria (Fabricius, 1775) (Slowakei)

Perconia Hübner, 1823
strigillaria (Hübner, 1787) (Mähren)

Cabera Treitschke, 1825
pusaria (Linnaeus, 1758) (Slowakei)
exanthemata (Scopoli, 1763) (Slowakei)

Lomographa Hübner, 1825
bimaculata (Fabricius, 1775) (Slowakei)
temerata ([Denis & Schiffermüller], 1775) (Slowakei)

Campaea Lamarck, 1816
margaritata (Linnaeus, 1767) (Slowakei)
honoraria ([Denis & Schiffermüller], 1775) (Böhmen)

Hylaea Hübner, 1822
fasciaria (Linnaeus, 1758) (Slowakei)

Puengeleria Rougemont, 1903
capreolaria ([Denis & Schiffermüller], 1775) (Slowakei)

Lignyoptera
thaumastaria Rebel, 1901 (Bosnien)

Theria Hübner, 1825
rupicapraria ([Denis & Schiffermüller], 1775) (Slowakei)
primaria (Haworth, 1809) (Deutschland)

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FOUR NEW GENERA OF MICROVELIINAE (HETEROPTERA) FROM NEW GUINEA

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Four new genera of Microveliinae are described from New Guinea. These genera and their constituent species are as follows: *Tanyvelia* gen. n. containing type species *T. missim* sp. n. from Papua New Guinea; *Aegilipsicola* gen. n. containing type species *A. rapida* sp. n. from Papua New Guinea; *Tarsovelia* gen. n. containing type species *T. alta* sp. n. from Papua New Guinea, plus *T. arfak* sp. n. from Irian Jaya, and *T. dani* sp. n. from Irian Jaya; and *Neusterinsifer* gen. n. containing type species *N. compacta* sp. n. from Papua New Guinea, plus *N. sepik* sp. n. from Papua New Guinea, *N. cyclops* sp. n. from Papua New Guinea, *N. nabire* sp. n. from Irian Jaya, and *N. gladius* sp. n. from Irian Jaya. Habitus figures of the above new genera are provided, accompanied by illustrations of the male genital structures and distribution maps for all new species.

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Key words. – Veliidae; Microveliinae; New Guinea; taxonomy; new genera; new species; keys; distribution.

The assemblages of Microveliinae occurring on the islands of the Malay Archipelago exhibit a profound shift in taxonomic composition as one progresses from west to east through the region. On the Greater Sunda Islands, Celebes and the Philippines such faunas are dominated by members of the genera *Pseudovelia* Hoberlandt and *Microvelia* Westwood, accompanied by several other more ecologically specialized and less speciose genera. On New Guinea and surrounding islands, by contrast, *Pseudovelia* is absent and there occurs instead a group of previously undescribed endemic genera which fill the typical *Pseudovelia* niches. In addition, New Guinea also supports numerous endemic species of in the genus *Microvelia* sensu lato, but as noted by Andersen (1982) this generic grouping is almost certainly polyphyletic. A detailed analysis on a world basis of the subgroups contained within it will be necessary before it can be certain that the Papuan and Australian species presently held in *Microvelia* are in fact congeneric with the Asian forms.

New Guinea thus represents a major center of diversification for the Microveliinae, with a fauna derived independently from that occurring in the Asian tropics. In the present report we describe four new genera of endemic Papuan Microveliinae, all of which are easily separable from *Microvelia* sensu lato on the basis of distinct apomorphies. The relationships among these genera are still unresolved, however, pending the completion of ongoing revisions of the diverse Australian and New Guinea *Microvelia* faunas.

Key to genera of New Guinea Microveliinae

1. Middle tarsi subequal in length to middle tibia (fig. 9); light markings on hemelytra restricted to basal angles; fore femur of male at least slightly modified for phoresy .... *Tarsovelia* gen. n.
– Middle tarsi distinctly shorter than middle tibia (figs. 1, 5, 17); light markings on hemelytra may be restricted to basal angles, or may occur also on distal portions; fore femur may or may not be modified for phoresy (figs. 3, 6, 24-26) 2
2. Claws extremely long; light hemelytral markings entirely bright greyish to light bluish pruinose; gula long, rostral cavity demarcated by strongly raised carina .... *Aegilipsicola* gen. n.
– Claws relatively short; light hemelytral markings not bright pruinose; gula short, rostral cavity not demarcated by strongly raised carina 3
3. Antennae extremely long (fig. 1); comb on fore tibia 3/4 the length of the tibia (fig. 3); only micropterous morph known .... *Tanyvelia* gen. n.
– Antennae not extremely long (fig. 17); comb on fore tibia less than 3/4 length of tibia (except in *Neuterinsifer compacta*), if comb on fore tibia 3/4 length of tibia then male proctiger bearing elongate process and female abdominal tergites VII

and VIII forming an anal plate (see below); only apterous and macropterous morphs known, latter with large hemelytral light markings basally, and often occurring in all closed cells 4

4. Female abdominal tergites VII-VIII deflected ventrad forming an anal plate (fig. 23); male genitalia highly modified, bearing a long sinuate anteriorly directed sword-like process (figs. 18-22) .... *Neusterinsifer* gen. n.
– Female abdominal tergites VII-VIII not deflected ventrad, not forming an anal plate; male genitalia may be modified, but without a long sword-like process .... *Microvelia* Westwood

Tanyvelia gen. n.
(figs. 1-4, 27)

Diagnosis

Size. – Micropterous form, length of males 2.73-2.91 mm, females 2.81-3.13 mm; general body characteristics and size sexually dimorphic, males smaller, female abdomen more robust.

Colour. – Ground colour blackish brown, tinged with orange brown, without silvery pubescence; anterior pronotal lobe yellowish, pruinose, sharply demarcated from dark collar and posterior lobe. Micropterous wing pads brown, set with anterolateral light streaks.

Structural characters. – Only micropterous form known, shape elongate (fig. 1). Eyes globose, exserted but usually not beyond anterolateral pronotal angles, separated by about twice the width of an eye, appressed to anterior pronotal margin, with short ocular setae. Head declivant anteriorly, recessed into pronotum, posterior margin sloping caudo-dorsally, with usual three pairs of facial trichobothria; gular region moderately long, plainly visible, rostral cavity closed posteriorly. Rostrum reaching to middle of mesosternum, segment I short, enclosed in rostral cavity, segments I and IV subequal in length and about three times longer than II, segment III about 8 times as long as II. Antennae slender, very long, about 3/4 of body length.

Pronotum slightly raised medially, with weak median longitudinal carina; collar weakly formed, set off by a ragged row of small dark foveae, terminating under eyes laterally; anterior and posterior lobes set off by a transverse row of small foveae, evanescent medially; anterior lobe with scattered stiff erect dark setae; posterior lobe with numerous small foveae, humeri not prominent, broadly rounded posteriorly, not modified, covering metanotum. Thoracic venter not diagnostic, with weakly formed tubercles on either side of mesosternal midline on posterior margin opposing an unmodified metasternum. Metasternal scent gland opening (omphalium) small but visible, marked by a small tubercle; scent channels prominent, curving slightly anterad to base of metacetabulae.

Abdomen without silvery setae or other adornment, except weak longitudinal pruinose line on midline of tergites IV-VII; with short paired longitudinal carinae on basal half of tergite II. Abdominal sternites set off from laterosternites by hair-free glabrous oval lacunae. Micropterous wing pads elongate.

Legs slender, long, hind legs very long; anterior femur set beneath with short light setae, unmodified in males; anterior tibia of male with a comb of minute black setae occupying 3/4 of tibial length; middle femora set ventrally with 4-5 very long slender setae; all tarsi long (fig. 3), claws moderately long; both up- and down curving arolia large, evident.

Male genital segments moderately large, protruding, modified; proctiger unmodified (fig. 4); parameres small, slender symmetrical, acuminate (fig. 2). Female tergite VIII on same plane as VII, truncate posteriorly; first gonocoxae small, barely exposed, plate-like; tergite IX of both sexes triangular, protruding posteriorly.

Type-species: *Tanyvelia missim* sp. n.

Remarks

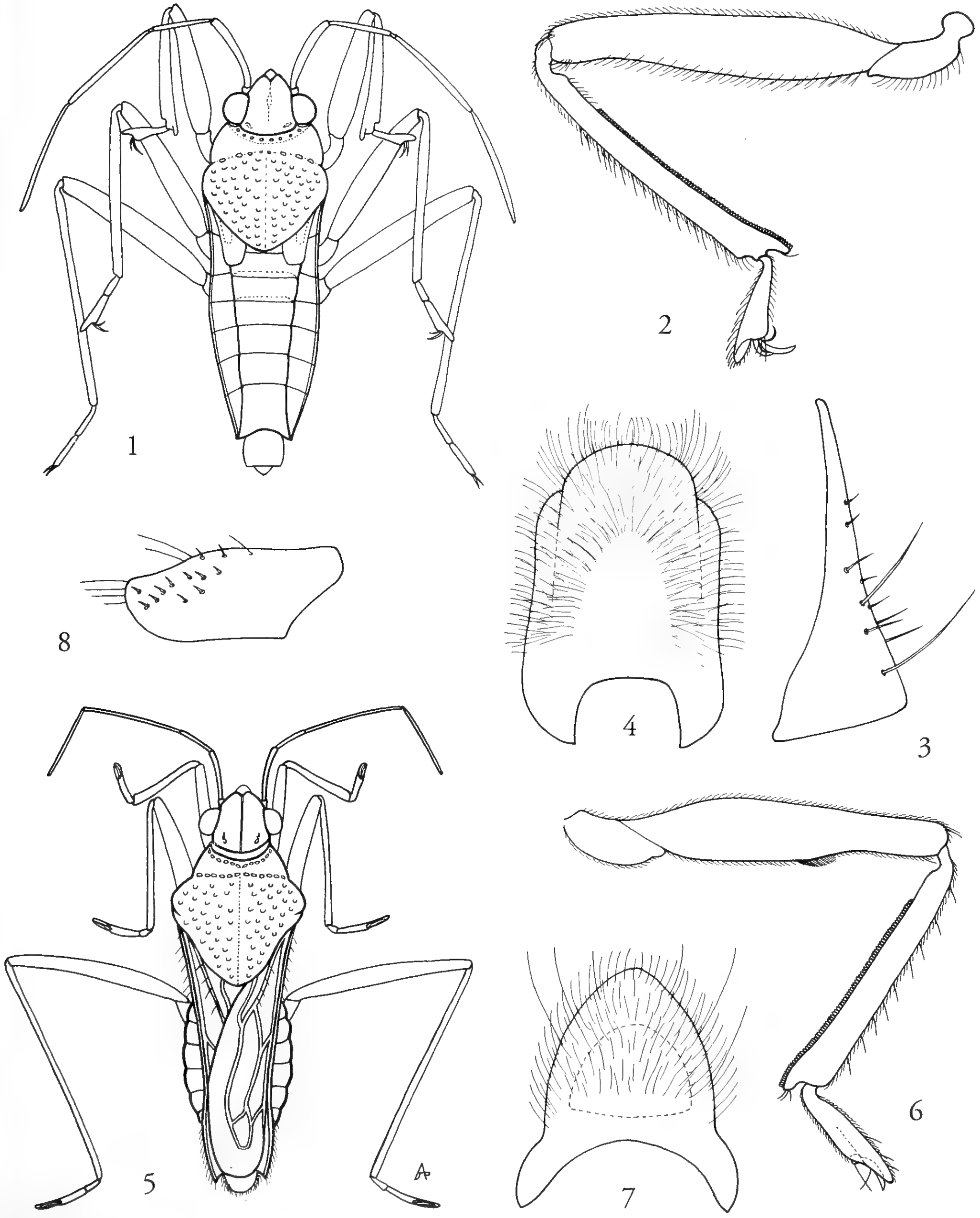
Comparative notes. – Separable from other genera of Papuan Microveliinae by the characters given in the key. Similar in general appearance and ecological habits to *Baptista* Distant, but distinguished by the presence of a long grasping comb that runs nearly the entire length of the male fore tibia (fig. 3), and the absence of modifications to abdominal sterna VI and VII. Among the Papuan genera, *Tanyvelia* appears most closely allied to *Aegilipsicola*, but the pronotal collar is not as pronounced, the legs, although long and slender, are slightly stouter, and the fore tibial grasping comb is shorter. The proctiger of *Tanyvelia* is broadly rounded distally rather than coming to a rounded point as in *Aegilipsicola* (compare figs. 4 and 7), and the paramere is slender and elongate rather than short and stout (compare figs. 2 and 8).

Etymology. – The generic name *Tanyvelia* is derived from *tany-* (Gr.), long, referring to the slender body shape, and *Velia*, the nominate genus of the family. Gender feminine.

Distribution. – New Guinea (fig. 27).

Tanyvelia missim sp. n.
(figs. 1-4, 27)

Type material: Holotype, micropterous male: Papua New Guinea, Morobe Prov., upper Poverty Creek on Mt. Missim, nr. Wau, 1600 m., 18 Sept.



Figs. 1-4. *Tanyvelia missim*, gen. n., sp. n. . – 1. Male, dorsal habitus; 2. Male foreleg; 3. Male paramere; 4. Male proctiger.
Figs. 5-8. *Aegilipsicola rapida*, gen. n., sp. n. – 5. Male, dorsal habitus; 6. Male foreleg; 7. Male proctiger; 8. Male paramere

1983, CL 1830, D. A. and J. T. Polhemus (BPBM). - Paratypes: 23 micropterous males, 12 micropterous females, same data as holotype (JTPC).

Diagnosis

Size. – Micropterous male, length 2.73-2.91 mm ($\bar{x}$ = 2.81, n = 10); width 0.79-0.90 mm ($\bar{x}$ = 0.86, n = 10). Micropterous female, length 2.81-3.13 mm ($\bar{x}$ = 2.96, n = 10); width 0.83-0.94 mm, ($\bar{x}$ = 0.88, n = 10).

Colour. – Micropterous male: ground colour black, venter and connexiva tinged with brown. Head black, brown ventrally; rostrum luteous on basal three segments, piceous distally. Pronotum with anterior lobe entirely yellowish including propleura, except narrowly embrowned medially; disc and collar black. Abdomen black, tergites mostly pruinose, lighter ventrally. Legs and antennae luteous to yellow brown, distally darker.

Structural characters. – Micropterous male: head of moderate length, declivant anteriorly; length 0.47; width of eye/interocular space, 0.16/0.30. Pronotum length:width, 0.74 : 0.81. Abdominal tergites not shining; tergites, II-VI subequal in length (0.16-0.19), VII longer (0.30). Abdominal venter set with short appressed setae; ventrite VII with a short V-shaped depression on caudal half. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Legs unarmed.

Antennal formula, segments I : II : III : IV; 0.51 : 0.40 : 0.70 : 0.70.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.79 : 0.77 : 0.30 : 0.0; of middle leg, 1.07 : 1.05 : 0.14 : 0.28; of hind leg, 1.16 : 1.47 : 0.23 : 0.30.

First genital segment with an antero-ventrally directed tuft of stiff dark setae. Paramere small, long, triangular (fig. 2).

Micropterous female: Similar to male in most respects, but somewhat larger; connexiva vertical or reflexed over dorsum except in gravid specimens.

Remarks

Comparative notes. – Recognized among the Papuan Microveliinae by its elongate form with long legs and antennae (fig. 1), relatively unmodified male foreleg with a long tibial grasping comb (fig. 3), acuminate paramere (fig. 2), and elongate male proctiger (fig. 4).

Biological notes. – Upper Poverty Creek at the Mt. Missim type locality was a small, rocky headwater stream dropping steeply through a boulder-strewn bed heavily shaded by primary rain forest.

Etymology. – The name '*missim*' is a noun in apposition and refers to the Mt. Missim type locality.

Distribution. – Eastern New Guinea (fig. 27).

Aegilipsicola gen. n.
(figs. 5-8, 28)

Diagnosis

Size. – Macropterous form, length of males 2.70-2.84 mm, females 3.16-3.31 mm, general body characteristics not sexually dimorphic, but males slightly smaller.

Colour. – Macropterous form: ground colour blackish brown, tinged with yellowish brown; dorsally dark brown on head and ventrally, wings black, brown to black beneath; anterior pronotal lobe narrowly yellowish on either side of midline, laterally dark but covered with silvery pubescence except medially, demarcated from dark collar and posterior lobe. Hemelytra black, bearing six elongate bluish-grey pruinose streaks, with two confined within the basal cells, and four others on distal third (fig. 5)

Structural characters. – Only macropterous form known. Form elongate, slender (fig. 5); eyes globose, exserted beyond anterolateral pronotal angles, separated by about twice the width of an eye, removed from anterior pronotal margin, with short ocular setae. Head moderately declivant anteriorly, recessed into pronotum, posterior margin sloping somewhat caudo-dorsally, with usual three pairs of facial trichobothria; gular region long, plainly visible, rostral cavity closed posteriorly by a strong carinate ridge. Rostrum reaching to middle of mesosternum, segment I short, enclosed in rostral cavity, I and IV subequal in length and about three times longer than II, segment III about 8 times as long as II. Antennae very slender, very long, about 2/3 of body length. Pronotum slightly raised medially, with weak median longitudinal carina marked by a line of golden pubescence; collar prominent, distinctly set off by a row of deep foveae, terminating laterally; near ventral eye margins; anterior and posterior lobes set off by a transverse row of foveae, evanescent medially; entire pronotum sparsely set with fine decumbent golden pubescence; posterior lobe with numerous obscure shallow foveae, humeri moderately prominent, almost triangular, narrowly rounded posteriorly. Thoracic venter not diagnostic, with weakly formed tubercles on either side of mesosternal midline along posterior margin opposing an unmodified metasternum. Metasternal scent gland opening (omphalium) not visible; scent channels prominent, curving anterad to base of metacetabulae.

Abdomen without silvery setae or other adornment; prominent paired longitudinal carinae present on basal half of tergite II in macropters (visible only after removal of wings). Abdominal sternites set off from laterosternites by hair-free glabrous oval lacunae. Female connexiva expanded, plate like along tergite VII. Macropters with five closed cells in hemelytra, venation of fore and hind wings similar to figs. 312-313 in Andersen (1982) except distal cell closed; fore wings set with fine semi-recumbent stiff setae on basal half; micropterous form unknown.

Legs slender, long, hind legs very long; anterior femur set beneath with short light setae, with ventral tubercle at distal 2/3 in males; anterior tibia of male with a fine line of minute black setae occupying 4/5 of tibial length; femora ventrally without long setae; all tarsi long (fig. 6), claws very long; both up- and down curving arolia long, slender.

Male genital segments moderately large, protruding, modified; proctiger unmodified (fig. 7); parameres small, slender, symmetrical (fig. 8). Female tergite VIII on same plane as VII, protruding posteriorly over tergite IX; first gonocoxae small, barely exposed, plate-like; tergite IX of both sexes button-like, protruding posteriorly.

Type-species: *Aegilipsicola rapida* sp. n.

Remarks

Etymology. – The generic name *Aegilipsicola* is derived from *Aegilips* (Gr.), sheer, steep, referring to the habitat, and *-cola*, (L.), inhabitant. Gender feminine.

Comparative notes. – In general facies *Aegilipsicola* most closely resembles the Neotropical genus *Aegilipsivelia*, however this similarity is apparently due to convergence. Although the two genera share many similar structures adapted to life on steep hygropetric habitats, such as long legs and extremely long claws, *Aegilipsivelia* lacks the carinate rostral cavity on the gula, the bright pruinose hemelytral markings, and the carinate female connexiva seen in *Aegilipsicola.* In addition, the collar in *Aegilipsivelia* is set off by a sulcus rather than a row of deep foveae, and the comb-like process on the male fore tibia is relatively short instead of almost as long as the tibia.

Among Papuan genera of Microveliinae *Aegilipsicola* is apparently most closely allied to *Tanyvelia* gen. n. (see discussion under *Tanyvelia*)

Distribution. – Eastern New Guinea (fig. 28).

Aegilipsicola rapida sp. n.
(figs. 5-8, 28)

Type material: Holotype, macropterous male: Papua New Guinea, Morobe Prov., seeps along Mt. Kaindi road nr. Kunai Creek, above Wau, 17 Sept. 1983, CL 1823, D. A. and J. T. Polhemus (BPBM). – Paratypes: 39 macropterous males, 37 macropterous females, 62 immatures, same data as holotype (JTPC); 4 macropterous males, 4 macropterous females, 2 immatures, Morobe Prov., Namie Creek, Mt. Kaindi, 17 Sept. 1983, CL 1829, J. T. & D. A. Polhemus (JTPC); 1 macropterous female, Morobe Prov., Kunai River, 1500 m, 10 Oct. 1966, Illies (ZBSM).

Diagnosis

Size. – Macropterous male, length 2.70-2.84 mm ($\bar{x}$ = 2.74, n = 10); width 0.86-0.97 mm ($\bar{x}$ = 0.94, n = 10). Macropterous female, length 3.06-3.31 mm ($\bar{x}$ = 3.16, n = 10); width 1.01-1.12 mm, ($\bar{x}$ = 1.04, n = 10).

Colour. – Macropterous male: ground colour black, tinged with yellowish brown ventrally. Head black; two longitudinal regions between eyes and medial furrow, posterior margin, brown. Pronotum with anterior lobe narrowly, transversely orange brown on either side of midline, extending to inner eye margins; posterior lobe uniformly black. Hemelytra blackish brown, long, extending beyond tip of abdomen. Abdomen brownish yellow ventrally, with a broad brown longitudinal stripe along sternal-laterosternal boundary. Legs yellowish, darker distally; antennae brown, segment I yellowish basally.

Structural characters. – Macropterous male: head of moderate length, declivant anteriorly; length 0.51; width of eye/interocular space, 0.14/0.30. Pronotum long, humeri evident but not raised; length : width, 0.84 : 0.91.

Abdominal venter set with very short appressed fine setae; venter VII depressed on either side of midline; first genital segment excavated ventrally, with three small brown sclerotized denticles distally. Legs, antennae thickly clothed with short inconspicuous setae, without longer setae. Legs unarmed, except fore femur set near distal 2/3 with patch of short stiff setae (fig. 6).

Antennal formula I : II : III : IV; 0.40 : 0.28 : 0.74 : 0.60.

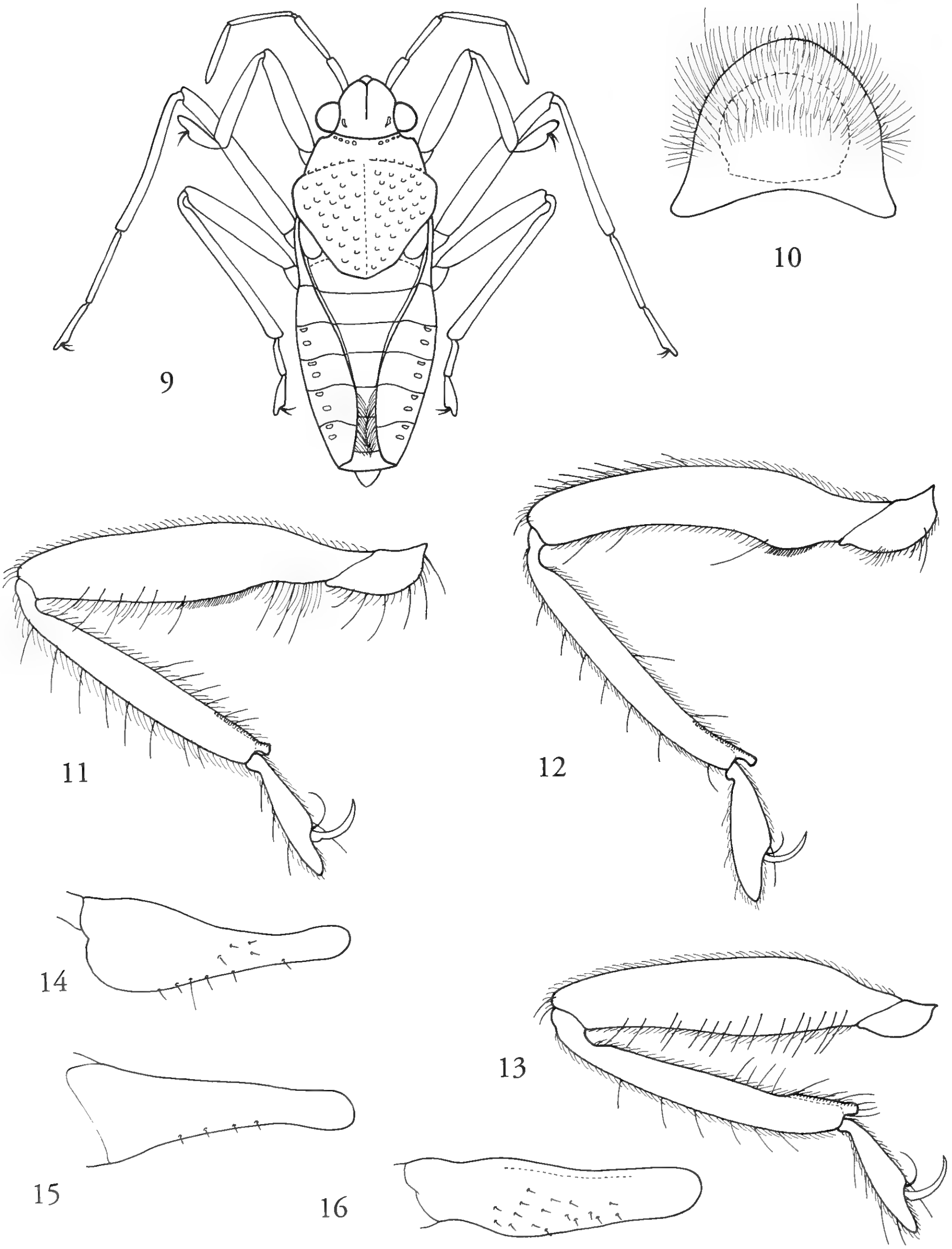
Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.74 : 0.60 : 0.28 : 0.0; of middle leg, 1.00 : 0.98 : 0.12 : 0.33; of hind leg, 1.44 : 1.74 : 0.09 : 0.40.

Paramere small, short, ovate (fig. 8).

Macropterous female: Similar to male in most respects, but somewhat larger. Connexiva vertical, strongly raised and plate-like along tergite VII, produced posteriorly along tergite VIII.

Remarks

Comparative notes. – Easily recognized among the Papuan Microveliinae by its elongate form (fig. 5), broadly pointed proctiger (fig. 7), short and broad paramere (fig. 8), elongate fore tibial grasping comb



Figs. 9-16. *Tarsovelia* gen. n. – 9. *Tarsovelia alta* sp. n., micropterous female, dorsal habitus; 10. *Tarsovelia dani* sp. n., male proctiger; 11-13. Male forelegs of *Tarsovelia* species, 11. *Tarsovelia arfak* sp. n.; 12. *Tarsovelia dani* sp. n.; 13. *Tarsovelia alta* sp. n.; 14-16. Male parameres of *Tarsovelia* species. 14. *Tarsovelia dani* sp. n.; 15. *Tarsovelia alta* sp. n.; 16. *Tarsovelia arfak* sp. n.

(fig. 6), and small tuft of black setae ventrally on the male fore femur (fig. 6).

Biological notes. – The type series was taken from wet seeping vertical rock faces formed by road cuts along the Mt. Kaindi road. The insects were abundant, and ran across the wet rocks and moss with great speed and agility.

Etymology. – The name '*rapida*' refers to the speed with which these insects can move across vertical rock faces.

Distribution. – Eastern New Guinea (fig. 28).

Tarsovelia gen. n.
(figs. 9-16, 29)

Diagnosis

Size. – Length of males 2.41-2.95 mm, females 2.77-3.45 mm, general body characteristics and size sexually dimorphic, males smaller, female abdomen more robust.

Colour. – Ground colour brown to blackish brown, often blackish above, without silvery pubescence; winged forms dorsally black, wings black, brown to black beneath. Anterior pronotal lobe and collar usually entirely yellowish to orange brown, only in *T. arfak* dark laterally.

Structural characters. – Form robust (fig. 9); eyes globose, exserted but usually not beyond anterolateral pronotal angles, separated by at least twice the width of an eye, appressed to anterior pronotal margin, with long ocular setae. Head declivant anteriorly, slightly recessed into pronotum, with usual three pairs of facial trichobothria; gular region moderately long, plainly visible, rostral cavity closed posteriorly. Rostrum reaching almost to metasternum, segment I short, enclosed in rostral cavity, segments I and IV subequal in length and about three times longer than II, segment III about 8 times as long as II. Antennae slender, long, about 1/2 of body length.

Pronotum of micropterous form slightly raised medially; collar weakly formed, set off by a ragged row of small dark foveae, terminating under eyes laterally; anterior and posterior lobes set off by a transverse row of small foveae in a weak transverse sulcus, evanescent medially; anterior lobe set with stiff erect setae; posterior lobe with numerous shallow depressions, humeri not prominent, broadly rounded posteriorly, not modified, covering metanotum. Pronotum of alate form longer, rounded posterior margin extending farther caudad, almost triangular, humeri more prominent. Thoracic venter not diagnostic, with weakly formed tubercles on either side of mesosternal midline on posterior margin opposing an unmodified metasternum. Metasternal scent gland opening (omphalium) not evident; scent channels prominent, angled slightly anterad to base of metacetabulae.

Abdomen without silvery setae or other adornment, except weak longitudinal pruinose line on midline of tergites IV-VII; prominent paired longitudinal carinae on tergite II of macropters (visible only after removal of wings), absent in micropterous form. Abdominal sternites set off from laterosternites by hair-free round or oval lacunae. Micropters with elongate white wing pads, often infuscated distally; macropters with four closed cells in dark hemelytra with white region basally; venation of fore and hind wings similar to figs. 312-313 in Andersen (1982); female fore wing Sc often terminating in a triangular thickened region, resulting in a slight to pronunced sinuosity of the wing margin; fore wings set with long dark stiff erect setae on basal half, much more pronounced in females.

Legs slender; anterior femur set beneath with short light setae, sometimes slightly modified in males (figs. 11-13); anterior tibia with a distal comb of many stiff setae; middle and anterior femora set ventrally with numerous long slender setae; middle tibia set with an evenly spaced row of about 10 erect setae beginning at basal third, very long basally, decreasing in length distally; middle tarsi extremely long (fig. 9); claws short; both up- and down curving arolia evident, but very slender.

Male genital segments small, not protruding, unmodified; proctiger unmodified; parameres small, slender symmetrical (figs. 14-16). Female tergite VIII on same plane as VII, truncate posteriorly; first gonocoxae small, barely exposed, plate-like; tergite IX small, button-like, protruding posteriorly.

Type-species: *Tarsovelia alta* sp. n.

Remarks

Comparative notes. – *Tarsovelia* is similar in general facies to *Microvelia*, but is easily separated from this genus and all other Microveliinae by the elongate middle tarsi (fig. 9), which are adapted for rowing rather than running. In addition, the light colored markings on the hemelytra of *Tarsovelia* are restricted to the basal angles, plus occasionally a weak medial fascia, whereas in the type-species of *Microvelia* (*M. pulchella* Westwood) the hemelytra also bear ovate light spots in every closed cell, plus a large bright spot in the open distal cell.

Biological notes. – *Tarsovelia* species are found along the margins of flowing pools on rocky mountain streams. They are swift and agile skaters if disturbed, and will fly readily if captured in a net.

Etymology. – The generic name *Tarsovelia* is derived from *tarsos* (Gr.), referring to the extremely long slender middle tarsi, and *Velia*, the nominate genus of the family. Gender feminine.

Distribution. – New Guinea (fig. 29).

Key to the species of *Tarsovelia*

Males

1. Fore femur with patch of short, stiff hairs on ventral surface (figs. 11, 12) 2
– Fore femur lacking patch of short, stiff hairs on ventral surface (fig. 13) .... *T. alta* sp. n.
2. Fore femur with patch of short, stiff hairs near middle of ventral margin (fig. 11) .... *T. arfak* sp. n.
– Fore femur with patch of short, stiff hairs near base of ventral margin (fig. 12) ..... *T. dani* sp. n.

Tarsovelia alta sp. n.
(figs. 9, 13, 15, 29)

Type material: Holotype, micropterous male: Papua New Guinea, Morobe Prov., bog nr. Mt. Kaindi summit, above Wau, 17 Oct. 1983, CL 1825, D. A. and J. T. Polhemus (BPBM). – Paratypes: 13 micropterous males, 14 micropterous females, 16 immatures, same data as holotype (ZMUC, JTPC, BPBM).

Additional material examined: 2 macropterous females, Papua New Guinea, Morobe Prov., Eddie Creek, 2050 m, 11 Oct. 1966, Illies leg. (ZBSM, JTPC); 1 macropterous female, Morobe Prov., Poverty Creek, Mt. Missim, 18 Sept. 1983, CL 1830, 1600 m, J. T. & D. A. Polhemus (JTPC); 9 macropterous males, 6 macropterous females, 2 immatures, Western Highlands Prov., rocky stream 17 km N. of Mt. Hagen on Baiyer River road, 6 and 8 Sept. 1983, CL 1780, D. A. and J. T. Polhemus (JTPC).

Diagnosis

Size. – Micropterous male, length 2.41-2.48 mm ($\bar{x}$ = 2.44, n = 10); width 0.83-0.89 mm ($\bar{x}$ = 0.85, n = 10). Micropterous female, length 2.81-2.88 mm ($\bar{x}$ = 2.84, n = 4); width 0.94-1.01 mm, ($\bar{x}$ = 0.99, n = 4).

Macropterous male, length 2.77-2.95 mm ($\bar{x}$ = 2.87, n = 9); width 1.10-1.15 mm ($\bar{x}$ = 1.14, n = 9). Macropterous female, length 3.31-3.45 mm ($\bar{x}$ = 3.36, n = 6); width 1.19-1.33 mm, ($\bar{x}$ = 1.28, n = 6).

Colour. – Micropterous male: ground colour orange brown, venter slightly lighter. Head dark orange brown, lighter beneath; rostrum luteous medially, piceous distally. Pronotum with anterior transverse band orange brown, extending onto propleura; disc dark brown, mottled with lighter brown. Abdomen orange brown, tergal margins darker, lighter ventrally. Distal segements of legs, antennae brown, basal segments lighter.

Structural characters. – Micropterous male: head of moderate length, declivant anteriorly; length 0.37; width of eye/interocular space, 0.14/0.30. Pronotum long, covering metanotum, humeri evident but not raised; length:width, 0.84 : 0.86. Abdominal tergites not shining; lengths of tergites, II : 0.14; III : 0.16; IV-VI : 0.19; VII : 0.26.

Abdominal venter not modified, set with short appressed setae. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Legs unarmed.

Antennal formula I : II : III : IV; 0.29 : 0.33 : 0.37 : 0.42.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.65 : 0.63 : 0.28 : 0.0; of middle leg, 0.98 : 0.93 : 0.42 : 0.35; of hind leg, 0.86 : 1.00 : 0.19 : 0.29.

Paramere small, long, slender (fig. 15).

Micropterous female: Similar to male in most respects, but somewhat larger; connexiva reflexed over dorsum except in gravid specimens.

Macropterous male: Similar to micropterous form in most respects. Pronotum with anterior lobe entirely orange brown, extending onto propleura; posterior lobe uniformly dark. Hemelytra blackish brown, basally entirely white except slight infuscation of Sc, white region extending beyond tip of pronotum.

Macropterous female: Very similar to macropterous male, except lateral hemelytral margin slightly sinuate at distal thickening of Sc. Posterior lobe of pronotum with two (1+1) tufts of erect stiff black setae on either side of midline at about middle. Connexival margin vertical.

Remarks

Comparative notes. – *T. alta* sp. n. may be separated from *T. dani* sp. n. and *T. arfak* sp. n. by the unmodified male fore femur (fig. 13), brownish coloration in wingless forms, male paramere shape (fig.15), and length of the second segment of the hind tarsi, which is about 1.5 times as long as the first (versus only slightly longer in the other two species). In *T. arfak* sp. n. the anterior femora are dark distally, and the middle and posterior femora plus all the tibiae and tarsi are dark brown to black, while in *T. alta* sp. n. and *T. dani* sp. n. all femora are largely light brown, and the tibiae and tarsi are dark brown but not black. In the macropters of *T. alta* sp. n. and *T. arfak* sp. n. the entire basal angle of the hemelytra is white (including the veins, although these are occasionally slightly darkened), whereas in *T. dani* sp. n. the veins are dark and the light coloring is often a sordid white.

We originally considered the micropterous and macropterous specimens at hand from Papua New Guinea to represent different taxa. However with two additional new species now available from Irian Jaya that show marked differences from the Papua New Guinea material, we have now concluded that the latter represent but a single, albeit somewhat variable, species. We have thus included all of the specimens from eastern New Guinea under *T. alta* sp. n., but the macropters are not named as paratypes. Macropterous specimens from Eddie Creek and Poverty Creek (not measured) have very long hemelytra, considerably exceeding the tip of the abdomen, and they are lighter in color than specimens from Mt. Hagen. Measurements of leg and antennal segments are not helpful, as they appear to vary randomly between populations, thus we defer the final decision about the specific distinctness of these populations from Papua New Guinea until more material, hopefully including both micropters and macropters in the same sample, is available.

Biological notes. – Near Mt. Hagen *T. alta* was found in a plunge pool below a small cascade, with individuals hiding in the crevices of a sheer rock wall. When disturbed the insects would skate rapidly over the water near the wall until disappearing into their hiding places once more. By contrast, the Mt. Kaindi specimens were taken from beneath a large, partly submerged log in a bog pool, where violent flushing was required to dislodge them. So far this species has been found only at altitudes above 1200 meters.

Etymology. – The name '*alta*' refers to the high elevation at which this species was taken.

Distribution. – Eastern New Guinea (fig. 29).

Tarsovelia arfak sp. n.

(figs. 11, 16, 29)

Type material: Holotype, macropterous male: Indonesia, Irian Jaya Prov., Saumarin River, nr. Warkomi, Arfak Mountains, 42 km S. of Manokwari, 90 m, water temp. 25° C, 18 Oct. 1991, CL 2647, D. A. and J. T. Polhemus (USNM). – Paratypes: 67 macropterous males, 48 macropterous females, 6 immatures, same data as holotype (JTPC).

Diagnosis

Size. – Macropterous male, length 2.45-2.77 mm ($\bar{x}$ = 2.62, n = 10); width 1.01-1.12 mm ($\bar{x}$ = 1.06, n = 10). Macropterous female, length 2.81-3.09 mm ($\bar{x}$ = 2.98, n = 10); width 1.15-1.19 mm, ($\bar{x}$ = 1.17, n = 10).

Colour. – Macropterous male: ground colour black, tinged with brown. Head black. Pronotum with anterior lobe and collar medially orange brown, extending to inner eye margins; posterior lobe uniformly black. Hemelytra blackish brown, long, extending beyond tip of abdomen, basally with broad elongate rectangular white region along outer margin, extending beyond tip of pronotum. Abdomen black, ventrally tinged with brown along connexival margins and caudally. Legs, antennae brown, fore femur yellowish except distally, mid and hind femora yellowish ventrally.

Structural characteristics. – Macropterous male: head of moderate length, declivant anteriorly; length 0.40; width of eye/interocular space, 0.12/0.33. Pronotum long, humeri evident but not raised; length:width, 0.86 : 1.00.

Abdominal venter not modified, set with short appressed setae. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae; all tibia, middle and hind tarsi set with rows of long setae dorsally, in addition to long ventral setae. Legs unarmed, except fore femur ventrally slightly excavate basally, set near middle with patch of short stiff setae (fig. 11).

Antennal formula I : II : III : IV; 0.28 : 0.33 : 0.35 : 0.40.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.65 : 0.51 : 0.28 : 0.0; of middle leg, 0.88 : 0.81 : 0.49 : 0.35; of hind leg, 0.81 : 0.95 : 0.23 : 0.28.

Paramere small, long, slender (fig. 16).

Macropterous female: Similar to male in most respects, but somewhat larger; hemelytra with lateral margin sinuate, thickened and set with long dense black setae at distal Sc. Connexiva vertical along tergites II-IV, slightly reflexed over tergites V-VII.

Remarks

Comparative notes. – Recognized by the patch of short stiff black setae on the ventral margin of the male fore femur (fig. 11), and the shape of the male paramere (fig. 16). For additional comparative notes see key, and discussion under *T. alta* sp. n.

Biological notes. – The Saumarin River at the type locality was a moderate sized stream dropping steeply to the sea off the flanks of the Arfak Mountains through a bed of boulders, cobbles and sand, heavily shaded by primary rain forest. The stream profile was punctuated by numerous small waterfalls, and *T. arfak* was most abundant on the plunge pools below these falls.

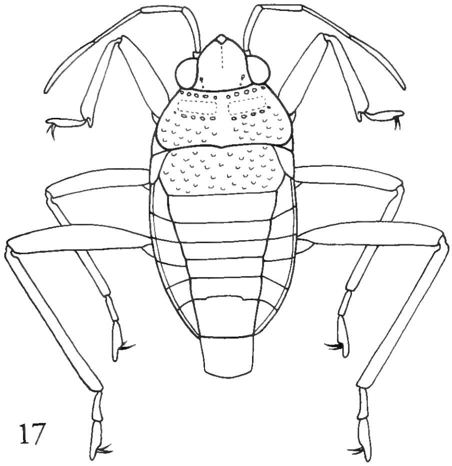
Etymology. – The name '*arfak*' is a noun in apposition and refers to the Arfak Mountain type area.

Distribution. – Western New Guinea (Vogelkop Peninsula) (fig. 29).

Tarsovelia dani sp. n.

(figs. 10, 12, 14, 29)

Type material: Holotype, macropterous male: Indonesia, Irian Jaya Prov., swift rocky stream in



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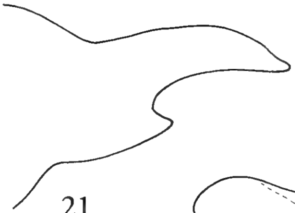

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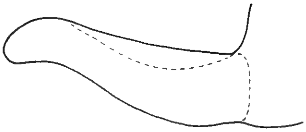

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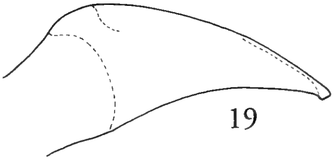

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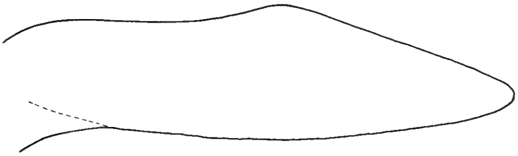

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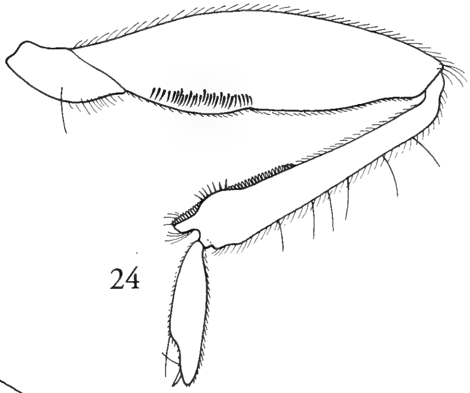

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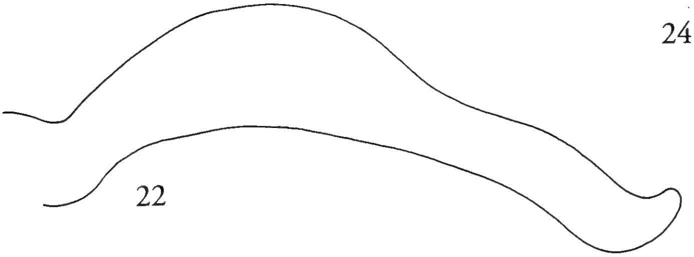

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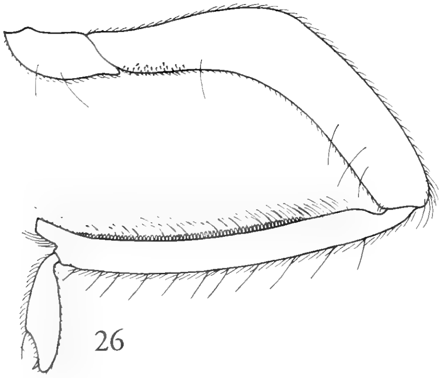

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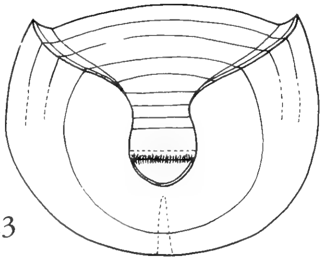

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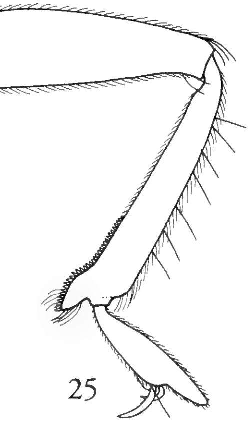

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upper Pass Valley, 52 km NE of Wamena, 2015 m., water temp. 14°C, 23 Sept. 1991, CL 2614, D. A. and J. T. Polhemus (USNM). - Paratypes: 61 macropterous males, 26 macropterous females, 28 immatures, same data as holotype (JTPC).

Diagnosis

Size. – Macropterous male, length 2.55-2.95 mm ($\bar{x}$ = 2.78, n = 10); width 1.01-1.15 mm ($\bar{x}$ = 1.09, n = 10). Macropterous female, length 2.99-3.45 mm ($\bar{x}$ = 3.12, n = 10); width 1.15-1.37 mm, ($\bar{x}$ = 1.22, n = 10).

Colour. – Macropterous male: Ground colour orange brown, marked with black. Head blackish brown dorsally, ventrally lighter. Pronotum with anterior lobe and collar orange brown, extending onto propleura, collar marked only laterally, demarcated by a row of dark foveae; posterior lobe uniformly black. Hemelytra blackish brown, basally with narrow elongate white stripe along costal margin, extending beyond tip of pronotum, plus a shorter sordid white region basally along pronotum; with elongate grayish brown streak in middle, barely visible in some specimens; length variable, shortest reaching barely onto tergite VII, longest almost covering genital segments. Abdomen orange brown. Legs, antennae brown, fore femur yellowish except distally, mid and hind femora, tibia yellowish ventrally.

Structural characteristics. – Macropterous male: head of moderate length, declivant anteriorly; length 0.38; width of eye/interocular space, 0.14/0.30. Pronotum long, humeri evident but not raised; length:width, 1.00 : 1.12.

Abdominal venter not modified, set with short appressed setae. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Legs unarmed, except fore femur flattened ventrally, curved, basally with a tuft of stiff setae (fig. 12).

Antennal formula I : II : III : IV; 0.30 : 0.35 : 0.42 : 0.42.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.74 : 0.72 : 0.30 : 0.0; of middle leg, 1.12 : 1.02 : 0.49 : 0.35; of hind leg, 0.98 : 1.07 : 0.26 : 0.33.

Paramere small, long, slender (fig. 14).

Macropterous female: Similar to male in most respects, but somewhat larger. Hemelytra length variable, shorter than in male, shortest not reaching tergite VII, longest reaching caudal margin of tergite VII; with lateral margin weakly sinuate, narrowly thickened and set with stiff setae at distal Sc. Connexiva vertical along tergites II-III, IV in transition, strongly reflexed over tergites V-VII.

Remarks

Comparative notes. – Recognized by the small tuft of black setae basally on the ventral surface of the weakly bowed male fore femur (fig. 12), and the shape of the male paramere (fig. 14). For additional comparative notes see key, and discussion under *T. alta* sp. n.

Biological notes. – The type series of *T. dani* was taken from pools along a very swift, cold mountain stream in a limestone bed bordered by *Nothofagus* and *Rhododendron* forest. The insects were most common along the pool margins, skating rapidly across the water if disturbed and flying readily if taken in a net.

Etymology. – The name '*dani*' is a noun in apposition and refers to the native Dani people who inhabit the type area.

Distribution. – Central New Guinea (fig. 29).

Neusterinsifer gen. n.
(figs. 17-26, 30)

Diagnosis

Size. – Form stout (fig. 17), length of males 1.87-2.48 mm, females 1.91-2.77 mm, general body characteristics and size sexually dimorphic, males smaller, female abdomen more robust.

Colour. – Ground color black, tinged with orange brown, heavily marked with silvery pubescence; anterior pronotal lobe orange brown on posterior half, with streak extending from near midline to middle of eyes, weakly demarcated from collar and posterior lobe.

Structural characteristics. – Both apterous and macropterous forms known. Eyes globose, exserted but usually not beyond anterolateral pronotal angles, separated by about twice the width of an eye, appressed to anterior pronotal margin, with moderately long ocular setae. Head strongly declivant anteriorly, recessed into pronotum, posterior margin almost vertical, with usual three pairs of facial trichobothria; gular region short, not visible, rostral cavity open posteriorly, with raised carinate bucculae. Rostrum reaching to middle of mesosternum, segment I short, enclosed in rostral cavity, I and IV subequal in length

Figs. 17-26. *Neusterinsifer* gen. n. – 17. *Neusterinsifer compactus* sp. n., micropterous male, dorsal habitus; 18-22. Processes arising from male proctigers of *Neusterinsifer* species, 18. *Neusterinsifer compactus* sp. n.; 19. *Neusterinsifer cyclops* sp. n.; 20. *Neusterinsifer sepik* sp. n.; 21. *Neusterinsifer nabire* sp. n.; 22. *Neusterinsifer gladius* sp. n.; 23. *Neusterinsifer compactus* sp. n., posterior view of female abdomen showing anal plate formed by tergites VII and VIII. 24-26. Male forelegs of *Neusterinsifer* species: 24. *Neusterinsifer sepik* sp. n.; 25. *Neusterinsifer gladius* sp. n.; 26. *Neusterinsifer compactus* sp. n.

and about two times longer than II, segment III about four times as long as II. Antennae slender, very long, about 2/3 of body length.

Pronotum almost flat, without median carina; collar very weakly formed, set off by a ragged row of small dark foveae, terminating under eyes laterally; anterior and posterior lobes set off by a transverse row of foveae; anterior lobe thickly set with appressed silvery setae except triangular median area; posterior lobe with numerous small foveae, humeri not formed, almost straight posteriorly, not modified, covering mesonotum. Metanotum almost as long as pronotum. Thoracic venter not diagnostic, with weakly formed tubercles on either side of mesosternal midline on posterior margin opposing an unmodified metasternum. Metasternal scent gland opening (omphalium) not visible, but marked by a tiny tubercle; scent channels prominent, curving slightly anterad to base of metacetabulae.

Abdomen with silvery setae laterally on tergites II, VII, VIII, covering most of tergites II-VI in females, less extensive in males; prominent paired longitudinal carinae on tergite II of macropters (visible only after removal of wings), absent in micropterous form. Abdominal sternites set off from laterosternites by small hair-free glabrous oval lacunae; laterosternite VII of both sexes set with small round tuft of stiff posterolaterally directed setae, near connexival margin at basal 2/5 in males, much closer to base in females.

Macropterous forms with four closed cells in dark hemelytra, occasionally with fifth distal cell closed; always with white elongate streak basally in outer basal cell, usually with faint to pronounced light areas in other cells; venation of fore and hind wings similar to figs. 312-313 in Andersen (1982).

Legs moderately stout, moderately long; anterior femur set beneath with short light setae, modified in males of some species, with a patch of stiff setae or denticles ventrally on basal half; anterior tibia of male with a comb of minute black setae occupying 2/5 to 1/2 of tibial length; all femora set ventrally with 7-12 long slender setae; all tarsi moderately long, claws moderately long; both up- and down curving arolia long, slender.

Male abdominal ventrites VI, VII modified; genital segments very large, protruding, highly modified, proctiger bearing a large sword-like appendage arising from anterior margin, directed antero-laterally beneath abdomen (figs. 18-22); segment IX, proctiger rotated by about 90°; parameres vestigial or absent. Female tergite VIII on same plane as VII basally, distally sharply deflected ventrad closing abdomen posteriorly except for protruding tip of proctiger (fig. 23); first gonocoxae hidden.

Type-species: - *Neusterinsifer compacta* sp. n.

Remarks

Comparative notes. – Very similar in general facies to *Microvelia* (fig. 17), but separated by sword-like projection on the male proctiger (figs. 18-22), the small tuft of stiff setae on laterotergite VII, and other characters as given in the generic key. Macropters differ from *Microvelia* and most other genera of Microveliinae in having a well defined long slender white streak basally in the outer cell (with only ill defined light areas in all other cells), and lacking the distal white spot that is characteristic of *Microvelia* and other closely related genera. The wing markings are similar to those of *Tenagovelia* Kirkaldy from Africa, but species in this latter genus are much larger and possess much longer legs.

Biological notes. – Species of *Neusterinsifer* are most commonly encountered in sheltered areas along the margins of stream pools, or on the surfaces of water filled potholes in bedrock exposures adjacent to flowing sections of streams.

Etymology. – The generic name *Neusterinsifer* is derived from *neuster* (Gr.), swimmer, and *ensifer* (L.), sword bearer. Gender masculine.

Distribution. – New Guinea (fig. 30).

Key to species of *Neusterinsifer*

1. Male process on proctiger bifurcate, short (fig. 21). Female abdomen strongly narrowed posteriorly, boat shaped .... *nabire* sp. n.
– Male process on proctiger not bifurcate, longer (figs. 18-20, 22). Female abdomen not strongly narrowed posteriorly, not boat shaped 2
2. Small species, male 1.87 mm, female 1.91 mm long. Male process on proctiger relatively short, broad, narrowly triangular distally (fig. 19 .... *cyclops* sp. n.
– Larger species, male at least 2.19 mm, female at least 2.27 mm long. Male process on proctiger long, relatively narrow, not triangular distally (figs. 18, 20, 22) 3
3. Relatively small species, males 2.19-2.27 mm, females 2.27-2.34 mm long. Process of male proctiger long, broad, expanded medially and distally (fig. 22); male fore femur with a row of 5-10 black spinules basally (fig. 25). Female connexival segment VII forming a small acute angle at level of caudal margin of tergite VII ...... *gladius* sp. n.
– Larger species, males 2.27-2.48 mm, females 2.37-2.77 mm long. Process of male proctiger long, narrow or broad, not expanded medially and distally (figs. 18, 20); male fore femur without a basal row of 5-10 black spinules, instead with either a basal row of many short stiff black setae, or unarmed. Caudal extreme of female con

nexival segment VII either forming an acute or obtuse angle, but without a small acute angle at level of caudal margin of tergite VII 4

4. Process of male proctiger long, slender, sharp distally (fig. 18); male fore femur strongly bowed, bearing small black denticles basally (fig. 26). Caudal extreme of female connexival segment VII forming an obtuse angle ..... *compactus* sp. n.

– Process of male proctiger long, broad (fig. 20); male fore femur not bowed, with a patch of black spinules basally (fig. 24). Caudal extreme of female connexival segment VII slightly produced posteriorly, forming an acute angle ... *sepik* sp. n.

Neusterinsifer compactus sp. n.

(figs. 17, 18, 23, 26, 30)

Type material: Holotype, apterous male: Papua New Guinea, Western Highlands Prov., Baiyer River, 53 km N. of Mt. Hagen, 6 and 8 Sept. 1983, D. A. and J. T. Polhemus (BPBM). - Paratypes: 19 apterous males, 12 apterous females, same data as holotype (JTPC); 1 apterous male, 3 apterous females, Western Highlands Prov., Baiyer River Bird Sanctuary, 8 Sept. 1983, CL 1792, J. T. & D. A. Polhemus (JTPC); 1 apterous male, Morobe Prov., Bamboo Creek, nr. Wau, 16 Sept. 1983, CL 1817, J. T. & D. A. Polhemus (JTPC); 4 apterous males, 1 apterous female, Morobe Prov., trib. to Bumbu River, N. of Lae, 20 Sept. 1983, CL 1836, J. T. & D. A. Polhemus (JTPC).

Diagnosis

Size. – Apterous male, length 2.37-2.48 mm ($\bar{x}$ = 2.43, n = 10); width 1.33-1.40 mm ($\bar{x}$ = 1.39, n = 10). Apterous female, length 2.63-2.77 mm ($\bar{x}$ = 2.70, n = 10); width 1.40-1.55 mm, ($\bar{x}$ = 1.50, n = 10).

Colour. – Apterous male: Ground colour blackish brown, venter slightly lighter, entire dorsum, laterotergites covered with fine appressed golden pubescence. Head black, orange brown beneath; rostrum fuscous medially, piceous distally. Pronotum with anterior transverse orange brown band barely interrupted medially; disc blackish brown. Abdomen blackish brown, lighter ventrally, connexiva margined with orange brown. Antennae brown; anterior legs yellowish, distally darkened; middle, hind legs dark brown, basally lighter; coxae, trochanters luteous.

Structural characters. – Apterous male: head of moderate length, declivant anteriorly, with weak impressed median line; length 0.40; width of eye/interocular space, 0.15/0.30. Pronotum long, covering metanotum, thickly set with obscure foveae, humeri depressed; length:width, 0.40 : 1.00. Metanotum length:width, 0.33 : 1.00. Abdominal tergites not shining; tergites II-VI subequal in length (0.14-0.16), VII longer (0.28).

Abdominal venter set with short appressed setae, and scattered longer setae caudally; venter VI posteriorly set with two (1+1) tufts of dense dark erect setae on either side of midline; venter VII broadly depressed medially, carinate along posterior margin. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Middle and hind legs unarmed; fore femur strongly bowed, bearing a patch of black denticles basally, fore tibia with grasping comb extending 3/4 the length of the tibia (fig. 26).

Antennal formula I : II : III : IV; 0.35 : 0.28 : 0.40 : 0.51.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.65 : 0.60 : 0.28 : 0.0; of middle leg, 0.86 : 0.86 : 0.16 : 0.30; of hind leg, 0.93 : 1.07 : 0.17 : 0.30.

Proctiger produced anteriorly into a long slender sinuate ensiform process (fig. 18). Parameres vestigial or absent.

Micropterous female: Similar to male in most respects, but somewhat larger; connexiva vertical, incurved and slightly refexed at caudal extreme, which forms an obtuse angle.

Remarks

Comparative notes. – A relatively large species for the genus, recognized by the short, blunt process on the male proctiger (fig. 18), and the strongly bowed male foreleg with a patch of black denticles basally on the ventral surface (fig. 26). Similar in size and general facies to *N. sepik* sp. n., but this latter species possesses an unbowed foreleg with a large patch of black denticles (fig. 24), and a much larger and more pointed process on the male proctiger (fig. 20).

Biological notes. – The Baiyer River at the type locality was a swift, deep river flowing in a rocky bed with wet mossy banks, and partially shaded by disturbed upland rain forest. *N. compactus* was taken here skating on the surface of water filled potholes in an exposure of igneous rock along the river margin.

Etymology. – The name *compactus* (L.) refers to the shape of this species.

Distribution. – Eastern New Guinea (fig. 30).

Neusterinsifer cyclops sp. n.

(figs. 19, 30)

Type material: Holotype, apterous male: INDONESIA, Irian Jaya Prov., small rocky stream and spring above Sentani, Cyclops Mountains, 325 m, 25 Sept. 1991, CL 2618, J. T. & D. A. Polhemus (JTPC, to be placed in USNM when more material is available).

Diagnosis

Size. – Apterous male, length, $\bar{x}$ = 1.87, n = 1; width, $\bar{x}$ = 0.79, n = 1. Apterous female, length, $\bar{x}$ = 1.91, n = 1; width, $\bar{x}$ = 0.90, n = 1.

Colour. – Apterous male: Ground colour deep brown, marked with brown, venter slightly lighter, entire dorsum, laterotergites covered with fine appressed golden pubescence; entire dorsum, pleura, sides of abdomen covered with moderate length erect setae. Head brown, orange brown beneath; rostrum fuscous medially, piceous distally. Pronotum with anterior transverse orange brown band embrowned medially; disc blackish brown. Abdomen blackish brown, lighter ventrally, connexiva margined with orange brown. Antennae brown, base of segment I lighter; legs yellowish, distally darkened; femora darker posteriorly; coxae, trochanters luteous.

Structural characters. – Apterous male: head of moderate length, declivant anteriorly, with weak impressed median line; length 0.33; width of eye/interocular space, 0.12/0.30. Pronotum long, covering metanotum, thickly set with obscure foveae, humeri depressed; length:width, 0.28 : 0.79. Metanotum length:width, 0.26 : 0.79. Abdominal tergites not shining; tergites II-VI subequal in length (0.12-0.14), VII longer (0.26).

Abdominal venter set with short appressed setae; venter VI posteriorly set with two (1+1) tufts of dense dark erect setae on either side of midline, between them a V-shaped depression open posteriorly; venter VII broadly depressed medially, sharply excavated on posterior half, carinate along anterior margin of excavation. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Middle and hind legs unarmed; foreleg lacking denticles or spinules, tibial comb extending for only 1/2 the length of the tibia.

Antennal formula I : II : III : IV; 0.21 : 0.19 : 0.33 : 0.40.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.51 : 0.44 : 0.19 : 0.0; of middle leg, 0.63 : 0.60 : 0.12 : 0.19; of hind leg, 0.74 : 0.86 : 0.12 : 0.26.

Proctiger produced anteriorly into a broad ensiform process (fig. 19). Parameres vestigial or absent.

Apterous female: Similar to male in most respects, but somewhat larger; connexiva vertical; caudal extreme gently curving ventrad.

Macropterous forms: unknown.

Remarks

Comparative notes. – Separable from all other *Neusterinsifer* species by its small size, and short, pointed process on the male proctiger (fig. 19).

Biological notes. – The type of *N. cyclops* was taken from a small, clear, spring fed stream at the margin of the remaining primary rain forest on the slopes of the Cyclops Mountains above Sentani. The stream flowed in a bed of metamorphic rocks intermixed with coarse grey sand, and was partially shaded by trees felled for garden clearings.

Etymology. – The name *cyclops*, a noun in apposition, refers to the mountain range where the species was found.

Distribution. – Northern New Guinea (Cyclops Mountains) (fig. 30).

Neusterinsifer gladius sp. n.
(fig. 22, 25, 30)

Type material: Holotype, apterous male: INDONESIA, Irian Jaya Prov., Nabire River and swift tributary, 5 km E. of Nabire, 60 m, 14 Oct. 1991, CL 2642, J. T. & D. A. Polhemus (USNM). - Paratypes: 2 apterous males, 2 apterous females, same data as holotype (JTPC).

Diagnosis

Size. – Apterous male, length 2.19-2.27 mm ($\bar{x}$ = 2.24, n = 3); width 0.90-0.94 mm ($\bar{x}$ = 0.91, n = 3). Apterous female, length 2.27-2.34 mm ($\bar{x}$= 2.30, n = 2); width 1.01-1.04 mm, ($\bar{x}$ = 1.03, n = 2).

Colour. – Apterous male: Ground colour blackish brown, venter slightly lighter, entire dorsum, laterotergites covered with fine appressed golden pubescence; entire body except thoracic venter covered with long erect setae. Head black, orange brown beneath; rostrum fuscous medially, piceous distally. Pronotum with anterior transverse orange brown band sometimes interrupted medially; disc blackish brown. Abdomen blackish brown, lighter ventrally, connexiva margined with orange brown. Antennae brown; anterior femora luteous, distally darkened; anterior tibia, tarsi brown, darker distally; middle, hind legs brown dorsally, ventrally yellowish, femora basally lighter; coxae, trochanters luteous, tinged with fuscous.

Structural characters.- Apterous male: head of moderate length, declivant anteriorly, with weak impressed median line; length 0.35; width of eye/interocular space, 0.15/0.28. Pronotum long, covering metanotum, thickly set with obscure foveae, humeri depressed; length:width, 0.37 : 0.86. Metanotum length:width, 0.28 : 0.86. Abdominal tergites not shining; tergites II-VI subequal in length (0.12-0.14), VII longer (0.28).

Abdominal venter set with short appressed setae; venter VI posteriorly set with two (1+1) widely separated tufts of dense dark erect setae on either side of

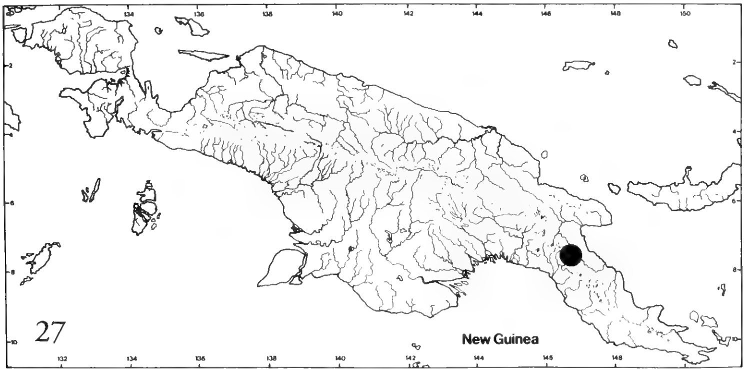

Fig. 27. Distribution of *Tanyvelia missim*, gen. n., sp. n.

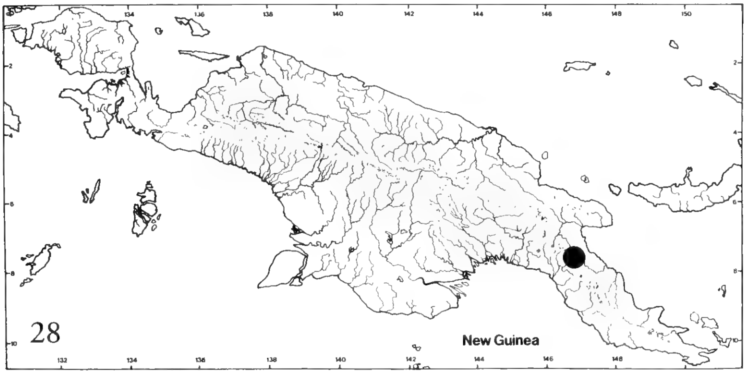

Fig. 28. Distribution of *Aegilipsicola rapida*, gen. n., sp. n.

midline, with shallow hair free sulcus between, extending the length of ventrites V-VI; venter VII broadly and strongly depressed medially. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Middle and hind legs unarmed; fore tibia bearing a row of 5-10 black spinules basally; fore femur with grasping comb extending 1/2 the length of the tibia (fig. 25).

Antennal formula I : II : III : IV; 0.35 : 0.28 : 0.35 : 0.47.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.60 : 0.51 : 0.28 : 0.0; of middle leg, 0.79 : 0.74 : 0.16 : 0.30; of hind leg, 0.84 : 1.02 : 0.16 : 0.30.

Proctiger produced anteriorly into a long broad sinuate ensiform process, expanded medially and distally (fig. 22). Parameres vestigial or absent.

Apterous female: Similar to male in most respects, but somewhat larger; connexiva vertical; caudal extreme of VII forming an acute angle; VIII gently curving ventrad.

Macropterous forms: Unknown.

Remarks

Comparative notes. – Similar in size to *N. nabire* sp. n., but easily separable by the elongate process on the male proctiger (fig. 22), the patch of stiff, black spinules basally on the ventral surface of the male fore femur (fig. 25), and the relatively unmodified female abdomen which is not laterally compressed or boat-shaped.

Biological notes. – The Nabire River at the type locality was a swift, clear, moderate sized stream flowing in a rocky bed, and shaded by primary lowland rain forest. The type series of *N. gladius* was taken downstream of a limestone waterfall, where the banks of the river included numerous boulders and bedrock exposures. The insects were taken from the surfaces of water filled potholes and on still pools amid the rocks.

Etymology. – The name *gladius* (L.), refers to the ensiform process of the male proctiger.

Distribution. – Western New Guinea (fig. 30).

Neusterinsifer nabire sp. n.
(figs. 21, 30)

Type material: Holotype, apterous male: INDONESIA, Irian Jaya Prov., Nabire River and swift tributary, 5 km E. of Nabire, 60 m, 14 Oct. 1991, CL 2642, J. T. & D. A. Polhemus (USNM). - Paratypes: 98 apterous males, 13 macropterous males, 72 apterous females, 35 macropterous females, 32 immatures, same data as holotype (JTPC).

Diagnosis

Size. – Apterous male, length 2.01-2.09 mm ($\bar{x}$ = 2.04, n = 10); width 0.79-0.83 mm ($\bar{x}$ = 0.81, n = 10). Apterous female, length 2.19-2.41 mm ($\bar{x}$ = 2.27, n = 10); width 0.79-0.90 mm ($\bar{x}$ = 0.83, n = 10). Macropterous male, length 2.23-2.34 mm ($\bar{x}$ = 2.29, n = 6); width 1.04-1.12 mm ($\bar{x}$ = 1.10, n = 6). Macropterous female, length 2.41-2.55 mm ($\bar{x}$ = 2.46, n = 6); width 1.08-1.15 mm, ($\bar{x}$ = 1.12, n = 6).

Colour. – Apterous male: Ground colour blackish brown, venter slightly lighter, entire dorsum, laterotergites covered with fine appressed inconspicuous pubescence; dorsum, body laterally covered with long erect setae. Head black, orange brown beneath; rostrum fuscous medially, piceous distally. Pronotum with anterior transverse orange brown band broadly interrupted medially; disc blackish brown. Abdomen blackish brown, slightly lighter ventrally, connexiva margined with orange brown. Antennae brown; anterior femora yellowish, distally darkened, tibia brown; middle, hind legs dark brown to piceous, femora basally lighter; coxae, trochanters luteous, tinged with fuscous.

Structural characteristics. – Apterous male: head of moderate length, declivant anteriorly, with weak impressed median line; length 0.33; width of eye/interocular space, 0.14/0.28. Pronotum long, covering metanotum, thickly set with obscure foveae, humeri depressed; length:width, 0.37 : 0.81. Metanotum length:width, 0.28 : 0.79. Abdominal tergites not shining; tergites II-VI subequal in length (0.12-0.16), VII longer (0.30).

Abdominal venter set with short appressed setae; venter V posteriorly set with two (1+1) tufts of dense dark erect setae on either side of midline; venter VI with caudal margin medially produced, set with a large quadrate tuft of dense dark erect setae; venter VII excavated medially along posterior margin. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Middle and hind legs unarmed; fore femur lacking denticles or spinules; fore tibia with grasping comb extending 1/2 the length of the tibia.

Antennal formula I : II : III : IV; 0.30 : 0.21 : 0.28 : 0.44.

Proportions of legs as follows: Femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.51 : 0.47 : 0.21 : 0.0; of middle leg, 0.70 : 0.63 : 0.12 : 0.23; of hind leg, 0.74 : 0.93 : 0.16 : 0.28.

Proctiger produced anteriorly into a bifurcate process (fig. 21). Parameres vestigial or absent.

Apterous female: Similar to male in most respects, but somewhat larger; abdomen narrowing posteriorly. Connexiva vertical, touching at caudal extreme; caudally rounded; thickly set along posterior margin with long stout dark setae; tuft of stiff posterolaterally directed setae near connexival margin of laterosternite VII of females pronounced, more so than in other species.

Macropterous male: Similar to apterous male in many respects, but broader, humeri more pronounced. Hemelytra always with light streaks in each of the two basal cells, often with light areas in all closed cells.

Macropterous female: Similar to apterous female in many respects, but broader, humeri more pronounced. Hemelytra with light areas in each of the four basal closed cells.

Remarks

Comparative notes. – Easily recognized by the bifurcate process on the male proctiger (fig. 21) and the laterally compressed, boat-shaped abdomen in females. This species is similar in size to *N. gladius* sp. n., and larger than *N. cyclops* sp. n., but smaller than either *N. compactus* sp. n. or *N. sepik* sp. n.

Biological notes. – See discussion under *N. gladius* sp. n.

Etymology. – The name '*nabire*', a noun in apposition, refers to the Nabire River type locality.

Distribution. – Northern New Guinea (fig. 30).

Neusterinsifer sepik sp. n.

(figs. 20, 24, 30)

Type material: Holotype, apterous male: Papua New Guinea, East Sepik Prov., Yemogu Creek, 2 km W. Tring, 12 Sept. 1983, CL 1805, J. T. & D. A. Polhemus (BPBM). - Paratypes: 11 apterous males, 6 apterous females, same data as holotype (JTPC); 1 apterous male, 4 apterous females, 1 macropterous female, East Sepik Prov., Mandi Creek, E. of Wewak, 10 Sept. 1983, CL 1797, J. T. & D. A. Polhemus (JTPC); 4 apterous males, 1 apterous female, East Sepik Prov., Brandi Creek, nr. Wewak, 10 Sept. 1983, CL 1796, J. T. & D. A. Polhemus (JTPC).

Diagnosis

Size. – Apterous male, length 2.27-2.41 mm ($\bar{x}$ = 2.35, n = 10); width 0.94-1.01 mm ($\bar{x}$ = 0.99, n = 10). Apterous female, length 2.37-2.63 mm ($\bar{x}$ = 2.48, n = 10); width 0.97-1.15 mm, ($\bar{x}$ = 1.04, n = 10). Macropterous female, length, $\bar{x}$ = 2.62, n = 1); width, $\bar{x}$= 1.15, n = 1)

Colour. – Apterous male: Ground colour blackish brown, venter slightly lighter, entire dorsum and la-

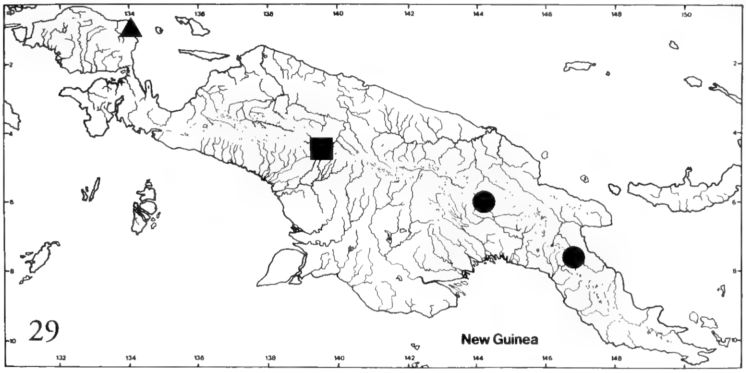

Fig. 29. Distribution of species of *Tarsovelia* gen. n. – Square = *Tarsovelia dani* sp. n.; Circles = *Tarsovelia alta* sp. n.; Triangle = *Tarsovelia arfak* sp. n.

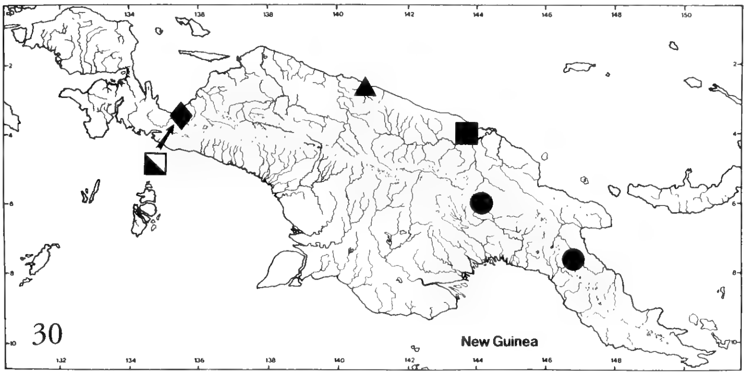

Figure 30. Distribution of species of *Neusterinsifer* gen. n. – Square = *Neusterinsifer sepik* sp. n.; Circles = *Neusterinsifer compactus* sp. n.; Triangle = *Neusterinsifer cyclops* sp. n.; Diamond = *Neusterinsifer nabire* sp. n.; Half filled square = *Neusterinsifer gladius* sp. n.

terotergites covered with fine appressed golden pubescence; entire body except thoracic venter covered with long erect setae. Head black, orange brown beneath; rostrum fuscous medially, piceous distally. Pronotum with anterior transverse orange brown band barely interrupted medially; disc blackish brown. Abdomen blackish brown, lighter ventrally, connexiva margined with orange brown. Antennae brown; anterior legs yellowish, distally darkened; middle, hind legs dark brown to piceous dorsally, ventrally yellowish, femora basally lighter; coxae, trochanters luteous, tinged with fuscous.

Structural characteristics. – Apterous male: head of moderate length, with weak impressed median line; length 0.27; width of eye/interocular space, 0.14/0.30. Pronotum long, covering metanotum, thickly set with obscure foveae, humeri depressed; length:width, 0.37 : 0.95. Metanotum length:width, 0.28 : 0.95. Abdominal tergites not shining; tergites II-VI subequal in length (0.14-0.16), VII longer (0.30).

Abdominal venter set with short appressed setae; venter VI posteriorly set with two (1+1) tufts of dense dark erect setae on either side of midline, with hair free sulcus between; venter VII broadly depressed medially, weakly carinate along posterior margin. Legs, antennae thickly clothed with short to moderate length setae, with scattered longer setae. Middle and hind legs unarmed; fore femur bearing an elongate patch of stiff erect black spinules basally; fore tibia with a swelling distally bearing 5-7 erect short stiff setae (fig. 24).

Antennal formula I : II : III : IV; 0.33 : 0.26 : 0.37 : 0.47.

Proportions of legs as follows: femur, tibia, tarsal 1, tarsal 2 of fore leg, 0.65 : 0.53 : 0.28 : 0.0; of middle leg, 0.84 : 0.79 : 0.16 : 0.28; of hind leg, 0.93 : 1.07 : 0.19 : 0.28.

Proctiger produced anteriorly into a long broad sinuate ensiform process (fig. 20). Parameres vestigial or absent.

Apterous female: Similar to male in most respects, but somewhat larger; connexiva vertical; caudal extreme forming an acute angle.

Macropterous female: Similar to apterous female in many respects, but broader, humeri more pronounced. Hemelytra with light areas in each of the four basal closed cells.

Remarks

Comparative notes. – Recognized by the large, elongate process on the male proctiger that comes to a rounded point (fig. 20), and the elongate patch of black denticles on the inner surface of the male foreleg (fig. 24).

Biological notes. – Yemogu Creek at the type locality was a slow flowing stream running through a rock bed, and containing numerous large pools shaded by slightly disturbed primary rain forest. *N. sepik* was found here in sheltered areas along the margins of the stream pools, and in similar habitats at Brandi River and Mandi Creek, two lowland rainforest streams entering the sea east of Wewak.

Etymology. – The name *sepik*, a noun in apposition, refers to the district of Papua New Guinea from which the type series was taken.

Distribution. – Northern New Guinea (fig. 30).

ACKNOWLEDGEMENTS

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Holotypes of all new species described herein are deposited in the Bishop Museum, Honolulu (BPBM), or the U.S. National Museum of Natural History, Washington, D. C. (-USNM); paratypes are held in the J. T. Polhemus collection, Englewood, Colorado (JTPC), and where numbers permit will be distributed to the institutions noted above as well as the Museum Zoologicum Bogoriense, Bogor, Indonesia (MZB), and the Universitets Zoologisk Museum, Copenhagen (ZMUC). We also thank Dr. Martin Baehr of the Zoogische Sammlung des Bayersichen Staates, Munich (ZBSM) for allowing us to examine specimens held under his care.

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ADULTS AND LARVAE OF TWO *PTECTICUS* LOEW FROM PENINSULAR MALAYSIA (DIPTERA, STRATIOMYIDAE)

Rozkošný, R. & D. Kovac, 1994. Adults and larvae of two *Ptecticus* Loew from Peninsular Malaysia, (Diptera, Stratiomyidae). – Tijdschrift voor Entomologie 137: 75 - 86, figs. 1-43. [ISSN 0040-7496]. Published 15 July 1994.

Descriptions and redescriptions of larvae and adults of *P. malayensis* sp. n. and *P. longipennis* (Wiedemann) are given, based on material from Malaysia. The phylogenetic relationships of the two species and the systematic position of the genus based on larval and adult characters are briefly discussed, and biological notes on larvae are provided. The diagnostic characters of the larvae and imagines, including the male genitalia, are illustrated. A generic key to the larvae of the subfamily Sarginae is given.

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Key words. – Peninsular Malaysia; Stratiomyidae; larvae, key; *Ptecticus*; new species, life history.

The genus *Ptecticus* Loew belongs to the subfamily Sarginae and differs in the adult stage from the closely related genus *Sargus* Fabricius by the distinctly prominent pedicel on the inner side of the antenna. According to the recent catalogue by James (1975), 31 valid species have been described from the Oriental region but many of them are poorly known. The male genitalia as the most important criterion for species discrimination, for example, have not yet been examined in most Oriental species and the taxonomic status of many species needs a re-evaluation.

The junior author, while studying insects on bamboo (*Gigantochloa scortechinii* Gamble) in Peninsular Malaysia, found larvae of Stratiomyidae living inside bamboo internodes. Following our study on *Camptopteromyia fractipennis* de Meijere (Rozkošný & Kovac 1991) the present paper represents the second modern contribution to the taxonomy, morphology and biology of the Oriental Stratiomyidae.

Two species are treated here, both reared from larvae found under semi-natural conditions. The first of them, *P. longipennis* (Wiedemann), is a well distinguishable species, but we decided on re-description in order to include important diagnostic characters not mentioned in the original description, including the male genitalia. The second species is described here as new; it differs from all known Oriental *Ptecticus* species. Larvae and puparia of both species are described for the first time, and their descriptions enable us to propose generic characters for *Ptecticus* in the larval stage.

Ptecticus longipennis (Wiedemann, 1824)

(figs. 1-10, 26-32)

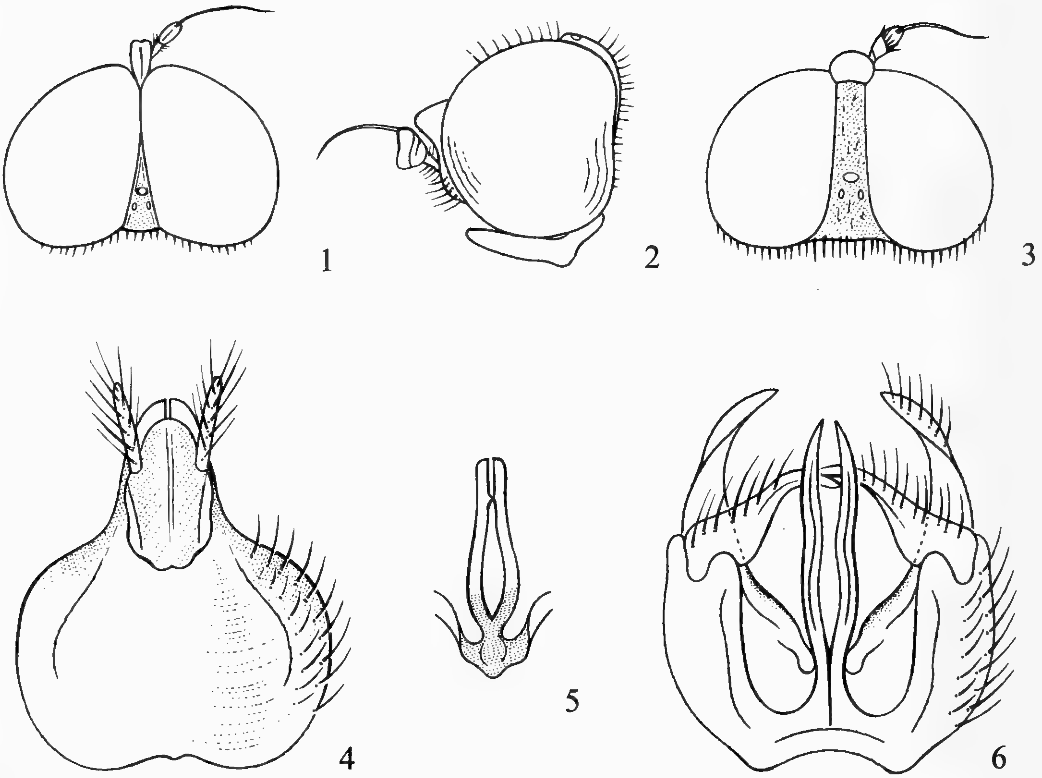
Diagnosis

An easily recognizable, chiefly blue black and yellow species from the *cingulatus*-group with conspicuously long, and apically darkened wings.

Measurements: Body 8.2-11.5 mm, wing 10.8-13.0 mm.

Male. – Head hemispherical, deeply concave posteriorly, bare eyes touching on frons (figs. 1-2). Upper part of frons elongate, triangular, subshining black and sparsely covered with fairly long brownish hairs. Ocellar triangle relatively narrow and low, barely visible in lateral aspect (fig. 2). Lower frons and face protuberant, white to pale yellow, white frontal callus slender, nose-shaped. Face with dense yellow hairs. Antennae yellow, arista brown, both basal segments yellow haired. Pedicel with prominent projection on inner side. Flagellum wider than long, about as long as pedicel. Postocular margin with a complete fringe of erect hairs. Proboscis pale yellow, somewhat swollen but relatively slender, with two-segmented labellae.

Thorax bright yellow in ground colour, with extensive dark pattern. Mesonotum chiefly shining bluish-black, leaving large anterior corners and postalar calli yellow. Scutellum dark, with margin broadly brownish or yellow. Pleura yellow, with large brownish to bluish-black spots on greater part of anepisternum,



Figs. 1-6. *Ptecticus longipennis*, adult characters. – 1, male head, dorsal view; 2, the same, lateral view; 3, female head, dorsal view; 4, dorsal part of male terminalia; 5, aedeagal complex; 6, ventral part of male terminalia.

lower half of katepisternum and anterior parts of anepimeron and katepimeron. Laterotergite shining brown and mediotergite behind scutellum completely bluish-black. Narrow subnotopleural stripe, upper margin of katepisternum, and, especially, propleuron pale, often whitish yellow.

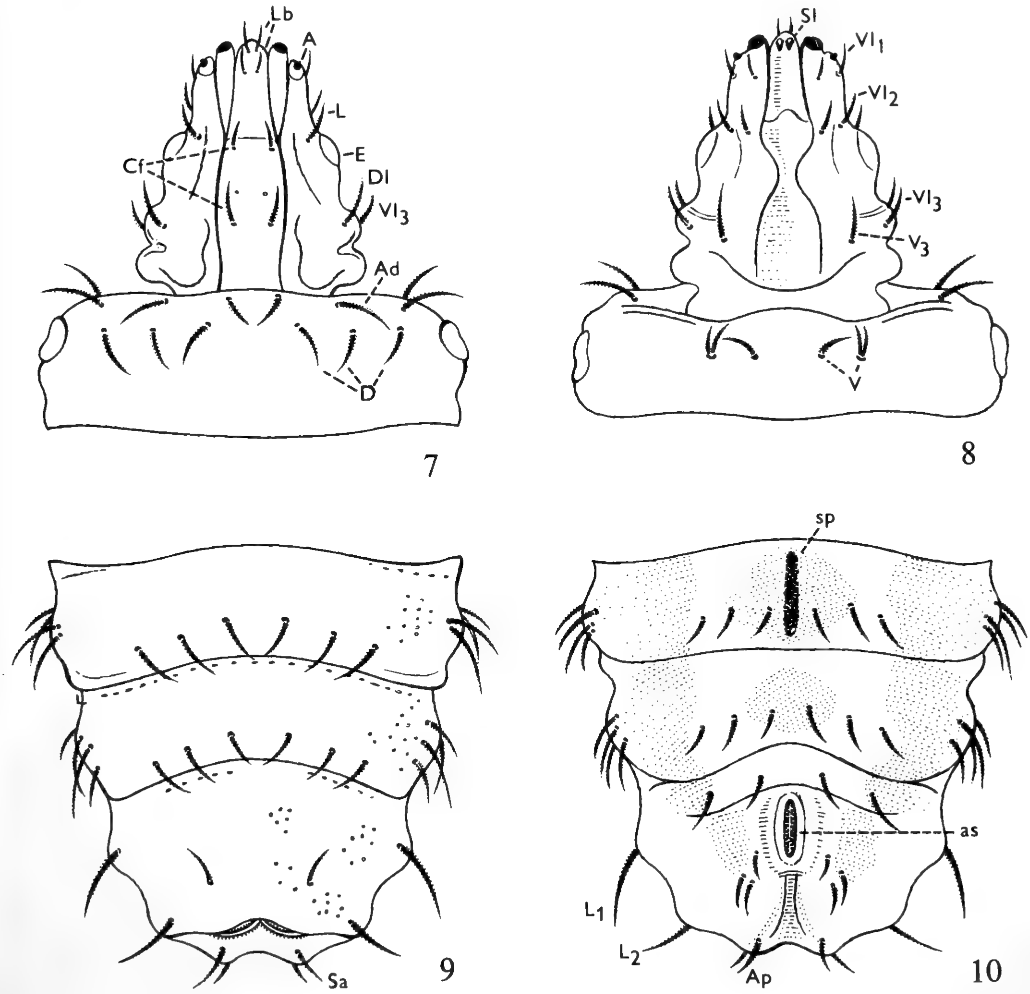
Wings slightly greyish infuscate, with yellow pterostigma and darkened apical part reaching almost half way between apex and discal cell. Dense microtrichia absent in wing base, alula, subcostal cell and greater part of posterior cubital cell. Anterior crossvein situated just at beginning of R_{3-5}, M_3 shortened, not reaching wing margin. Narrow squamae white to yellow, pale yellow haired. Halteres yellow, with darkened knob.

Legs including coxae chiefly yellow, only hind pair partly darkened. All femora distinctly thickened in basal half. Hind coxa and femur yellow as in fore and middle legs, hind tibia and narrow base of basitarsus dark brown to black. Rest of basitarsus and all following tarsal segments white, with whitish hairs at least on dorsal side.

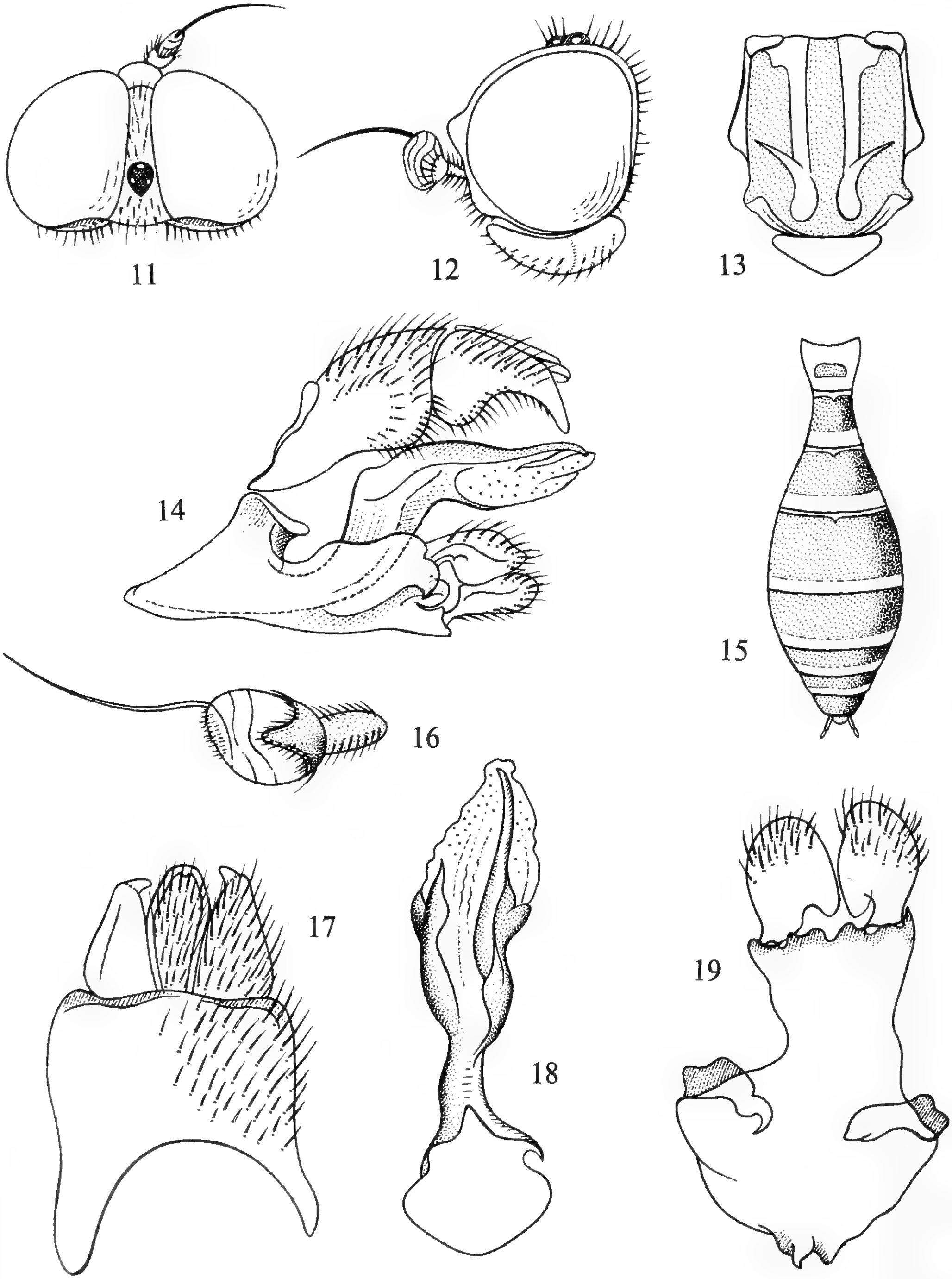
Abdomen shining bluish-brown to black, with yellow transverse stripes and pleural membrane. Transverse stripes broad on the posterior, and narrow on the anterior margin of each tergum of segments 2-4, apical terga completely black. Transverse stripes sometimes reduced to broad yellow sidemarkings on posterior corners of segments. Male genitalia (figs. 4-6) rotated by 90° along longitudinal axis, so that epandrium is in right lateral position. Apart from this, hypopygium symmetrical. Epandrium almost round and compact, tightly connected with paraprocts posteroventrally. Epiproct of proctiger narrow, bearing slender, rodlike cerci. Synsternum deeply emarginate, with slender and bipartite medial process shielding short, symmetrical, partly reduced aedeagal complex from ventral side.

Female. – Eyes separated by shining black frontal stripe being anteriorly somewhat broader than ocellar triangle (fig. 3). White frontal callus bulbose, wider than in male. Scutellum dark, its posterior margin slightly yellowish. Dark pleural spots as in male but partly reduced on katepisternum. Abdomen shining bluish black, with transverse yellow stripes at posterior margins of terga 2-4 extending to anterior margins of following terga. Yellow stripes about half as wide as dark stripes between them, somewhat broader than in male. Dark pattern of hind legs as in male. Cerci with two segments, slender and relatively long.

Larva (and puparium). – Subcylindrical, with prominent head, slightly arched lateral margins of body segments and distinctly angulate though generally rounded anal segment. Cuticle with usual mosaic appearance, some cells somewhat larger and darker, forming almost complete double rows at boundary of body segments and groups in sublateral position. General colour yellowish brown, with diffuse brown pattern consisting of broad, longitudinal, undulate bands. Anal segment yellow, with large anterodorsal brownish spot. Ventral side paler, especially in median third where brownish spots are almost indistinct. Head (figs. 7-8, 26-27) moderately flat, subconical. Vestiges of mandibular-maxillary complexes about as



Figs. 7-10. *Ptecticus longipennis*, larval characters. – 7, head and first thoracic segment, dorsal view (A, antenna; Ad, anterodorsal setae; Cf, clypeofrontal setae; D, dorsal setae; Dl, dorsolateral setae; E, eye prominence; L, lateral setae; Lb, labral setae; VL3, posterior ventrolateral setae); 8, the same, ventral view (Sl, sublabral setae; V, ventral setae; VL1-3, ventrolateral setae; V3, posterior ventral setae); 9, last abdominal segments, dorsal view (Sa, subapical setae); 10, the same, ventral view (Ap, apical setae; as, anal slit; L1 + L2, lateral setae; sp, sternal patch).



Figs 11-19. *Ptecticus malayensis* sp. n., adult characters. – 11, male head, dorsal view; 12, the same, lateral view; 13, mesonotum pattern, dorsal view; 14, male terminalia, lateral view; 15, female abdomen, dorsal view; 16, antenna, inner side; 17, dorsal part of male terminalia; 18, aedeagal complex; 19, ventral part of male terminalia.

long as labrum in dorsal view, low and rounded antennae placed anteriorly, their apical segment about as high as broad at base. Eyes relatively little prominent, posterior part of head with two rounded protuberances on each side.

Three thoracic segments about same shape as abdominal segments 1-7, first thoracic segment with lateral vestiges of prothoracic spiracles. Thoracic segment 3 and abdominal segments 1-7 with small, round, dorsolateral, probably non-functional larval spiracles. In puparia, abdominal segments 2-5 with very inconspicuous, short, rodlike pupal respiratory horns near lateral margin. Very slender and long midsternal patch on abdominal segment 6 consisting of 112-114 pale cells (figs. 10, 31). Rounded and much smaller sternal patch with 18-19 cells usually at posterior margin of abdominal segment 5 (fig. 32). Anal segment (figs. 9-10, 28) distinctly emarginate between insertions of marginal setae, with a pair of low protuberances distally. Opening of spiracular chamber with undulate posterior margin and short pennate setae (figs. 29-30). Anal slit on ventral side with somewhat swollen marginal lips, boundered proximally by usual transverse fold. Two low symmetrical protuberances developed around insertions of posterior ventral setae.

General scheme of chaetotaxy as in other known genera of Sarginae (cf. Rozkošný 1982). All setae on head short, labral setae not longer than others, spinelike sublabral setae well developed. Anterior clypeofrontal setae inserted almost at level of eye prominences. Setae on thoracic and abdominal segments arranged in transverse rows (3 pairs of dorsal and 2-3 pairs of ventral setae) and lateral groups (2-4 setae). Thoracic segment 1, on each half, with 2 anterodorsal, 3 dorsal, 1 dorsolateral and 1 ventrolateral seta. All 3 thoracic segments only with 2 pairs of ventral setae. Lateral group of setae on thoracic segments consisting of 2 setae only (1 dorsolateral and 1 ventrolateral).

On lateral side of abdominal segments, 4 setae (1 dorsolateral, 2 lateral and 1 ventrolateral) on abdominal segments 1 and 6-7, but only 2 setae (probably 1 ventrolateral and 1 lateral) on abdominal segments 2-5. All marginal setae on anal segment of about same length, virtually not longer than setae on preceding abdominal segments. Five pairs of ventral setae on anal segment well visible, two distal pairs inserted closely together (fig. 10). Especially dorsal and ventral setae on body segments distinctly pubescent. Length 9.3-10.6 mm, maximum width 2.6-3.0 mm (based on 4 puparial exuviae).

Material examined. – Peninsular Malaysia, University of Malaya Field Studies Centre, Ulu Gombak, Selangor (3°20'N, 101°45'E, altitude 250 m), 1♂ from 10 May, 2♂ from 12 May and 1♀ from 16 June 1991, all specimens ex puparia, D. Kovac leg. Material deposited in the Forschungsinstitut Senckenberg, Frankfurt (SMFD) (2♂), and in the Faculty of Science, Masaryk University, Brno (MUB) (1♂ and 1♀).

Remarks

Distribution. – India, Malaya, Sumatra, Java, Borneo, Philippines.

Discussion. – According to Brunetti (1923) this slender species with long legs and wings belongs to the *cingulatus* species group. It differs from the other species of this group by the darkened wing tip, a diagnostic character shared only with *P. sumatranus* Enderlein. The latter species, however, possesses the normal, not elongate wings and its mesonotum is reddish yellow, not dark with a metallic shine. Of the few *Ptecticus* species in which the male genitalia have been illustrated, only *P. okinawensis* Ôuchi may belong to the same group, as shown by the compact epandrium and deeply emarginate synsternum (cf. Nagatomi 1975).

Ptecticus malayensis sp.n.

(figs. 11-25, 33-39)

Type material. – Holotype, male: Peninsular Malaysia, University of Malaya Field Studies Centre, Ulu Gombak, Selangor (3°20'N, 101°45'E, altitude 250 m), ex puparium 15 November 1991, D. Kovac leg., SMFD. – Paratypes 3♂ 2♀: Same locality, 3♂ reared 15 November, 1♀ 23 November, 1♀ 20 December 1991; 1♂ 1♀ SMFD, 2♂ 1♀ MUB.

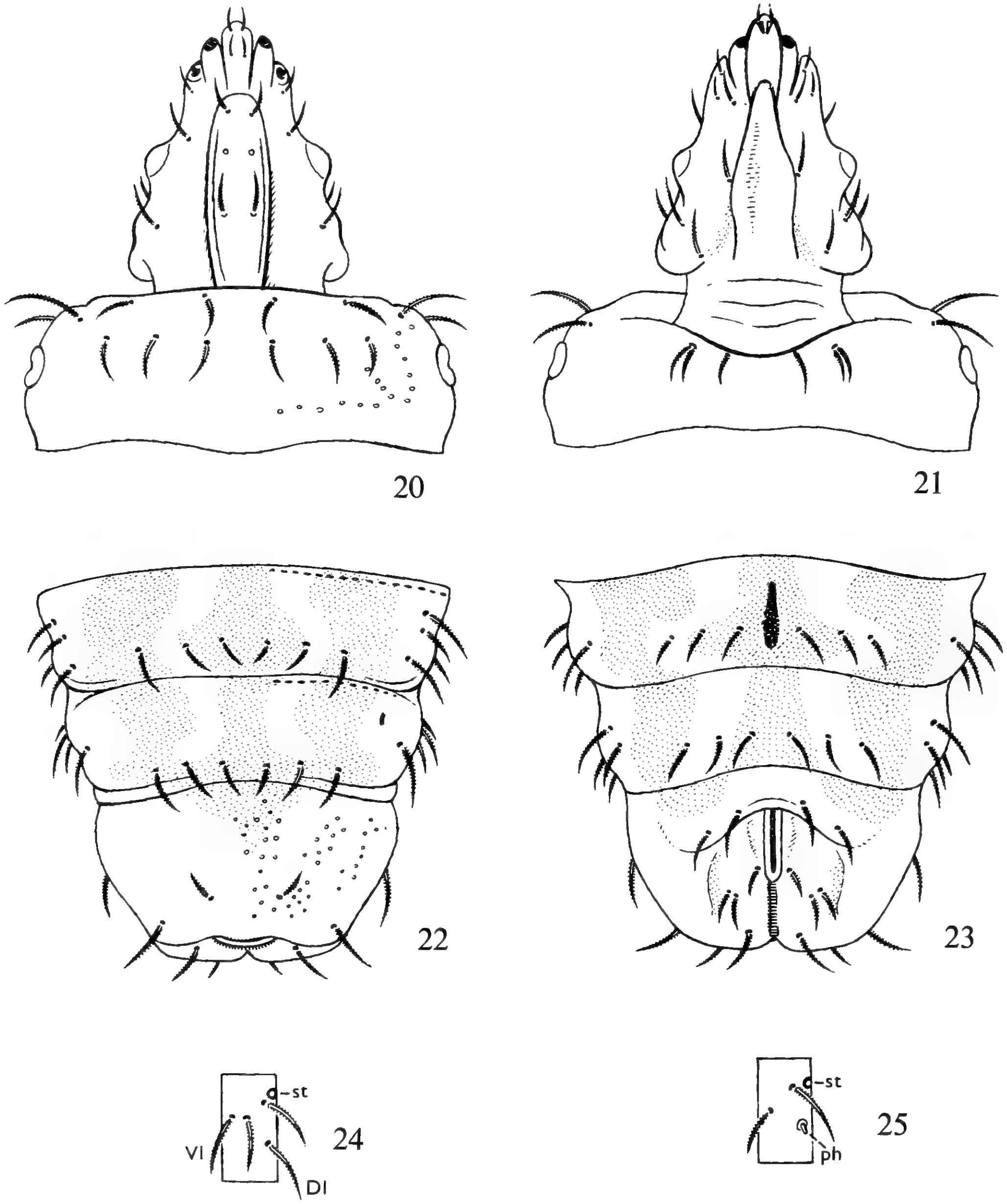
Diagnosis

A species of the *cingulatus* group with longitudinally striped mesonotum and a conspicuously spindle-shaped abdomen in both sexes.

Measurements: Body 11.2-12.5 mm, wing 11.8-12.2 mm.

Male (holotype). – Head hemispherical, with conspicuously protuberant white frontal callus (figs. 11-12). Eyes separated by yellow, sparsely black-haired frontal stripe being in its narrowest point about as wide as distance between outer margins of posterior ocelli. Postocular area narrowly protuberant in dorsal view. Postocular hairs fine and moderately long, in several rows. Antennae ochrous yellow, scape and pedicel black-haired. Pedicel with elongate process on inner side (fig. 16), annulation of flagellum barely visible. Arista in subapical position, bare. Bi-partite labellae of proboscis distinctly swollen, white in ground colour and with short white hairs. Posterior part of head deeply concave.

Thorax yellow in ground colour, with extensive



Figs. 20-25. *Ptecticus malayensis* sp.n., larval characters. – 20, head and first thoracic segment, dorsal view; 21, the same, ventral view; 22, last abdominal segments, dorsal view; 23, the same, ventral view; 24, scheme of setae on lateral wall of 6th abdominal segment (Dl, dorsolateral seta; st, larval spiracle; Vl, ventrolateral seta); 25, scheme of setae on lateral wall of abdominal segment 3 (ph, pupal respiratory horn; st, larval spiracle).

brown to blackish pattern. Mesonotum (fig. 13) with 3 broad black stripes reaching its posterior margin. Pleura predominantly yellow with several brownish to black spots in central part of anepisternum, anterior side and posterior corner of katepisternum, posterior half of katepimeron and anterior third of laterotergite. Also posterior margin of mediotergite broadly brownish. Thoracic pubescence short and mostly adpressed, yellow on pleura and predominantly brown to black on mesonotum and scutellum.

Wings shaded with grey, veins along anterior margin including discal cell yellow, other veins brown except for bases. Anterior cross-vein placed at basis of radial fork $R_{3-5,}$ M_3 not reaching wing margin. Dense microtrichia covering virtually the whole wing membrane, only wing base, alula and posterior cubital cell mostly bare. Squamae very narrow and inconspicuous, with brownish margin and yellow hairs. Halteres with yellow stem and blackish knob.

Legs yellow with extensive blackish pattern on hind pair. Both anterior pairs mainly yellow, including coxae, only apical half of mid-femora somewhat brownish. Hind coxae brownish on anterior side, hind femur mainly dark except for both ends. Also hind tibia chiefly brown but this darkening more pronounced along dorsal side and in mid-ring. Hind tarsi black but basal two thirds of basitarsus and last tarsal segment pale yellow.

Abdomen spindle-shaped, broadest behind middle, yellow with brownish black transverse bands on terga (fig. 15). First tergum yellow with a transverse brown spot in middle and following terga with relatively broad posterior margin and narrow anterior margin yellow. Venter yellow but more brownish in apical half. Genitalia (figs. 14, 17-19) brown, distinctly asymmetrical, although dorsal part only slightly so. Cerci pointed, with tips oriented ventrally (figs. 14, 17). Synsternum strongly asymmetrical in proximal half, dististyli almost hoodlike in ventral view (fig. 19). Aedeagal complex almost S-shaped in lateral aspect (fig. 14), right paramere conspicuously reduced (fig. 18).

Female. – As male but with broader wings and somewhat wider abdomen in apical half. Frontal stripe only slightly broader than in male, particularly in anterior half, white frontal callus distinctly bipartite and lower, antennae relatively larger. Colours of thorax, legs and abdomen virtually the same, only darkening of hind legs more extensive, leaving only bases of femora and knees yellow. Hind tarsi coloured as in male. Terminalia dark brown, cerci with two narrow black segments (fig.15).

Larva (and puparium). – Larvae on average stouter and longer than those of *P. longipennis,* often predominantly reddish brown, though dark pattern consisting of dark undulate longitudinal bands, especially in puparia, mostly distinct. Integument rough and sclerotised, with usual mosaic surface structure. Some cuticular cells forming inconspicuous pattern as in preceding species. Head (figs. 20-21, 33-34) prominent, strongly sclerotised, partly retracted into first thoracic segment, distinctly longer than wide and conspicuously flattened, rather subtriangular in dorsal view. Antennae very small and low, distinctly closer to eye prominences than in *P. longipennis,* apical segment barely prominent. Eyes conspicuously protuberant, posterolateral tubercles less distinct, not doubled as in *P. longipennis.*

Tracheal system as in larva of *P. longipennis,* including vestiges of larval spiracles and very small lateral pupal respiratory horns on abdominal segments 2-5. Sternal patch in middle of abdominal segment 6 drop-like to elongate oval, consisting of 90-116 cells (fig 23). Similar but much smaller and rounded sternal patch at posterior margin of sternum 5 formed by 17-20 cells. Anal segment (figs. 22-23, 35) almost round posteriorly, with a small incision in middle of distal margin. Opening of posterior spiracular chamber with arched and finely fringed posterior margin (-figs. 36-37). Anal slit distinctly emarginate, somewhat longer than one third of anal segment.

General scheme of chaetotaxy as in *P. longipennis* although setae relatively shorter and more pubescent, especially in marginal setae of anal segment. Anterior clypeofrontal setae inserted almost between eye prominence and tip of labrum (fig. 20). Configuration of setae on lateral wall of abdominal segments and ventral side of anal segment identical with those of preceding species and probably confirming generic characters in this way: 4 setae on lateral wall of abdominal segments 1 and 6-7, 2 setae on abdominal segments 2-5 (figs. 24-25) and 5 pairs of ventral setae on anal segment present (fig. 23). Length 10.0-13.4 mm, maximum width 3.6-5.0 mm (based on 2 larvae, 5 puparia and 3 puparial exuviae).

Discussion

The new species presumably belongs to the *cingulatus* species group as defined by Brunetti (1923). Three species of this group have dark longitudinal stripes on the thorax: *P. brevipennis* Rondani, *P. intensivus* Brunetti and *P. kambangensis* de Meijere. The first was redescribed by van der Wulp (1885) and Brunetti (1923). It is, in contrast to *P. malayensis* sp. n., characterized by the shining blue black frontal stripe and by much narrower and shorter stripes on the mesonotum, the black tibiae and bases of the basitarsi of the hind leg. *P. intensivus* is, according to the original description by Brunetti (1927), closely related to *P. brevipennis* and like that species should have a black frontal stripe. Moreover, it also differs in the coloration of the leg (the fore tarsi are partly black, only the basal third of the hind femur is darkened and the hind tarsi are completely black). *P. kambangensis* distinctly differs by the pleura being shining blackish

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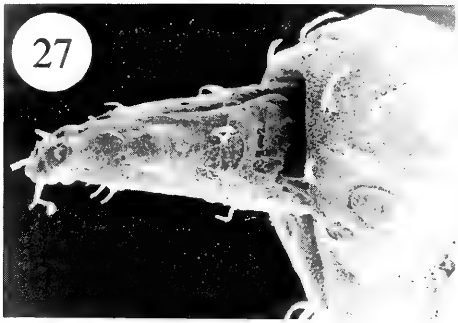

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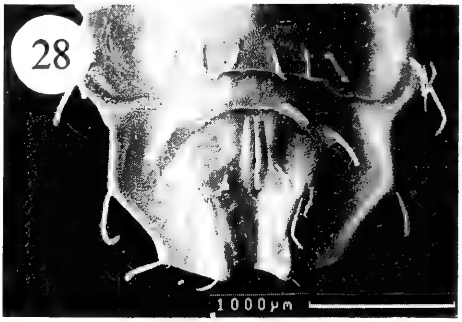

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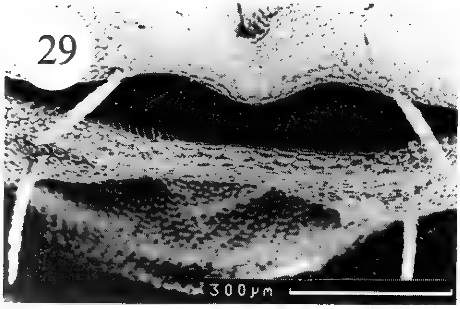

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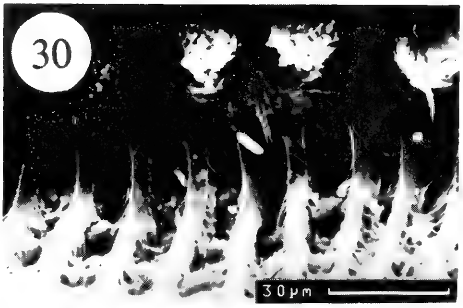

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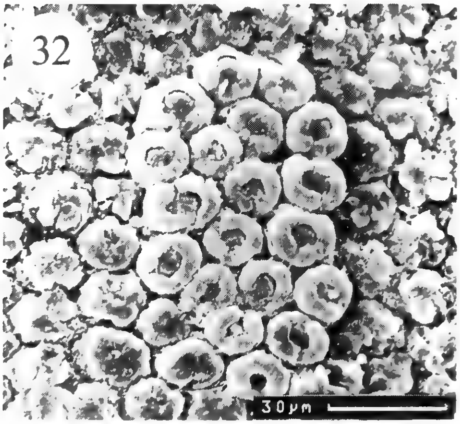


brown with a yellow band, and by the hind basitarsus, which is completely whitish as is the basis of the following tarsal segment.

From the other Oriental *Ptecticus* species only *P. tricolor* van der Wulp displays the longitudinally striped mesonotum. Brunetti (1923) considered this species to be an intermediate form with uncertain relationships. According to the original description and illustration (van der Wulp in de Meijere 1904) *P. tricolor* differs from the new species by the colouring of the legs (hind tibia and tarsi completely black) and abdomen (segments 2-4 entirely red).

The colour of the leg and partly also the male genitalia of the new species resemble the East Palaearctic *P. sinchangensis* Ôuchi redescribed and figured recently by Nagatomi (1975). However, this species does not have a striped mesonotum, and its male genitalia, including the well developed aedeagal complex, are symmetrical.

BIOLOGICAL NOTES

The larvae of *Ptecticus longipennis* were found in felled bamboo culms whose internodes – now lying in the horizontal position on the ground – had been sawn in such a way that the upper half formed a hinged lid that could easily be opened for inspection and than closed again. Two lateral slits, about 2 mm wide, provided access to the interior. The internodes were partly filled with water, and the larvae stayed in the moist part above the water surface (fig. 43). They appeared about two months after the culms had been felled. During the six-months study period larvae of *Ptecticus longipennis* were found only in three out of over one hundred internodes prepared in the described manner; moreover, these three internodes were adjacent to each other, i.e. the eggs were probably laid by the same female. This indicates that bamboo internodes are only an occasional habitat for the larvae of *Ptecticus longipennis.*

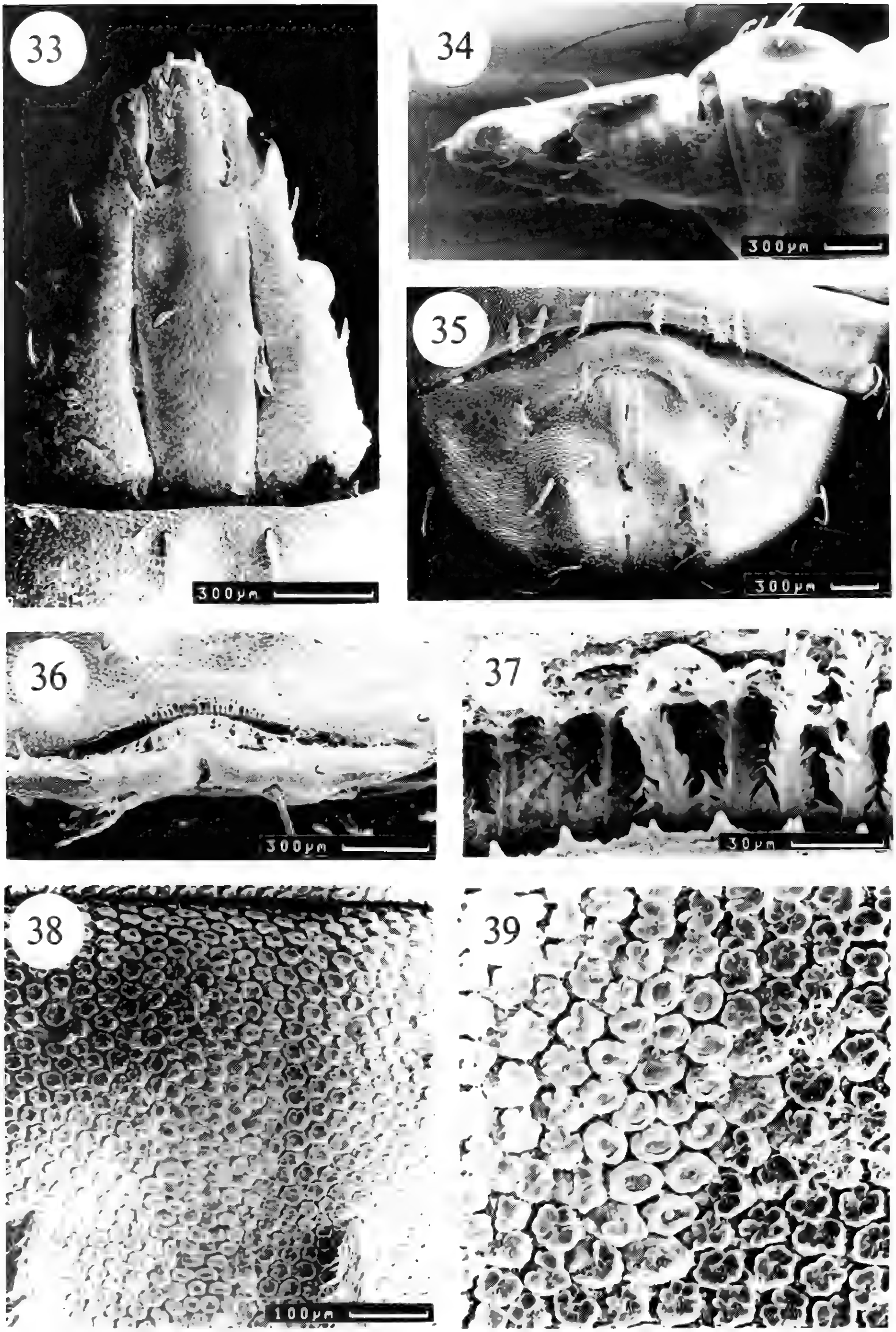
Ptecticus malayensis, in contrast, was found in bamboo more frequently. The larvae of this species were restricted to bamboo shoots that had died recently (fig. 40). Judging from the traces of insect attack found in the internodes, death of the shoots was probably caused by a weevil, *Cyrtotrachelus* sp. (Coleoptera, Curculionidae), adults of which had been observed on bamboo shoots. The dead shoots were 2.5 m to 6 m high. At the time of felling the lower internodes were still green while the upper part had turned dark brown and begun to decay. In the lower part the rotten section (c. 1 m from the top) in some cases a small hole (diameter c. 1-2 mm) was found which led into the interior of the culm. Beginning at this hole a groove in the inner wall led upwards, piercing the node septa (usually c. 10-15) and gradually becoming wider and deeper (fig. 42). At several points along this depression there were holes through the internode wall to the outside which were covered by the culm sheets and therefore hidden from outside view. Just below the shoot tip there was no segmentation into internodes. In this section, which was moist and gave off a putrid smell, the culm sheets had been penetrated with a circular opening c. 1.5 cm in diameter. In one case 2 grooves and circular openings were found in the same shoot.

Apparently the *Cyrtotrachelus* larva had worked itself up all the way to the nutritious apical meristem from the small entrance hole bored by the female, feeding and grooving along the way. After feasting on the apical meristem the fully grown larva then probably broke to the outside tu pupate in the soil, as described by Witt (in Beeson 1941: 209) for *Cyrtotrachelus longipes* F.

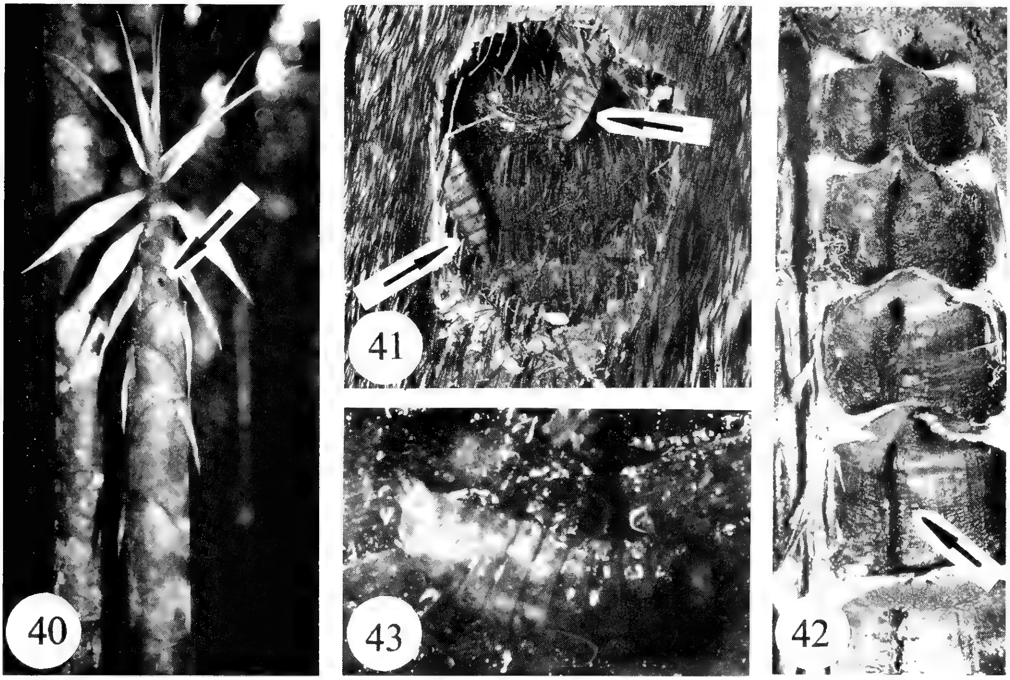
Ptecticus malayensis probably uses a fresh *Cyrtotrachelus* emergence hole to enter the bamboo shoot. Although all shoots attacked by *Cyrtotrachelus* died, there was probably still some limited growth after departure of the weevils as indicated by a shift of the holes in the different culm sheets relative to each other (fig. 41). Consequently, at the time of felling there was no longer a contiguous opening all the way to the interior of the culm. The larvae of *Ptecticus malyensis* were found in all internodes connected by holes. In the lower internodes with punctured septa water usually accumulated, and dead stratiomyid larvae were found there on several occasions. Pupation of *Ptecticus malayensis* took place in the upper section of the shoot, behind the *Cyrtotrachelus* escape hole (fig. 41). Probably the freshly eclosed flies had to sqeeze themselves past the sheets to escape from the bamboo. The adult flies left before the rotten shoot tips fell to the ground. Five out of twelve investigated bamboo shoots were occupied by *Ptecticus malayensis,* with a maximum number of 22 larvae per shoot. In two shoots larvae of *Solva completa* de Meijere (Xylomyidae, Diptera) were found together with *Ptecticus malayensis.*

Only a few literature accounts on larvae of *Ptecticus* are available. Lindner (1928), who superficially de-

Figs. 26-32. *Ptecticus longipennis,* larval structures (SEM-photographs). – 26, head and fore margin of first thoracic segment, dorsal view; 27, the same, lateral view; 28, last abdominal segments, ventral view; 29, opening to spiracular chamber, posterior view; 30, short pennate setae on ventral lip of spiracular chamber opening; 31, sternal patch on abdominal segment 6; 32, sternal patch on abdominal segment 5.



Figs. 33-39. *Ptecticus malayensis* sp.n., larval structures (SEM-photographs). – 33, head and fore margin of first thoracic segment, dorsal view; 34, head and two thoracic segments in lateral view; 35, last abdominal segments, ventral view; 36, opening to spiracular chamber, posterior view; 37, pennate setae on lips of spiracular chamber opening; 38, sternal patches on abdominal segment 6; 39, sternal patch on abdominal segment 5.



Figs. 40-43. Habitat of the larvae of *Ptecticus malyensis* sp.n. and *P. longipennis*. – 40, dead shoot tip of *Gigantochloa scortechinii*. The arrow points to the emergence hole of the weevil larva, *Cyrtotrachelus* sp., which was probably used by *P. malayensis* to enter the hollow interior of the shoot; 41, emergence hole of *Cyrtotrachelus* sp. after removal of several culm sheets. Two puparia of *P. malayensis* are visible (arrows). As can be seen, the openings of the culm sheets have shifted relative to each other; 42, the hollow interior of the shoot. Arrow points to a groove made by the larva of *Cyrtotrachelus* sp.; 43, larva of *Ptecticus longipennis* on the moist interior wall of an internode laying on the ground.

scribed a larva of *P. testaceus* Fabricius from South America, pointed out that larvae were found in decaying cactuses, oranges and lemons. Engel & Cuthbertson (1939), who examined a larva of African *P. posticus* Wiedemann, found the larvae in the semi-liquid mass of decaying *Conopharyngia johnstoni* Stapf. (Apocynaceae) fruits together with other dipterous larvae.

Larvae of North-American *Ptecticus trivittatus* (Say) were collected from a corn compost pile, decaying tomatoes, garbage and fruit, from watermelon rinds, rotting paper and a fungus (McFadden 1967).

Our observations suggest that *P. longipennis* and *P. malayensis* are unspecialized phytosaprophages. These findings conform to the previously reported larval mode of life within the subfamily Sarginae: saprophagy with some tendency to coprophagy as known in many European species.

RELATIONSHIPS OF *Ptecticus* LOEW

Only one reliable character separates the genus *Ptecticus* Loew from the related *Sargus* Fabricius, viz. the shape of the pedicel projecting into the elongate process on the inner side of the antenna. However, this character may be indistinct in some species, and its generic relevance therefore seems disputable. A comparison of the structure of the male genitalia is not possible for all species of the two genera because it has not been included in all descriptions. It may nevertheless be stated that the differences found among some *Ptecticus* species seem to be more pronounced than those among the European genera of the Sarginae. This fact indicates the necessity of a revision of the generic concept of *Ptecticus*.

Judging from the description of the larva of North-American *P. trivittatus* (Say) by McFadden (1967) and the descriptions of the two larvae presented here, *Ptecticus* appears, on the other hand, well separated from the genera of Sarginae in the larval stage. First of all, in addition to a long and slender sternal patch on abdominal segment 6, a small and rounded sternal patch on abdominal segment 5 is developed. Relatively short setae on the head as well as on the anal segment, the configuration of setae on the lateral wall of abdominal segments and the presence of five pairs of ventral setae on the anal segment are cosidered diagnostic generic characters. So, the known larvae of Sarginae may be distinguished according to the following identification key:

1. Setae on anal segment shorter than length of penultimate segment 2
– At least some setae on anal segment longer than penultimate segment 4
2. Eye prominence anterior to protruding lateral tubercle (according to McFadden 1967) .... *Merosargus* Loew
– Eye prominence on protruding lateral tubercle 3
3. Abdominal segment 5 without sternal patch, four pairs of ventral setae on anal segment, 2-4 setae on lateral wall of abdominal segment 1, 6-7, and always one seta less or equal number of setae on abdominal segments 2-5 .... *Sargus* Fabricius
– Abdominal segment 5 with a small but distinct sternal patch in addition to sternal patch on segment 6, five pairs of ventral setae on anal segment, four setae on lateral wall of abdominal segments l, 6-7, and only two setae on abdominal segments 2-5 (i.e. two setae less) ... *Ptecticus* Loew
4. Anterior labral setae short, apical lobes on anal segment prominent .... *Chloromyia* Duncan
– Anterior labral setae strikingly long, apical lobes on anal segment less distinct .. *Microchrysa* Loew

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THE ODONATA OF SULAWESI AND ADJACENT ISLANDS

Part 3. The genus *Macromia* Rambur (Corduliidae)[1]

Tol, J. van, 1994. The Odonata of Sulawesi and adjacent islands. Part 3. The genus *Macromia* Rambur (Corduliidae). – Tijdschrift voor Entomologie 137: 87-94, figs. 1-25, table 1 [ISSN 0040-7496]. Published 15 July 1994.

The *Macromia* species of Sulawesi (Celebes) are detailed, and a key to the species is provided. One new species, *Macromia celebica* sp. n., and the hitherto unknown female of *M. irina* Lieftinck are described. The occurrence on Sulawesi of *M. moorei fumata* Krüger is considered doubtful. The phylogenetic relationships of the Indo-Australian species of *Macromia* are analysed. The Sulawesi species are shown to have a sister group relationship to the monophyletic group of the Papuan species. *M. chalciope* from Halmahera is considered the most recently evolved taxon. These results are compared with recent reconstructions of the geological history of the region.

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Key words. – Odonata; Corduliidae; *Macromia*; new species; phylogeny; biogeography; Indonesia; Sulawesi; New Guinea.

[1] Part 2: Zoologische Mededelingen [1987] 61 (13): 160-176.

Hitherto, only two species of the rheophilic dragonfly genus *Macromia* Rambur have been mentioned from Sulawesi (Celebes), viz. *M. moorei fumata* Krüger and *M. irina* Lieftinck (Lieftinck 1950: 714-716). Specimens of *Macromia* that were recently collected in the southern part of Central Sulawesi, appear to belong to a species as yet undescribed. The number of species reliably recorded from this island, however, remains two, since the only record of *Macromia moorei fumata* must be regarded doubtful (see below).

The dragonflies of the virtually cosmopolitan genus *Macromia* are remarkable insects in many respects. With more than 120 species, several of which polytypic, *Macromia* is one of the largest genera of the Anisoptera. They are especially speciose in the tropical areas of the Old World. In Europe (one species), North America (nine species) and Australia (two species), they are far less numerous. All other species are confined to Africa and Southeast Asia.

Our present knowledge of the *Macromia* species of Southeast Asia is mainly based on the studies of Krüger (1899) and especially Lieftinck (1929, 1950, 1971a; see also 1954).

Due to their elusive behaviour, most species are poorly represented in collections. In fact, many are only known from the type series, often consisting of one specimen only. Most species are fierce flyers. The larvae seem to be quite stenotopic, so that larvae as well as adults can only be found in very restricted parts of streams. Notwithstanding their strong flying capabilities, many species have small ranges, apparently due to the fact that they seldom fly far from their breeding sites.

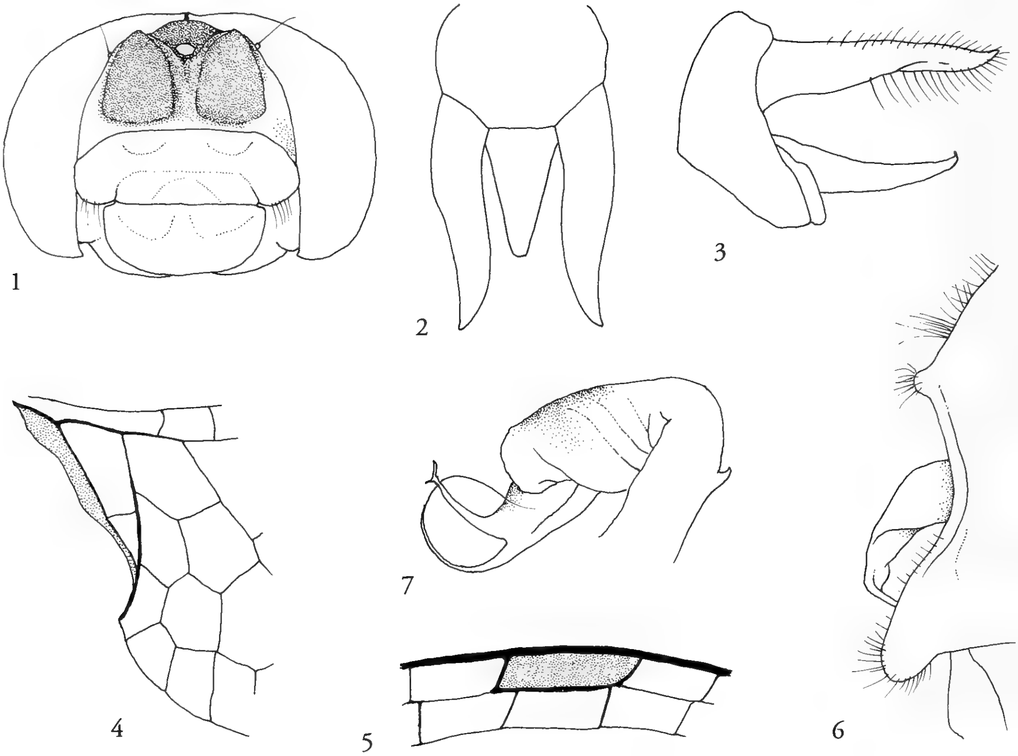
In the present paper I describe the new species from Sulawesi, provide some new observations on *M. irina*, and give a key to species recorded from Sulawesi. Finally, after having analysed the affinities of the Sulawesi species to those of the Oriental and the Papuan regions, I propose a hypothesis for a scenario of the biogeographical history of this genus in the Indo-Australian region.

SYSTEMATIC PART

Key to the *Macromia* species of Sulawesi

1. Outer margin of superior appendage of male with well-developed tooth-like tubercle approximately halfway (cf. fig. 18); vertex bilobed (cf. figs. 22, 23); thorax green with metallic lustre .... *M. moorei fumata*
   [Occurrence on Sulawesi doubtful].

– Outer margin of superior appendage of male



Figs. 1-7. *Macromia celebica* sp. n. – 1, Head in frontal view; 2, Anal appendages of male, dorsal view; 3, Idem, left lateral view; 4, Base of right hind wing, male; 5, Pterostigma of right fore wing; 6, Accessory genitalia of male, left lateral view; 7, Fourth segment of penis, left lateral view.

somewhat curved inwards, in some specimens with very small teeth along the margin, but especially in dorsal view not a conspicuous extero-lateral tooth (figs. 2, 9); vertex dorsally smoothly rounded, without a paired tubercle (figs. 1, 8); thorax green or brown 2

2. Appendix inferior distinctly shorter than superiors (figs. 2, 3); coloration at least on synthorax green with greenish blue metallic shine; frontal side of head brownish black .... *M. celebica* sp. n.

– Appendix inferior approximately as long as superiors (figs. 9, 10); coloration without any indication of metallic lustre, but body generally orange-brown; head orange-brown with some middle-brown parts, but without conspicuous brownish black frons .... *M. irina*

Macromia celebica sp. n.
(figs. 1-7)

Type material. – Holotype ♂. Indonesia. Southern Central Sulawesi. Puncak Palopo. 600-1000 m. October 1993. Leg. Yohan R. (JvT 6007) (MBBJ). – Paratypes: 2♂, same data (JvT 5930-5931) (RMNH).

Description. – A medium-sized *Macromia*, with green thorax and dark abdomen.

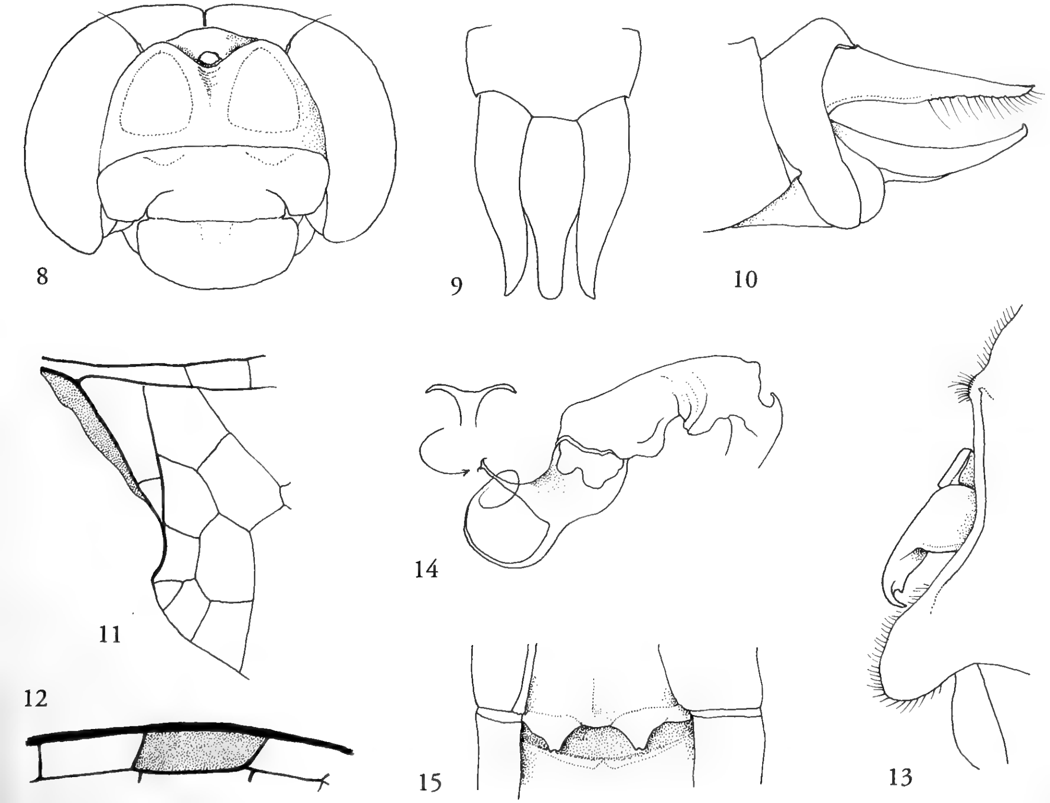
Male. Head with labium, labrum and clypeus orange-brown, especially clypeus without yellow markings, labrum with outer corners darker. Pyramidal processes of frons high and subacute (fig. 1); frontal side very flat, more or less triangular, with very fine transverse striae from upper-inner to lower-outer corner of each side; frontal and upper parts of frons shiny black with blue metallic lustre; frons against eyes orange-brown as lower part of face; vertex black with fine punctation, the paired dorsal tubercles hardly discernable, the lateral angles tapering into small projecting cones on top of which the lateral ocelli are situated (shape as in *irina*; *westwoodii* has somewhat more pronounced dorsal tubercles), covered with thin setae. Occiput shiny black with very fine punctation. Antennae brownish black.

Thorax. Brilliant metallic green, densely covered with long and slender creamish white setae; antehumeral stripe yellow and distinct, somewhat tapering dorsally, extending dorsally to ca. three-seventh of mesepisternum, ventrally continuing over mesinfraepisternum; yellow stripe over spiracle rather narrow, tapering in width dorsally and nearly reaching the upper margin of episternum. Pale stripe on lateroventral part of metepimeron covering anterior anterior half (stripe absent in *chalciope*). Legs long and slender, hind femur 10 mm, reaching to base of posterior hamulus, colour brown, keel on fore leg very short, ca. 1 mm, not reaching the apex, middle tibia without keel, hind tibia with long keel from ca. 2 mm from base of tibia to less than 1 mm from its apex.

Wings relatively short, fore wing with 17-18 Ax, 8 Px; hind wing with 11 Ax, 11-13 Px; fore wing with 7 Cux, hind wing with 5 Cux (incl. subtriangle); anal loop 7-9 cells without central cell; anal triangle relatively short (fig. 4; cf. *M. chalciope*, fig. 19); discoidal triangle of hind wing very narrow; pterostigma (fig. 5) reddish brown, anterior side ca. 2.0 mm.

Abdomen brownish black with some blue-green metallic lustre especially on first few segments; yellow spot on anterior side of segment 7; general shape anteriorly slender, especially segment 7-9 significantly widened; tergites ventro-anteriorly somewhat paler, dark or middle-brown. Spot on segment 7 consisting of a complete ring covering anterior one-fourth of segment, medio-dorsally extending posteriorly for another one-eighth segment length and ca. one-third the segment's width. Segment 10 rather short, middorsal process not spine-like, but consisting of a low triangular-shaped subterminal tubercle. Appendages (figs. 2-3) with superiors in dorsal view rather slender, significantly longer than inferior, basal two-fifths rather straight, then innerside slightly tapering posteriorly and outerside strongly tapering, caudalmost part somewhat curved outwards; no trace of a lateral tubercle on superior appendage.

Secondary genitalia: anterior side margin of tergite 2 with dense setae, a mixture of strong and soft setae, longer than in *irina*; also tuft of setae on ventral tu-



Figs. 8-15. *Macromia irina* Lieftinck. – 8, Head in frontal view; 9, Anal appendages of male, dorsal view; 10, Idem, left lateral view; 11, Base of right hind wing, male; 12, Pterostigma of right fore wing; 13, Accessory genitalia of male, left lateral view; 14, Fourth segment of penis, left lateral view; 15, Valvula vulvae, female.

bercle of tergite longer; genital lobe directed posteriorly, elongate, and tapering towards the top, but tip not acute; posterior hamulus glossy brown, basally coloured brown, the straight outer part pale brown, and the endhook reddish brown, curved strongly (90°) inwards, endhooks in ventral view slightly diverging, the tip reaching ca. two-thirds of genital lobe.

Measurements. – Abdomen, incl. appendages 48 (paratypes 46-48) mm, hind wing 42 (paratypes 42-43) mm

Female. – Unknown.

Differential diagnosis. – Differs clearly from the only other Sulawesi *Macromia* by the presence of green metallic lustre, the black markings on the frons, the presence of an antehumeral stripe; structurally the short inferior appendage, and shape of abdominal segment 10 are diagnostic. Both Sulawesi species can be distinguished from other Indo-Australian *Macromia* by the intermediate sized pterostigma, the very narrow discoidal triangle of the hind wing, and especially the rounded (not bilobed) vertex. Also, the superior appendages lack an extero-lateral tooth, but are not particularly slender. The Papuan *Macromia* have extremely slender superiors with or without an extero-lateral tooth (fig. 20), while the Oriental species have rather solid appendages with a more or less conspicuous extero-lateral tooth (fig. 18).

Remarks. – Although this species differs in many respects from *M. irina*, I consider it the sister species of *M. irina*. This view is based on shared, presumably apomorphous, character states in the structure of vertex and superior appendage of male (see below).

Distribution. – Only the southwestern part of Central Sulawesi. Collected between 600-900 m.

Macromia irina Lieftinck
(figs. 8-15)

Macromia irina Lieftinck, 1950: 714-716. Holotype male 'S Celebes, foot of Mt Lompobatang, Borong Rapao, 800 m, 12.viii. 1949, leg. A. Diakonoff' in RMNH [examined]. – Lieftinck 1971b: 94 [note on type]; Askew et al. 1989: 118 [records Northern Sulawesi, Dumoga Bone National Park].

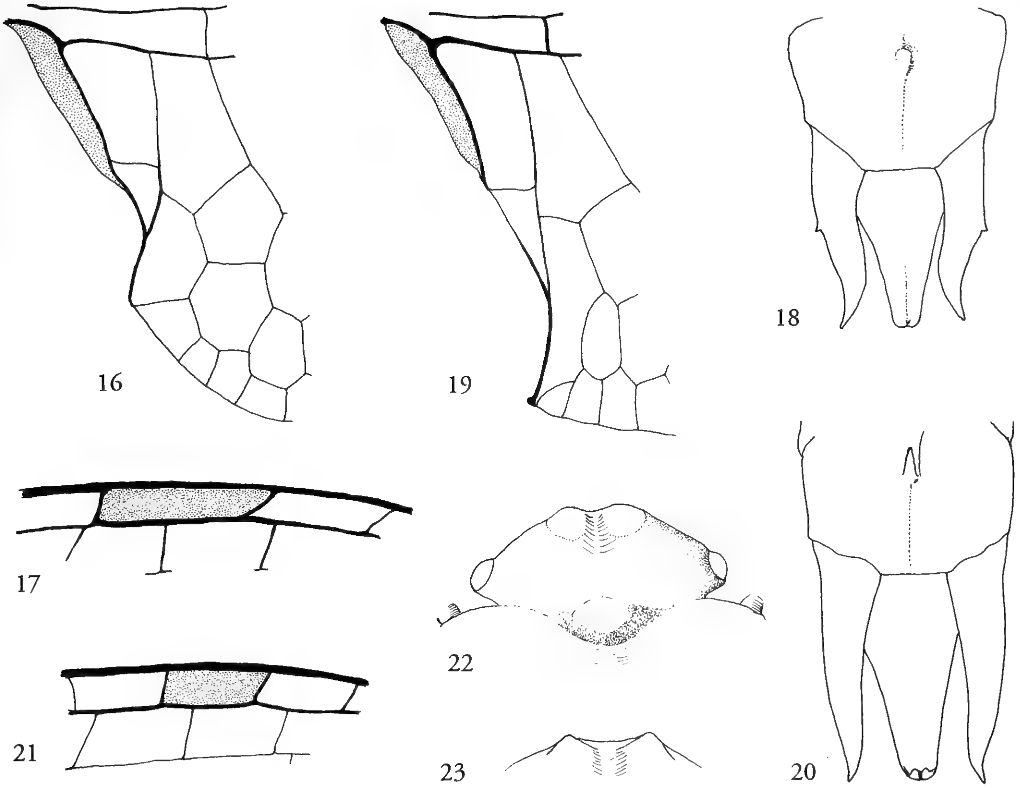
Diagnosis. – Unmistakable among Indo-Australian *Macromia*: head, thorax and abdomen brown without any metallic lustre. Structural characters: wing base with anal angle sharp, but not angulated (fig. 11); the anal triangle rather short (long in *moorei fumata*), membranula ending circa halfway between anal crossvein and base of anal triangle; pterostigma rather short (fig. 12), circa twice as long as high (more than three times in *moorei fumata*); anal appendages of male with superiors with rather smooth outer margin, without any indication of tooth (figs. 9-10) (cf. *moorei fumata* and *westwoodii*); inferior appendage approximately as long as superiors (clearly shorter in *celebica*).

Description. – Little can be added to the extensive description of the male in Lieftinck (1950). Live colour of eye dark green. Since Lieftinck did not provide any illustration, I have added here drawings of the head, wing base, anal appendages and secondary genitalia (figs. 8-14). The up to now undescribed female was collected in Southeast Sulawesi.

Female. – General coloration as the male, and structurally very similar to the male, although more robust. Head and thorax not differing from male. Wings somewhat broader, especially at base; membranula fully opaque white or only greyish in most narrow part; rusty brown base of wings more extensive than in male, in costal and subcostal area of fore and hind wing reaching to first Ax or even somewhat beyond; some less extensive rusty brown at base of medio-anal space; Arculus at Ax2 in fore wing and just beyond Ax2 in hind wing; fore wing 16-17 Ax, 9 Px, 7 Cux; hind wing 10-12 Ax, 11 Px, 5 Cux. Abdomen of the coloration ('Mikado-brown') as male; segment 1 dorsum dark brown and lateral parts brown; segment 2 brown, somewhat darker above than laterally, as the male with two narrow transverse yellow streaks, one over transverse carina halfway abdominal segment and the other pair more oblique running just before posterior margin; segment 3 anteriorly brown to transverse carina, somewhat darker above, posteriorly dark brown except for space just before segment 4; segments 4-7 similar to segment 3, but dark patch anterior to transverse carina gradually increasing in size, and posterior paler brown ring also increasing from segment 4 to 7; segment 8 brown with dorsal carina black and some darkening against dorsal carina; segment brown, dorsal carina dark; segment 10 brown; appendages middle brown, rather short, acute. Valvula vulvae short, approximately four times as wide as long, with wide triangular emargination, the tips just bifid, somewhat curved inwards (fig. 15).

Other material examined. – Sulawesi Tenggara. S of Sanggona: Gunung Watuwila. Sunggai Lalonduwasi near Centipede camp. c. 1050 m. 2-4 Nov 1989 (J. van Tol) 3♂ 1♀ (JvT 5932-5935); Sulawesi Tengah, ca. 10 km WNW Palopo near Tojambu. 800-1000 m, c. 2°56'S 120°07'E, Jul/Aug 1991 (Yohan R.), 1♀ (JvT 5936), all in RMNH. I have also studied one of the specimens collected by Askew et al. (1989): 1♂, in RSME.

Remarks. – I collected this species myself along a small, shaded stream in a steep valley in the Mengkoko mountain area. The insects appeared immediately after sunrise, and were active for approxi-



Figs. 16-23, *Macromia* species. 16-18, 22, *M. westwoodii*; 19-21, 23, *M. chalciope*. – 16, 19, Base of right hind wing, male; 27, 21, Pterostigma of right fore wing; 18, 20, Anal appendages of male, dorsal view; 22-23, Vertex in frontal view (fig. 23 dorsal-most part only).

mately one hour. Males as well as females flew low over the water up and down the stream, more or less in a straight line. With a rather slow and small wing beat, they were not extremely fast. The specimens could be collected at a site where a big log of more than one meter diameter was laying in the stream. *Macromia* specimens crossed the log at just a few centimeters height to return immediately to the water surface. The female was caught on a dark day at 16.30 h, i.e. 1.5 hours before sunset.

Macromia moorei fumata Krüger

Macromia fumata Krüger, 1899: 333-335 (Java) [not examined].

Macromia moorei fumata. – Lieftinck 1950: 678 (key, mentioned Celebes); Lieftinck 1954: 119, 185 (references, geographical distribution); Lieftinck 1971a: 29 (geographical distribution).

Remarks. – I have been able to check the specimen (in SMFD) at which Lieftinck's notice of this taxon on Sulawesi was based. Although this specimen can be assigned to *M. moorei fumata* without doubt, I consider its occurrence on Sulawesi still doubtful. The 'Lompo Battau' labels of Fruhstorfer have on many occasions proved to be incorrect (see van Tol 1987: 163). *M. moorei fumata* is rather common on Java, where Fruhstorfer also collected during his long journey through the former Dutch Indies.

Material examined. – Lompa Battau, S. Celebes, III. 1896 (H. Fruhstorfer) '16764' (in green ink) 1 ♂ [label in Ris' hand] [identified by M.A. Lieftinck as *Macromia moorei fumata*, Jan. 1928].

PHYLOGENETIC RELATIONSHIPS

Introduction

The so-called Papuasian representatives of *Macromia* share at least four characters (Lieftinck 1952, 1971a), viz., an exceptionally small discoidal triangle of the hind wing, a minute pterostigma of ca. one mm, a sharply acute anal angle of the hind wing in

Table 1 Character matrix for taxa of *Macromia* of the Indo-Australian archipelago.

(1)	extero-lateral tooth superior appendage	12	(present/absent)
(2)	vertex	12	(bilobed/rounded)
(3)	hamulus	12	(shorter/longer lobus)
(4)	superior appendages	12	(normal/very slender)
(5)	pterostigma	123	(long/intermediate/ very short)
(6)	postclypeus	12	(unicolorous/yellow markings)
(7)	antehumeral stripe	12	(present/absent)
(8)	anal angle	12	(sharp/angulate)
(9)	discoidal cell	12	(wide/narrow)
(10)	general coloration	12	(green/brown)
(11)	dorsal spine abdominal segment 10	123	(slender/absent/broad)
(12)	curvature superior appendages	123	(curved inward/outward/straight)

Character	1	2	3	4	5	6	7	8	9	10	11	12
Species												
amymone	1	1	2	2	3	2	2	2	2	1	2	2
celebica	2	2	1	1	2	1	1	1	2	1	2	2
chalciope	3	1	2	2	3	1	1	2	2	1	1	3
irina	2	2	1	1	2	1	2	1	2	2	2	2
melpomene	1	1	2	2	3	1	2	2	2	1	1	3
moorei fumata	1	1	1	1	1	1	2	1	1	1	2	1
terpsichore	3	1	2	2	3	2	1	2	2	1	2	3
westwoodii	1	2	1	1	1	1	1	1	1	1	3	2

the male, and long and slender genital hamules in the male. Lieftinck (1971a: 30-32) distinguishes three groups among the Papuan *Macromia* species, viz. *M. terpsichore*, *M. melpomene*, and *M. chalciope*, with the last one consisting of one species only.

The species assigned to these groups, which the exception of *viridescens* described from Cape York (Australia), are confined to the islands of New Guinea (*astarte* Lieftinck, *celaeno* Lieftinck, *eurynome* Lieftinck, *melpomene* Ris, *terpsichore* Foerster, *viridescens* Tillyard (= *amymone* Lieftinck)), the Bismarck Archipelago (*lachesis* Lieftinck), Waigeu (*euphrosyne* Lieftinck, *sophrosyne* Lieftinck) and Misool (*hermione* Lieftinck). *M. chalciope* Lieftinck is restricted to Schouten Is, and the Moluccan islands of Halmahera and Bacan (Lieftinck 1971a). No species of *Macromia* have been mentioned from any of the other Moluccan islands up to now. According to Lieftinck (1952: 460) *M. chalciope* can be considered 'an immediate derivative of the eastern cluster', i.e. that the sister-species of *chalciope* could be discovered among the species of New Guinea and adjacent islands.

The Malay peninsula and the Greater Sunda Islands are inhabited by 15 species of *Macromia* (see Lieftinck 1971a: 29). Although Lieftinck (1929) attempted to distinguish species groups in the western Malesian species, this author (1950: 716) had to admit that the groups had an artificial character. Variation in morphology among the species of western Malesia is more prominent than that among the Papuan representatives.

Finally, the Philippine islands are inhabited by at least one endemic species, viz. *M. negrito* Needham & Gyger from Luzon. The widespread *M. cincta* is reported from Palawan (Lieftinck 1929: 92), and Tawi Tawi (Lieftinck 1974), while also *M. gerstaeckeri* may

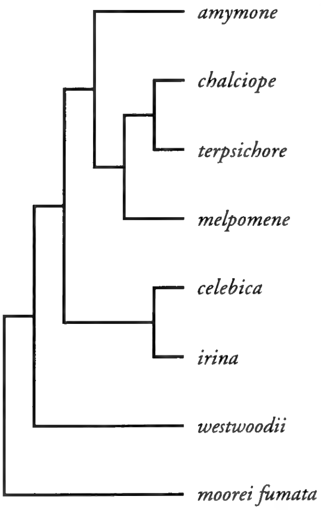


Fig. 24. Tree for *Macromia* species of the Indo-Australian archipelago.

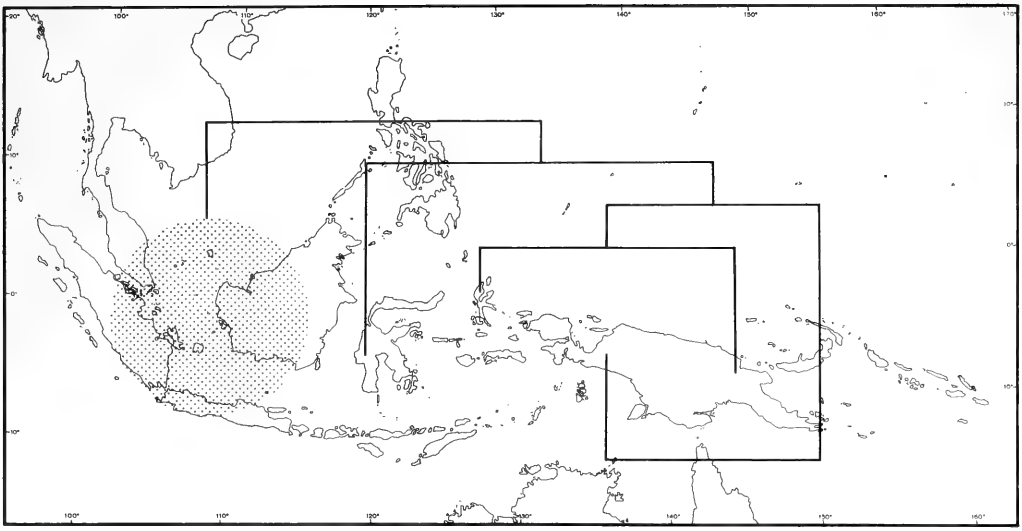


Fig. 25. Phylogenetic relationships of *Macromia* species (groups) represented on the map of Malesia.

occur in the Philippines (Lieftinck 1971a: 29).

I present here the results of a preliminary investigation of the phylogeny of the *Macromia* of the Indo-Australian region, mainly based on the characters used by Lieftinck to establish his Papuan species groups, or to distinguish the Oriental and Papuan groups. As outgroups I have added *M. moorei fumata* Krüger and *M. westwoodii* Selys, both considered closely allied to *M. irina* (Lieftinck 1950). For the present study only a limited number of the Papuan species have been included. Unfortunately, *M. negrito* Needham & Gyger from Luzon, was not available for study. A more extensive phylogenetic study, involving more of the Oriental as well as the Papuan species, has to wait for the future.

Methods and results

The matrix (table 1) was analysed with PAUP, version 3.1.1 (Swofford 1993), using 'exhaustive search'. *Macromia moorei fumata* was designated as outgroup, but the results appeared to be similar when *M. westwoodii* was selected as such. The analysis resulted in one tree of 20 steps (CI=0.800, RI=0.818).

This tree (fig. 24) shows that all Papuan species form a monophyletic group, with the Sulawesi species as sister group. The Papuan groups as defined by Lieftinck (1971a) are not corroborated by the present analysis. It is of interest to notice the sistergroup relationship of *M. terpsichore* from NE New Guinea, and *M. chalciope* from Halmahera.

Homoplasies in the present tree expecially occur in two non-structural characters, viz. character 7 (antehumeral stripe) and to a lesser extent character 6 (postclypeus).

Discussion and biogeography

The results of the phylogenetic analysis partly confirm earlier suggestions by Lieftinck on relationships among Indo-Australian *Macromia* species. Lieftinck (1950) considered *M. irina* from Sulawesi closely related to *M. moorei* and *M. westwoodii*, both rather widespread in Southeast Asia, including Borneo. The rather solid build of the superior appendage, in combination with the absence of an extero-lateral tooth, ranks the Sulawesi representatives in an intermediate position between the Oriental and the Papuan species. This intermediate position can also be recognized in the shape of the pterostigma.

The rather distant relationships of the Sulawesi and Halmahera species are of interest in a biogeographical context. Although the geological history of Wallacea and Halmahera is still under debate (e.g. Daly et al. 1991, Honza 1991), there is general agreement that there is no shared history for the North Moluccas (Halmahera) and Sulawesi. Reconstructions prior to 10-15 million years ago (Ma) are highly uncertain because of the very complicated plate movements. In the reconstruction of Daly et al. (1991) (see also Nichols & Hall 1991) Halmahera was formed at the margin of the Pacific and the Philippine plates, north of New Guinea, with a westward progression from c. 5 Ma to its present position. At least some parts of

Sulawesi have a much longer (65 million years) history above sea level on a far more western position. In other words, from approximately 60 to 5 Ma, the Oriental region + Sulawesi have shared (in some respects) a common history, while Halmahera shares its history mainly with New Guinea. The close contact of the Oriental and Papuan region is more recent than 5 Ma.

Given these phylogenetic relationships, and our present knowledge of the geological history of the area, the following historical scenario may be outlined. All *Macromia* species in the Indo-Australian region originate from an Oriental ancestor. The ancestor of the Sulawesi + Papuan species groups possibly inhabited Sulawesi, while the ancestor of the Halmahera *M. chalciope* + New Guinea *M. terpsichore* species groups apparently lived in north(eastern) New Guinea. The occurrence of two relatively remotely allied species on Sulawesi and Halmahera can be attributed to the westward movement of Halmahera during the last ten million years.

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THE GENUS *DIPSEUDOPSIS* WALKER FROM ASIA (TRICHOPTERA: DIPSEUDOPSIDAE)

Weaver, J. S., III & H. Malicky, 1994. The genus *Dipseudopsis* Walker from Asia (Trichoptera: Dipseudopsidae). – Tijdschrift voor Entomologie 137: 95-142, figs. 1-55. [ISSN 0040-7496]. Published 15 July 1994.

The genus *Dipseudopsis* Walker from Asia is revised, and a phylogeny of Hydropsychoidea is provided showing the relationships of its family taxa and the genera of Dipseudopsidae. Presently 36 Asian species of *Dipseudopsis* are recognized, having a distribution including Pakistan, India, Sri Lanka, Nepal, Bangladesh, Burma, Thailand, Cambodia, Vietnam, China, Japan, Philippines, Malaysia and Indonesia, including Sumatra, Java, Borneo, and Sulawesi. Six new species are described, *Dipseudopsis adiaturix* sp. n., *D. flinti* sp. n., *D. lucasi* sp. n., *D. malaisei* sp. n., *D. martynovi* sp. n., and *D. schmidi* sp. n., and one new subspecies, *D. robustior andamanensis* ssp. n. The identities of several problematic species are resolved, with 16 species names recognized as new junior synonyms (cf. species checklist p.102). *D. nervosella* Ulmer stat. n. is elevated from former subspecies status. New descriptions are provided for all species, including figures of the male hind mesoapical tibial spur (the modified spur), the male genitalia, and other notable characteristics of the head, thorax and wings, except two species recognized as nomina dubia, *D. onychophora* Navás, and *D. orientalis* (Navás). New lectotypes are designated for *D. contorta* Banks, *D. morosa* Banks and *D. triclavata* Martynov. A pictorial atlas is provided for rapid species identification. The genus *Eodipseudopsis* Marlier is removed from the Dipseudopsidae.

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Key words. – Asia, *Dipseudopsis*, Dipseudopsidae, Hydropsychoidea, phylogeny, systematics, Trichoptera.

The genus *Dipseudopsis* Walker exhibits a number of characteristics that are quite remarkable among the Trichoptera. The adults are the only members of the suborder Annulipalpia Martynov having siphoning mouthparts, with the lacinia forming a proboscis, a parallel modification of the galea in the higher Lepidoptera. Sexual dimorphism is conspicuous in the genus, with the males having highly contrasting colour patterns in their wings and bodies, and the females less striking in comparison. Also, males have the mesoapical spur of the hind tibia modified, often twisted and/or branched. The function of the modified spur is unknown, but it has been used almost exclusively for species determinations, to the extent that customary descriptions of the male genitalia often have been omitted from species descriptions. The convention of using the modified spur as the basis for species descriptions was established by Ulmer (1907b: 180): 'Bei *Dipseudopsis* sind die Genitalien aller Species ganz gleich' (i.e: In *Dipseudopsis* the genitalia of all species are totally alike). Hence, the modified spur became the primary characteristic used to recognize species; e.g. this is the main distinguishing character in every couplet of Ulmer's (1951) key to eleven species of *Dipseudopsis* of the Sunda Islands.

The precise orientation of the modified spur must be made apparent for species identification, because slight rotations of the tibia will show different perspectives of the spur. Some of the previous species descriptions based on the modified spur were ambiguous, because the figure of the spur did not show the remainder of the leg, and hence the actual orientation of the spur was uncertain. This problem accounts for several of the synonyms that we discovered in the course of this study. The figures of the spur herein are usually of the left leg and include the adjacent apicolateral spur and a portion of the tibia and tarsus to provide proper comparison of other specimens in the same perspective.

It seems somewhat ironic that the taxonomy of this genus, which exhibits so many fascinating character-

Table 1. List of character states. 0 = Plesiomorphic in respect to the outgroup Philopotamidae. 1 = Synapomorphic character.

1. Adult dorsal ocelli present = 0; ocelli absent = 1 (cf. Schmid 1980).
2. ♂ segment IX completely sclerotized cylinder = 0; IX jawlike with articulation between tergum & sternum = 1 (cf. Schmid 1980).
3. ♀ segment X without lateral papillae = 0; X with lateral papillae = 1 (cf. Schmid 1980).
4. ♀ segment IX normal = 0; IX long completely sclerotized cylinder = 1 (cf. Schmid 1980).
5. Larva spinneret short = 0; spinneret longer than other mouthparts = 1 (cf. Wiggins 1977).
6. ♀ sternum VIII normal, undivided = 0; sternum VIII divided into a pair of lateral lobes = 1 (cf. Schmid 1980).
7. ♂ inferior appendages 2-segmented = 0; 1-segmented = 1 (cf. Schmid 1980).
8. Adult bases of antennae distant = 0; bases close together = 1 (cf. Crichton 1957).
9. Larva tarsi nearly cylindrical, pretarsal claws long = 0; tarsi flattened, claws short = 1 (Ulmer 1957, Gibbs 1968, Wiggins 1977, Wells & Cartwright 1993).
10. Larval retreat differs from the following = 0; larva with branched tube-dwelling and filter-feeding behaviour as in *Phylocentropus* (Wallace et al. 1976, Wiggins 1977).
11. Adult labial palps present = 0; absent = 1 (Ulmer 1951).
12. Adult pronotum normal = 0; pronotum enlarged and with deep median fissure = 1.
13. Adult with head and thorax setous = 0; head and thorax glabrous = 1.
14.. Adult tegula knoblike = 0; tegula fattened like epaulets = 1.
15. Adult with galea short, vestigial = 0; modified into proboscis = 1.
16. Larva labrum expanded and more membranous = 1, autapomorphy for Philopotamidae (cf. Wiggins 1977).
17. Larva trochantin broad, either with blunt apical angle or truncate = 1, autapomorphy for Psychomyiidae (cf. Wiggins 1977).
18. Larva with mesopleural lobes = 1, autapomorphy for Xiphocentronidae (cf. Wiggins 1977).
19. Larva with tibiae and tarsi of legs fused = 1, autapomorphy for Xiphocentronidae (cf. Wiggins 1977).
20. Larva with ventral thoracic gills whorled = 1, autapomorphy for Hydropsychidae (cf. Wiggins 1977).
21. Larva epidermis with modified setae, especially on sternum VIII & IX and tergum = 1, autapomorphy for Hydropsychidae (cf. Wiggins 1977).
22. Larva head with ventrolateral bands of transverse ridges used in stridulation = 1, autapomorphy for Hydropsychidae (cf. Wiggins 1977).
23. Larval head and body flattened dorsoventrally = 1, autapomorphy for Ecnomidae (cf. Lepneva 1964).
24. Larva lateral fringe dense = 1, autapomorphy for Ecnomidae (cf. Lepneva 1964).

istics, should have become so confused at the species level. This is chiefly because Banks, Martynov, Navás, and Ulmer from 1905 to 1937 proposed descriptions of 25 different species from Asia and the species descriptions by Banks and Navás are poor. Another factor might be that specimens of *Dipseudopsis* are not particularly abundant in museum collections, even though adults are attracted to light traps.

The primary objective of this work is to clarify the taxonomy of the Asian species of *Dipseudopsis.* To accomplish this we have examined the types of most of the species as well as other specimens from several museums and private collections. The species descriptions have been expanded beyond the characteristics of the modified spur to include colouration of the body and wings and illustrations of the male genitalia. Hence, most of the redescriptions of species herein provide the first illustrations of the male genitalia. We recognize 36 species of *Dipseudopsis* from Asia, 30 previously described species and six new species, and one new subspecies. We also recognize the names of 16 species and one subspecies as new junior synonyms. Two additional Asian species, *D. onychophora* Navás and *D. orientalis* (Navás), are recognized as nomina dubia, because both were poorly described and their types could not be located for examination.

Depositories

The depositories of material are abbreviated as follows: BMNH, Natural History Museum (formerly the British Museum of Natural History), London; BPBM, Bernice Pauahi Bishop Museum, Honolulu; CASC, California Academy of Sciences, San Francisco; CNCI, Canadian National Collection, Ottawa; CLDD, collection of D. G. Denning (now deposited at CASC); CLHM, collection of H. Malicky; CLJW, collection of J. S. Weaver III; MCZC, Museum of Comparative Zoology, Harvard University, Cambridge; MNHN, Muséum National d'Histoire Naturelle, Paris; MZBS, Museu de Zoologia, Barcelona; MZLU, Museum for Zoology, University of Lund; NHMW, Naturhistorisches Museum Wien; NHRS, Naturhistoriska Riksmuseet, Stockholm; NZSI, National Zoological Collection, Zoological Survey of India, Calcutta; RMNH, Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden; SOFM, National Museum of Natural History, Sofia; UOPJ, Entomological Laboratory, University of Osaka Prefecture, Sakai; USNM, Smithsonian Institution, United States National Museum of Natural History, Washington; ZRAS, Zoological Institute of the Russian Academy of Sciences, St. Petersburg; ZMAN, Zoologisch Museum, Amsterdam; ZMHB, Zoologisches Museum der Humboldt-Universität Berlin; ZMUC, Zoologisk Museum København; ZMUH, Zoologisches Museum der Universität Hamburg; and ZSMC, Zoologische Staatssammlung München.

METHODS

Taxonomy

The morphological terminology of wing venation and genitalic characters mostly follows that of Schmid (1980), and Schuster & Hamilton (1984). The species synonymies are complete listing all original species descriptions, but subsequent references listed in Fischer's Trichopterorum Catalogus (1962, 1972) are not included. Locality names in current use are provided for specimens examined, where old names taken from labels are in quotes. For the type data, the term 'holotype' is used when the type specimen has actually been labelled or cited as such, otherwise it is listed as 'type'. An asterisk (*) designates types of previously described species examined by the authors.

Phylogenetics

Hennig86 (Farris 1988) is used for phylogenetic analysis to determine the relationship of Dipseudopsidae within the Hydropsychoidea *s. str.* Weaver, and the relationships of the proposed dipseudopsid genera. Twenty four character states (table 1) are selected, and with polarity determined for twelve taxa, using Philopotamidae Stephens as an outgroup, the data matrix (table 2) is produced. These data are analyzed using the 'mhennig*' command of Hennig86 for calculating trees. All characters have default values, weight = 1, active and additive, except weight = 2 for character 6.

DIPSEUDOPSIDAE ULMER

The family Dipseudopsidae is included in the suborder Annulipalpia Martynov, in the infraorder Curvipalpia Weaver (Weaver 1984, Weaver & Morse 1986). The family name, Dipseudopsinae Ulmer (1904b), including only the nominative genus, was first proposed as a subfamily of the Hydropsychidae Curtis, but was later placed within the Polycentropodidae Ulmer (1906), as it has been recognized by several others (Tsuda 1942, Marlier 1962, Ross & Gibbs 1973, Wiggins 1977, Schuster & Hamilton 1984). However, some workers in the past have recognized Polycentropodinae and the Dipseudopsinae as subfamilies of Psychomyiidae Curtis (Ross 1956, Ross & Kingsolver 1959), and more recently, some still recognize the Polycentropodinae as such (Flint 1991). The Dipseudopsidae were first given full family status by Ross (1967), and later concurred by Gibbs (1968), Wiggins (1982), Weaver (1984), Scott (1985), Weaver & Morse (1986), and Wells & Cartwright (1993).

The genus *Protodipseudopsis* Ulmer (1909) from the Afrotropical Region was the first addition to the subfamily, a relationship later confirmed by Ross & Kingsolver (1959). Two additional genera from the Afrotropical Region were placed in the Dipseudopsinae, *Eodipseudopsis* Marlier (1959) by original designation, and *Limnoecetis* Marlier (1955) originally placed in the Leptoceridae Leach, but later moved to the Dipseudopsinae (Marlier 1961). Ross & Gibbs (1973) transferred *Phylocentropus* Banks (1907) from Polycentropodinae to Dipseudopsinae, based predominantly on synapomorphic larval characteristics. They recognized only three genera in the Dipseudopsinae, *Dipseudopsis*, *Phylocentropus*, and *Protodipseudopsis*, and did not consider the status of *Eodipseudopsis* and *Limnoecetis*. However, Schmid (1980) later

Table 2. Data matrix for the families of Hydropsychoidea and genera of Dipseudopsidae, including outgroup Philopotamidae.

	Character				
		1	11111	11112	2222
	12345	67890	12345	67890	1234
Taxon					
Philopotamidae	00000	00000	00000	10000	0000
Psychomyiidae	11011	00000	00000	01000	0000
Xiphocentronidae	11011	00000	00000	00110	0000
Hydropsychidae	11100	10000	00000	00001	1100
Polycentropodidae	11100	11000	00000	00000	0000
Ecnomidae	11100	11000	00000	00000	0011
Dipseudopsis	11101	01111	01111	00000	0000
Protodipseudopsis	11101	01111	01110	00000	0000
Phylocentropus	11101	01111	00000	00000	0000
Limnoecetis	1110?	011??	01110	?????	????
Hyalopsyche	11101	01111	10000	00000	0000
Hyalopsychella	11???	?1???	10000	?????	????

made the novel assignment of placing *Phylocentropus* in the family Hyalopsychidae Lestage, on the basis of adult characteristics shared with the genus *Hyalopsyche* Ulmer (1904b). Wells & Cartwright (1993) recently concurred with the position of Ross and Gibbs, and based on the morphology of the larva and female of *Hyalopsyche*, added this genus to the Dipseudopsidae, and accordingly proposed the suppression of the family group name Hyalopsychidae. Our phylogenetic analysis tests the classifications of Ross & Gibbs and Wells & Cartwright, versus that of Schmid.

Results

Phylogeny. – The analysis of the data matrix via Hennig86 generated three trees with different topologies, having length 28, CI 0.89, RI 0.91 (fig. 55). All three trees depict Dipseudopsidae as a monophyletic group, comprising six genera. The first tree has the fewest number of ancestors, having 18 nodes, and is also identical to the strict consensus tree (fig. 56) of the three trees. The consensus tree depicts ((Psychomyiidae, Xiphocentronidae Ross) ((Hydropsychidae, Ecnomidae Ulmer, Polycentropodidae) Dipseudopsidae)), thus supporting monophyly of the Hydropsychoidea. The clade comprising Hydropsychidae, Polycentropodidae, Ecnomidae is recognized as the sister group of the Dipseudopsidae. A few differences are noted among the three original trees: 1) trees 0 and 2 depict the trichotomy (Hydropsychidae, Ecnomidae, Polycentropodidae), which is resolved as (Hydropsychidae (Ecnomidae, Polycentropodidae)) in tree 1; 2) trees 0 and 1 each have a basal and a distal trichotomy among the genera of Dipseudopsidae, both of which are resolved in tree 2.

Characters. – The combination of characteristics of the female genitalia as exhibited in the Dipseudopsidae (having synapomorphy 2, lateral papillae of segment X present, but lacking synapomorphy 6, abdominal sternite VIII not subdivided into lateral lobes) does not represent an apomorphic state, but only a unique combination of characteristics which happens to define the family very well, but only in a taxonomic sense. Synapomorphy 7, inferior appendage one-segmented is a homoplasy in Polycentropodidae and Ecnomidae. Three synapomorphies 8-10 support monophyly of Dipseudopsidae, and the first of these, antennal bases close together, is not unique, but within the Hydropsychoidea is also present in Hydropsychinae and Macronematinae (Hydropsychidae). However, since this characteristic is absent for the most part in Arctopsychinae and Diplectroninae, it is not part of the groundplan of Hydropsychidae, and thus is a homoplasy. A more accurate description of this condition as a homologue is that the antennal scapes of Dipseudopsidae are not merely close together but rather are so enlarged that they occupy most of the space between the eyes along the anterodorsal margin of the head (fig. 13).

Conclusions. – Monophyly of the Dipseudopsidae, including *Dipseudopsis*, *Hyalopsyche*, *Hyalopsychella* Ulmer (1930), *Limnoecetis*, *Phylocentropus*, and *Protodipseudopsis*, is unequivocal. Two clades are recognized among these genera, (*Hyalopsyche* + *Hyalopsychella*) supported by synapomorphy 11 (cf. table 1), and (*Dipseudopsis* + *Protodipseudopsis* + *Limnoecetis*) supported by synapomorphies 12-14. Hence, the sister group of the genus *Dipseudopsis* is unclear. The adult of *Limnoecetis*, a monotypic genus endemic to Lake Tanganyika, are quite remarkable, having unique adaptations to walk on water. The striking autapomorphies of *Limnoecetis* present a formidable challenge in resolving the trichotomy (*Dipseudopsis* + *Protodipseudopsis* + *Limnoecetis*). One obvious prediction based on our phylogeny, is that the unknown larval forms of *Hyalopsychella* and *Limnoecetis* probably share many similarities with the dipseudopsid larvae known. The phylogeny also provides evidence for removing *Eodipseudopsis* from the Dipseudopsidae (cf. final section of text).

The sister group relationship of the genus *Phylocentropus* remains uncertain. *Phylocentropus* phenetically agrees closely with *Hyalopsyche*, but the similarities of these two genera are predominantly plesiomorphic. Thus, the phylogenetic analysis above does not provide supporting evidence for Hyalopsychidae *s. str.* Schmid (1980) and in fact, infers that this taxon might be paraphyletic. Therefore we concur with Ross and Gibbs for the most part on the classification of *Phylocentropus*, and Wells and Cartwright on the placement of *Hyalopsyche* and the suppression of the Hyalopsychidae, a taxon that presently serves no useful purpose in phylogenetics.

Keys to genera of Dipseudopsidae

Larvae

The larvae of *Hyalopsychella* Ulmer and *Limnoecetis* Marlier are unknown.

1. Mandibles with apicolateral teeth; head capsule short, with lateral margins nearly parallel and its total length less than its maximum width (Ulmer 1957, Gibbs 1968) 2
– Mandibles without apicolateral teeth; head capsule long, with lateral margins tapering anteriad, and with its length slightly greater than its maximum width (Wiggins 1977, Wells & Cartwright 1993) 3

2. Frontoclypeal suture V-shaped with lateral lines tapering irregularly posteriad toward the dorsal coronal suture (Ulmer 1957) .... *Dipseudopsis* Walker
– Frontoclypeal suture with the posterior portion U-shaped, and the anterolateral lines nearly parallel between the eyes and then curving mesad to meet the coronal suture posteriad (Gibbs 1968) .... *Protodipseudopsis* Ulmer
3. Frontoclypeal suture sessile in respect to posterior margin, posterior 1/3 nearly regular V-shaped and without hourglass-shaped constriction (Wells & Cartwright 1993) .. *Hyalopsyche* Ulmer
– Frontoclypeal suture with short petiole joining posterior margin, posterior 1/3 more irregular V-shaped and with hourglass-shaped constriction (Wiggins 1977) .... *Phylocentropus* Banks

Adults

1. Pronotum with setaceous warts conspicuous and without deep median fissure 2
– Pronotum with setaceous warts inconspicuous and with deep median fissure 4
2. Labial palps present; forewing with fork I long and sessile .... *Phylocentropus* Banks
– Labial palps absent; forewing with fork I short and petiolate or absent 3
3. Fore and hind wings with fork I short and petiolate .... *Hyalopsyche* Ulmer
– Fore and hind wings with fork I absent ....*Hyalopsychella* Ulmer
4. Tibial spurs 1, 2, 2; female with maxillary palps three-segmented; one species endemic to Lake Tanganyika .... *Limnoecetis* Marlier
– Tibial spurs 3, 4, 4; female with maxillary palps five-segmented; Africa and Asia........................ 5
5. Mouthparts with maxilla modified into a proboscis; hindwing with median cell closed; male hind mesoapical tibial spur modified, often twisted and/or branched; Asia and Africa .... *Dipseudopsis* Walker
– Mouthparts without a proboscis; hindwing with median cell open; male hind mesoapical tibial spur normal; Africa ...... *Protodipseudopsis* Ulmer

SYSTEMATIC PART

Dipseudopsis Walker, 1852

Dipseudopsis Walker, 1852: 91. – Type species: *Dipseudopsis capensis* Walker (monobasic).

Nesopsyche McLachlan 1866: 168. – Type species: *Neopsyche flavisignata* McLachlan (monobasic).

Esperona Navás 1915: 397. – Type species: *Esperona orientalis* Navás (monobasic).

Bathytinodes Iwata 1927: 235. – Type species: *Bathytinodes albus* Iwata (monobasic).

Dipseudopsodes Lestage 1936: 170 (invalid, type species not designated).

The genus *Dipseudopsis* was proposed by Walker (1852) with the description of *D. capensis* from South Africa and placed in the family Sericostomatidae Stephens, a family designation which was common for caddisflies, exhibiting bizarre characteristics, that did not agree with the diagnoses of other families. Later when McLachlan (1863) added a second species to the genus, *D. collaris* from China, he placed *Dipseudopsis* in the family Rhyacophilidae. Brauer (1868) placed it in the Hydropsychidae *s. lat.*, near *Cyrnus* Stephens. However, after examination of the adult mouthparts, Ulmer (1904a, b) placed the genus in the Polycentropodidae, subfamily Dipseudopsinae. Accordingly, most workers have placed the genus in Polycentropodidae (Navás 1913, Martynov 1935, Schmid 1949). However, Banks (1931b) maintained a conservative approach, having never recognized the full family status of Polycentropodidae, and followed Brauer's placement of the genus in the Hydropsychidae *s. lat.*

Etymology. – *Dipseudopsis:* Greek *di*, two; *pseudos*, false; *ops*, eye; feminine. The actual etymology is uncertain. The basis of this name is uncertain also, since there are no noticeable characters such as wing spots present in the type species of the genus, *D. capensis.* Perhaps it was based on the appearance of the pronotum, having the setal areas expanded and divided by a deep median fissure.

Adult

Head and thorax (figs. 12A-B, 13, 14): The head has a sparse number of short inconspicuous setae and is nearly glabrous; sometimes it is glossy and very glabrous. The setal areas of both the head and thorax are not raised like typical setaceous warts, but are flush with other surrounding sclerites. The setae of the body and wings are mostly short sparse and inconspicuous, giving the imago a glabrous appearance. The pronotum is raised to the same level as the head and mesonotum and is divided by a deep median furrow, probably resulting from modifications of the lateral setal areas, which have remained separate, but have become both enlarged and glabrous. The tegula are flat and sit like epaulets on the bases of the forewings. Legs with tibial spur formula complete: 3, 4, 4. The head, thorax, and sometimes the anterior segments of the abdomen have patterns of yellowish or orangish brown contrasting with dark brown. The forewing is narrow, length ranging from 10 to 20 mm, usually mostly brown with a hyaline spot at m-cu and the arculus, and sometimes with a pattern of translucent bands or spots against a dark background, or with a striped pattern of dark veins against lighter translucent membranes; fork I is either short and petiolate or absent, II and IV are long and sessile, III and V are long and petiolate, and the discal and medial cells are closed. The hindwing is shorter and sometimes broader than the forewing, being somewhat triangular and lighter in colour, sometimes nearly translucent; forks II and V are long and sessile, forks I, III, IV absent, the discal cell closed, and unlike other dipseudopsid genera described the median cell is closed. The scent glands of sternum V are present in the female and absent in the male, their openings are rather inconspicuous and lack exterior projections. This condition differs in *Phylocentropus placidus* (Banks) examined, having the scent gland absent in both sexes.

The mouthparts (fig. 12B, 13, 14) have been described by Ulmer (1904a), Cummings (1913) and Crichton (1957: fig. 53), and are quite unique, having the lacinia modified into a proboscis, functioning as a siphoning tube. The two processes which form the proboscis are not held together in preserved specimens, but curl away from each other distally. Each process is shaped like half of a long slender straw, with its longitudinal edges fringed with numerous short scalelike setae, having many transverse ridges along its shaft (thus being semiannulate), and having several mesal dentations at its base. The proboscis is at least as long as the first 2-4 segments of the maxillary palps, or usually about the same length as the labium, including base plus palps. The haustellum is slender, about as long as the base of the labium, and its apex is bilobed. The frontoclypeus is large and slightly bulbous, apparently well-developed to support a pumping organ. *Protodipseudopsis* differs noticeably from *Dipseudopsis* by lacking a well-developed proboscis (fig. 12C); its frontoclypeus is shorter and less bulbous and apparently the pumping organ is reduced.

Male. – The male is dark brown, sometimes with contrasting patterns in the wings and body, and more striking than in the female. The mesoapical spur of the hind tibia is modified, often twisted like a corkscrew and sometimes branched into two or more processes. It is interesting to note that the same spur is also modified in *Phylocentropus auriceps* (Banks), (Schuster & Hamilton 1984), being exceptional among the other dipseudopsids.

Genitalia (fig. 17): The male genitalia are blunt, generally lacking in conspicuous characteristics, and the processes of the genitalia are retracted and obscured by the large blunt preanal appendages. This blunt appearance of the male terminalia, especially in dry material, probably is why males sometimes have been mistaken as females, e.g. the types of *D. flavisignata* (McLachlan, 1866) and *D. benardi* Navás (1930). Segment IX with articulation between tergite and sternite, resembling an open jaw in lateral view; the tergum and sternum also articulate with the preanal appendages. The tergum of segment IX is much smaller than the sternum and usually overhangs segment X, and its apical margin may be triangular, rounded, or bilobed in dorsal view. The sternum of segment IX is heavily sclerotized and is the most massive feature of genitalia, providing support for the inferior appendages, the phallus, and the ventral articulation of the preanal appendages. The sternum of segment IX is a simple structure except for the mesosuperior processes that, along with segment X, form a hood that hangs over the dorsal portion of the phallus which is mostly membranous. Segment X is inferior to segment IX, and subequal in length to the phallus. The phallus is mostly membranous dorsad and heavily sclerotized ventrad. Hence, segment X and the phallus appear to function in concert, with segment X providing dorsal coverage and support to the phallus. The inferior appendages are thumblike, with apices directly dorsad, perhaps modified to hold segment X and the phallus together, as well as clasping the female during copulation.

Female. – Females are usually lighter in colour than the males, and as a result they are more dull and have fewer contrasting colour patterns in their wings and bodies. However, the contrasting colouration of an unidentified female specimen (fig. 2) may be exceptional. In several species, such as *D. nervosa* (figs. 3, 4), where the males have brown wings with large translucent spots, the females have striped forewings with dark veins against a translucent background. Sometimes females have forewings with faded indistinct spots that are remotely similar to translucent spots in the forewings of males. However, the female forewings are most often dull brown and show no striking colour patterns.

Genitalia (figs. 15-16): Sternum VIII forms a single plate, not divided into lateral lobes as in the Polycentropodidae. Segment IX has a well-sclerotized tergite, as in some species such as *D. recta* (fig. 15), but is more membranous in others (fig. 16); the sternum is mostly membranous. The vaginal apparatus and the vulval scale are attached to the sternum of segment IX by sclerotized bands and membranous folds. Both the vaginal apparatus and the vulval scale are sclerotized. The length of the vaginal apparatus is variable, being long in *D. recta*, where it extends anteriad reaching the anterior margin of sternite VIII (fig. 15), but is much shorter in other species (fig. 16). The genitalia are generally similar to those of *Phylocentropus* (Schmid 1980, Schuster and Hamilton 1984), except that segment IX is more heavily sclerotized. This diagnosis is provisional, because the females of most species remain undescribed. We observe that the females of some species can be distinguished from others by colour patterns of the body and wings, and characteristics of the genitalia.

Larva

The larva of *Dipseudopsis* was first described by Iwata (1927), although under a different name. A key separating the larvae of *Dipseudopsis* and *Protodipseudopsis* was provided by Ulmer (1957), and a similar key was provided by Marlier (1962), whereby the larvae of *Dipseudopsis* and *Protodipseudopsis* were distinguished by the gular sclerite, mandibles, and hind tarsal claw. *Protodipseudopsis* and *Dipseudopsis* are unique in having mandibles with apicolateral teeth, a probable synapomorphy (Ulmer 1957: f. 401; Gibbs 1968: fig. 1; Marlier 1962: fig. 50; Marlier 1979: fig. 5). The known larvae of *Dipseudopsis* known can be distinguished from those of other dipseudopsids by having head capsule short, lateral margins nearly parallel with total length less than its maximum width, frontoclypeal suture V-shaped and the lateral lines tapering irregularly and posteriad toward the dorsal coronal suture, and mandibles with apicolateral teeth.

Larval behaviour and habitat. – The larval tube-dwelling and feeding-behaviour have been described for *Protodipseudopsis* (Gibbs 1968) and *Phylocentropus* (Wallace et al. 1976, Wiggins 1977). The larvae of these genera live in the bottom substrates of streams or lakes and construct a somewhat Y-shaped silken tube composed of sand grains and detritus. The ends of the two upper branches, usually one vertical and the other inclined, are open and exposed to the stream current, the rest of the tube is located within the bottom substrate, and the end of the bottom branch is closed. The opening of the vertical branch is an intake and the inclined branch an outlet, through which a directional flow is established via rapid oscillations of the larva. This forced flow enables a fine capture net, within an enlarged chamber of the outlet branch, to collect fine organic food particles for the larva to eat. The larval tubes of *Hyalopsyche* are branched and appear to be similar to those of *Phylocentropus* (Wells & Cartwright 1993), as are the tube-dwellings of *Dipseudopsis.* Therefore, since branched tube-dwellings are characteristic for the larvae of *Dipseudopsis, Hyalopsyche, Protodipseudopsis,* and *Phylocentropus,* this type of larval retreat and its associated mode of feeding-behaviour is a synapomorphy of Dipseudopsidae. The larva retreat of the hydropsychid genus *Macrostemum* Kolenati (Wiggins 1977, as *Macronema* Pictet) is generally similar, but differs in many details and is certainly a homoplasy.

Ulmer's (1957: 303) description of the larval retreat and biology of *Dipseudopsis* is translated as follows: 'Larvae and pupae live in calm pools of rivers, also in lakes and lake-outflows, in the mud or fine sandy substrates; the larvae not free-living there, but construct tubes out of secretions, covered with mud etc., in the depths; these tube-dwellings are more or less bent and twisted, elastic and flexible, but nevertheless fairly resistant; sometimes they are branched into 2 or 3 tubes, but only one of the branches reaches the [substrate] surface and there it is closed, while the other lower ends are open.' It seems obvious that Ulmer's orientation of the tube-dwelling is upside down; his description should depict the two open ends reaching the surface, and the one closed branch completely buried in the substrate. This would agree more with the tube-dwellings described in detail for *Phylocentropus* and *Protodipseudopsis,* and the description by Scott (1985: 334) for *Dipseudopsis* in southern Africa: 'The larvae are bottom dwellers in standing or slow-flowing water where they construct U-shaped silk-lined tubes with a transverse net in mud or silt or on submerged branches, filtering out algae and organic particles on which they feed.'

The larvae and pupae of *Dipseudopsis* inhabit a range of freshwater habitats, including the sandy depositional zones of lakes and the pool areas of rivers and streams. Marlier (1953, 1962) reports that immatures in Africa were found in shallow water, while Tsuda (1939) reported that larvae in Japan were discovered at a depth of 90 m. The collections of *D. diehli* Malicky & Weaver, at elevations of 1,400 m in Sumatra, devoid of large rivers and lakes, suggests that some species also live in mountain streams.

Distribution

Dipseudopsis is known to occur generally throughout the old world tropics of Africa and Asia. The African fauna recorded from the northern Nile River Valley, including Egypt, Sudan, and throughout most of the Afrotropical Region, from Ethiopia and Kenya to Nigeria, Ghana and Sierra Leone, and to Zaire, Mozambique, South Africa, and Madagascar. The genus is represented by 42 described species, 23 from the African continent, and 19 from Madagascar. However, in light of the problems discovered in this work, we suspect that the African species are in need of a thorough taxonomic revision. The Asian fauna with 36 recognized species is known throughout most of the Oriental Region and part of the southeastern Palearctic Region, including Pakistan, India, Sri Lanka, Nepal, Bangladesh, Burma, Thailand, Cambodia, Vietnam, China, Japan, Philippines, Malaysia, and Indonesia, including Sumatra, Java, Borneo and Sulawesi.

Checklist of *Dipseudopsis* from Asia

adiaturix **sp. n.**	p. 102
benardi Navás, 1930.	p. 104
langana Navás, 1930 **syn. n.**	
arculata Navás, 1931 **syn. n.**	
ulmeri Schmid & Denning, 1979 **syn. n.**	
bicolorata Martynov, 1935.	p. 107
collaris McLachlan, 1863.	p. 109
stellata McLachlan, 1875 **syn. n.**	
alba (Iwata, 1927).	
bakeri Banks, 1916 **syn. n.**	
discors Navás, 1924 **syn. n.**	
contorta Banks, 1931b.	p. 110
diehli Malicky & Weaver, 1988.	p. 112
digitata Ulmer, 1907a.	p. 112
doehleri Ulmer, 1929 (*döhleri*).	p. 115
elongata Banks, 1920.	p. 116
flavisignata (McLachlan, 1866)	p. 116
flinti **sp. n.**	p. 116
immaculata Ulmer, 1905.	p. 118
moesta Banks, 1931b **syn. n.**	
indica McLachlan, 1875.	p. 120
buddha Banks, 1913 **syn. n.**	
i. sindica Martynov, 1935 **syn. n.**	
infuscata McLachlan, 1875.	p. 120
knappi Schmid & Denning, 1979.	p. 121
lamellata Martynov, 1935.	p. 121
lucasi **sp. n.**	p. 123
maculata Ulmer, 1907a.	p. 123
malaisei **sp. n.**	p. 124
martynovi **sp. n.**	p. 124
modesta Banks, 1911.	p. 124
pallida Martynov, 1935 **syn. n.**	
morosa Banks, 1924.	p. 125
nebulosa Albarda, 1881.	p. 127
nervosa Brauer, 1868.	p. 127
luctuosa Banks, 1913.	
venosa Navás, 1931 **syn. n.**	
nervosella Ulmer, 1951 **stat. n.**	p. 128
nieuwenhuisi Ulmer, 1909.	p. 130
notata (Fabricius, 1781).	p. 130
horni Ulmer, 1915 **syn. n.**	
recta Martynov, 1935.	p. 131
bombayana Martynov, 1935 **syn. n.**	
robustior robustior Ulmer, 1929 **stat. n.**	p. 132
akhila Schmid & Denning, 1979 **syn. n.**	
thailandica Schmid & Denning, 1979 **syn. n.**	
junki Marlier, 1979 **syn. n.**	
robustior andamanensis **ssp. n.**	p. 134
schmidi **sp. n.**	p. 134
spectabilis Banks, 1931a.	p. 134
stabatensis Malicky & Weaver, 1988.	p. 135
tonkinensis Navás, 1921.	p. 135
triclavata Martynov, 1935.	p. 137
varians Ulmer, 1929.	p. 138
petersorum Schmid & Denning, 1979 **syn. n.**	
voluta Ulmer, 1906.	p. 138
onychophora Navás, 1935 **nomen dubium**	p. 139
orientalis (Navás, 1913) **nomen dubium**	p. 139

Dipseudopsis adiaturix sp. n.
(fig. 18)

Type material. – Holotype ♂: INDONESIA: Sumatra, Huta Padang, 26.I.1990, Diehl (CLHM).

Male. – Head with dorsum and frontoclypeus dark brown, almost black, but posterior dorsal warts yellowish brown. Basal segments of antennae brown (type with distal parts of antennae and mouthparts missing due to ant attack). Thorax, tergites and sternites dark brown. Coxae of fore and mid legs brown, coxa of hind legs yellowish brown. Basal ½ of fore femora dark brown, femora of mid and hind legs with basal ½ brownish; distal ½ of all femora, tibia of fore and mid legs, and all tarsi yellow; distal ½ of hind tibia brown. Modified spur (fig. 18) long and slender, more than ½ as long as adjacent tarsal segment, more than 2x longer than outer spur, distal claw about ⅛ as long as spur and bent obliquely laterally, and with short lateral thorn at ⅔ length from base. Forewing 16 mm, slender, dark brown, but with nervation darker, having hyaline lunula at m-cu, and indistinct translucent spots between M_4 and Cu_1 and near apex of 1A and 2A. Hindwing 10 mm, dark brown, with hyaline lunula at m-cu. Abdomen yellowish brown. Genitalia (18A-D): Tergum IX broad and bilobate with median sized cavity below in dorsal view; sternum IX with mesosuperior process fingerlike in lateral view. Dorsal edge of segment X with strong incision in lateral view, but apex not incised. Preanal appendages long and triangular in lateral view. Inferior appendages curved dorsad in lateral view, with distal part slightly clavate and basolateral mesal margins squarish in caudal view. Phallus calyx-like in ventral view, about ⅔ as long as segment X.

Etymology. – A noun in apposition: named after a Celt who lived in Austria 2000 years ago.

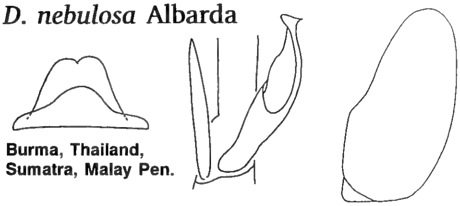
Distribution. – Indonesia: Sumatra.

Remarks. – This species is only known from the unique type. It has a modified spur similar to *D. flavisignata*, being long slender, acuminate, slightly sinuate and bearing a short subapical lateral thorn. However, it differs in having the male modified spur with the lateral thorn closer to its apex, rather than near the base, the male forewings mostly dark brown and without a striking pattern of translucent stripes and by characteristics of the male genitalia.

Pictorial atlas (p. 103-106)

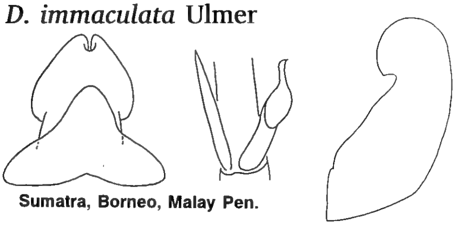
A pictorial atlas is provided for quick species determination. The figures of the following male characters are provided for each species: 1) dorsal aspect of segment IX and X, 2) shape and relative size of the left modified spur, and 3) caudal aspect of the right inferior appendage (but for subspecies, only figures of the modified spur). The distributional data are listed below the figures. Possible identifications should be confirmed with the complete species descriptions and figures in the text.

D. nebulosa Albarda



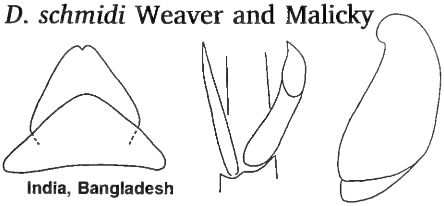
Burma, Thailand, Sumatra, Malay Pen.

D. immaculata Ulmer



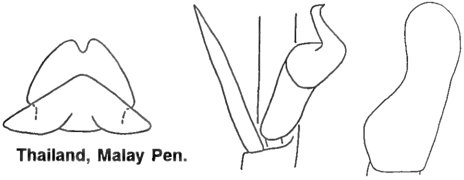
Sumatra, Borneo, Malay Pen.

D. schmidi Weaver and Malicky



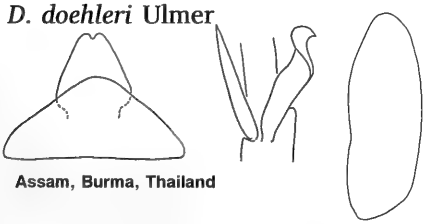
India, Bangladesh

D. varians Ulmer



Thailand, Malay Pen.

D. doehleri Ulmer

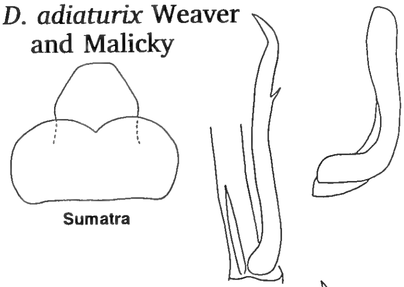


Assam, Burma, Thailand

D. flavisignata (McLachlan)

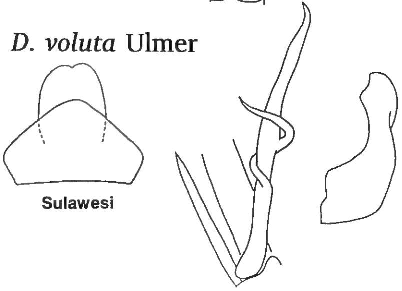
Sulawesi

D. adiaturix Weaver and Malicky



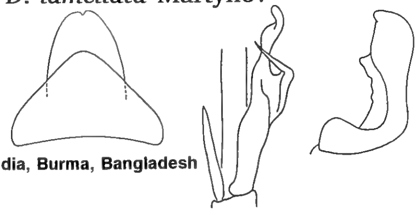
Sumatra

D. voluta Ulmer



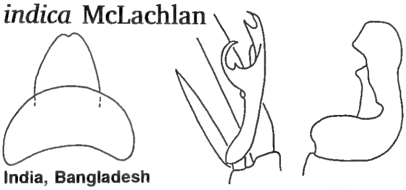
Sulawesi

D. lamellata Martynov



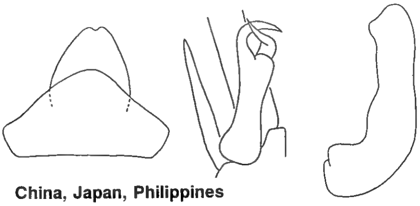
India, Burma, Bangladesh

D. indica McLachlan

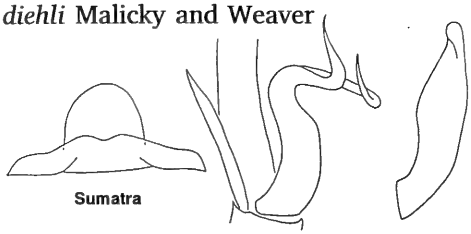


India, Bangladesh

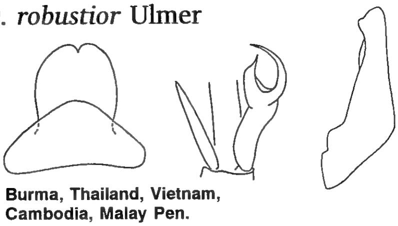
D. collaris McLachlan



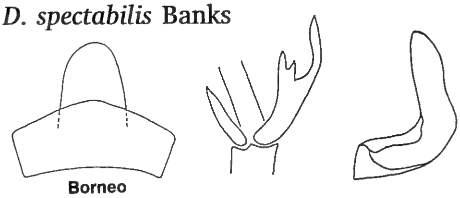
D. diehli Malicky and Weaver



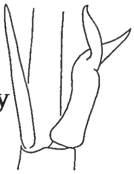
D. robustior Ulmer



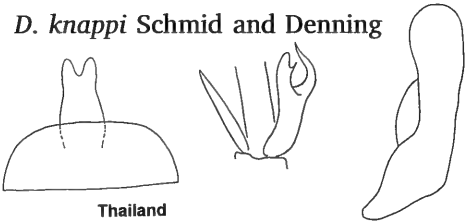
D. spectabilis Banks



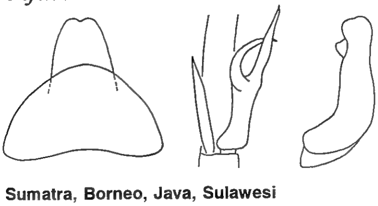
D. r. andamanensis Weaver and Malicky



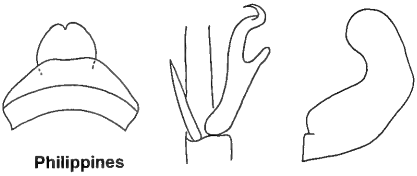
D. knappi Schmid and Denning



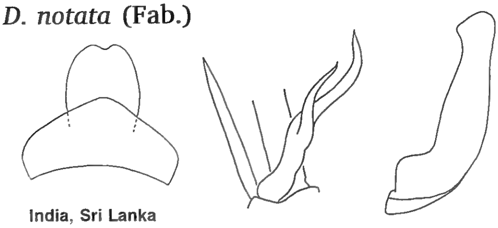
D. infuscata McLachlan



D. nervosa Brauer



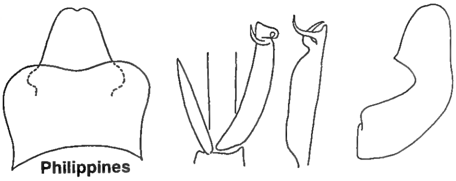
D. notata (Fab.)



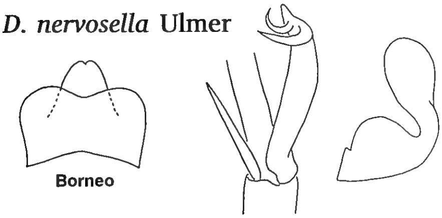
Dipseudopsis benardi **Navás, 1930**
(figs. 10, 19)

Dipseudopsis stellata. – Ulmer 1905: 96, fig. 75b [misdet].
Dipseudopsis benardi Navás, 1930: 141, Type ♂*, VIETNAM 'Tonkin': Phu Lang Thuong, 1909, det. P. Navás S. J., G. Benard (MNHN); 1♂*, same data (MNHN). – Fischer 1962: 5; Fischer 1972: 3.
Dipseudopsis langana Navás, 1930: 141, Type ♀*, VIETNAM 'Tonkin': Phu Lang Thuong, 1909, det. P. Navás S. J., G. Benard (MNHN). – Fischer 1962: 10; Fischer 1972: 5. Syn. n.
Dipseudopsis arculata Navás, 1931: 85-86, Holotype ♂*, CHINA: Guangfong: 'Cong-tcheou' Canton (MZBS). – Fischer 1962: 5; Fischer 1972: 2. Syn. n.

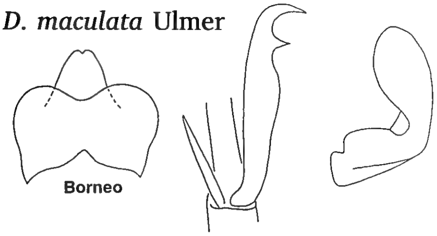
D. morosa Banks



D. nervosella Ulmer

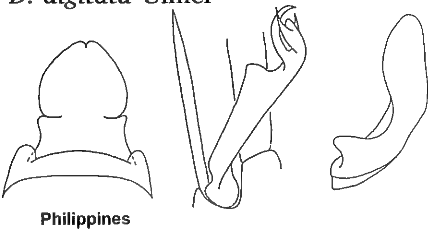


D. maculata Ulmer

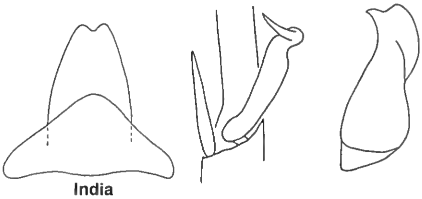


D. nieuwenhuisi Ulmer

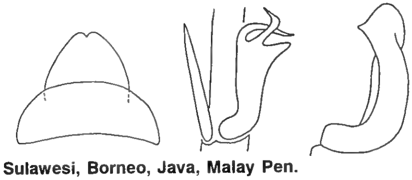
D. digitata Ulmer



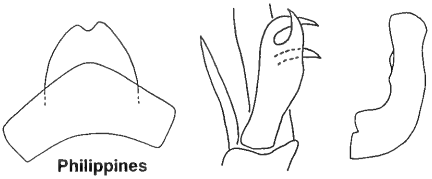
D. bicolorata Martynov



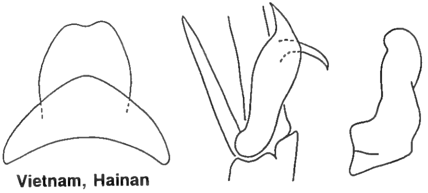
D. contorta Banks



D. martynovi Weaver and Malicky



D. tonkinensis Navás

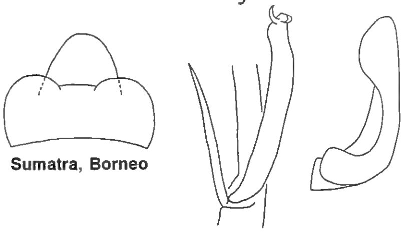


Erratum: *D. contorta*, read Sumatra for Sulawesi.

Dipseudopsis moesta. – Ulmer 1951: 128 [misdet].
Dipseudopsis ulmeri Schmid & Denning, 1979: 243, fig. 1a-e, Holotype ♂*, THAILAND: Chiang Mai Prov., E fork Mae Ping, 56km N of Chiang Mai, 1300ft, at light, 24.XI.1964, Peters (CLDD). Syn. n.

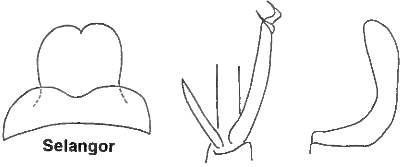
Specimens examined. – CAMBODIA: 1♂ 2♀, 'Cambodge' Pavie, 1886 (MNHN). – CHINA: Fujian: 1♂, 'Foochow' Fuchou, 1936-37, det. *D. stellata* by Mosely, M. S. Yang (-BMNH). – THAILAND: 2♂, Chiang Mai, 19.V.1952, D. & E. Thurman (USNM). 1♂, Doi Sutep, 1952, D. & E. Thurman (MCZC). 1♂, Bangkok, 5.X.1929, H. Smith (MCZC). 1♂, Ping River, Chiang Mai, 9.IV.1989, Malicky (CLHM). 2♂, Ping River near Lampun, 20.XII.1989, Malicky (CLHM).

D. stabatensis Malicky and Weaver



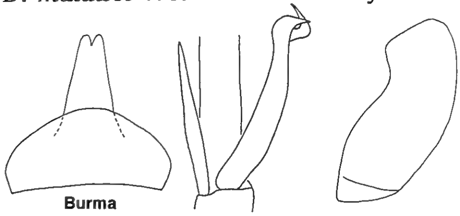
D. modesta Banks

D. flinti Weaver and Malicky

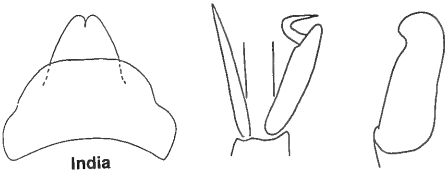


D. triclavata Martynov

D. malaisei Weaver and Malicky



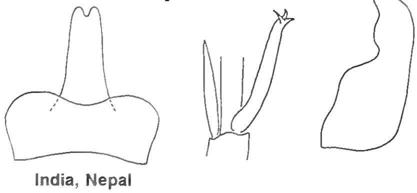
D. lucasi Weaver and Malicky



D. benardi Navás

D. elongata Banks

D. recta Martynov



1♂, Chiang Mai Zoo, light trap, 24-31.X.1988, Chantaramongkol & Malicky (CLHM). 2♂, Kanchanaburi, Sai Yok, 400ft, 4.V.1990; 6♂, 14.V.1988; Allen (CLHM). 2♂, Kwei river, 11.X.1979 (CLHM).

Male. – Head dorsum mostly dark brown but posterior warts light brown; frontoclypeus light brown but dorsal portion darker; antennal scape and pedicel light brown, flagellum dark. Pronotum, mesonotum and tegula dark brown. Forewing (fig. 10): 13.5-16.5 mm, mostly dark brown, but with translucent spots: distinct small translucent spot just distal of r; small

1

2

Figures 1-2. – Fig. 1, *Dipseudopsis bicolorata* Martynov, male, dorsal. Fig. 2, *Dipseudopsis sp.* female, dorsal, India, Manipur, Nungha.

faded spots just distal of transverse cord, hyaline lunula at m-cu, large translucent spot at arculus. Legs brown. Modified spur (fig. 19): basal ¾ unmodified and apical ¼ bifid with two short acuminate points curved, spiraling opposite each other distally, each point slightly longer than width of main shaft. Genitalia (fig. 19): Tergum IX with posterior margin curved in dorsal view, with posterior ½ extending over segment X in lateral view; sternum IX having mesosuperior process with short dorsal triangular point and long slender distal point, extending above basal ½ of phallus in lateral view. Segment X tapering distally into slender lobe in lateral view, extending posteriorly distal to preanal appendages about as far as inferior appendages, apex bilobed. Preanal appendages with posterior margin not distinctly incised in lateral view, having blunt dorsal point, dorsal and ventral margins converging to truncate posterior margin. Inferior appendages thumblike with obtuse midventral angle in lateral view.

Distribution. – Cambodia; China: Guangdong, Fujian; Thailand; Vietnam.

Remarks. – This species can be recognized by having the modified spur with two short apical points spiraling opposite from each other, and the forewing longer and darker brown than most other species in southern China and Indochina. The types of *D. benardi*, *D. arculata*, *D. langana*, and *D. ulmeri* were examined, and the latter three are recognized as junior synonyms of *D. benardi*. The type of *D. benardi* is a male, not a female as previously reported by Navás (1930). The type of *D. langana* is recognized as a female of *D. benardi*, because it is has an identical locality label as the type of *D. benardi* and is similar in size and general appearance.

Ulmer (1905: fig 75b) provided a figure of the male modified spur of an undetermined specimen of *Dipseudopsis* from 'Cambodscha, Museum Paris' and Ulmer (1951: 128) later identified this figure as *D. moesta* (syn. n. of *D. immaculata*). Ulmer's figure is more similar to the spur of *D. benardi*, and is probably not *D. immaculata* because this species is unknown from Cambodia. Also, we have examined a male specimen of *D. benardi* from Cambodia in the MNHN, which might be the same specimen figured by Ulmer.

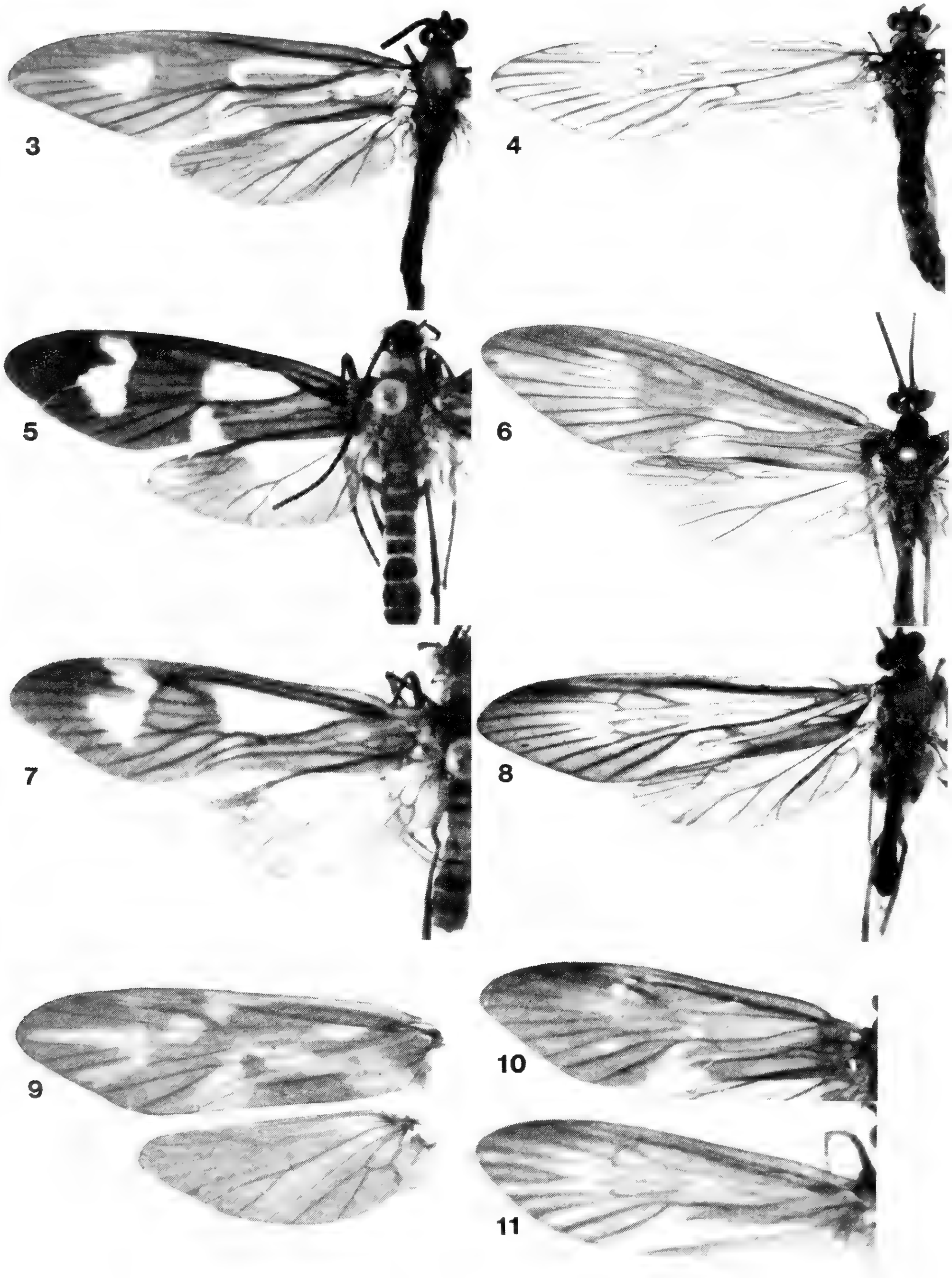
***Dipseudopsis bicolorata* Martynov, 1935**

(figs. 1, 20)

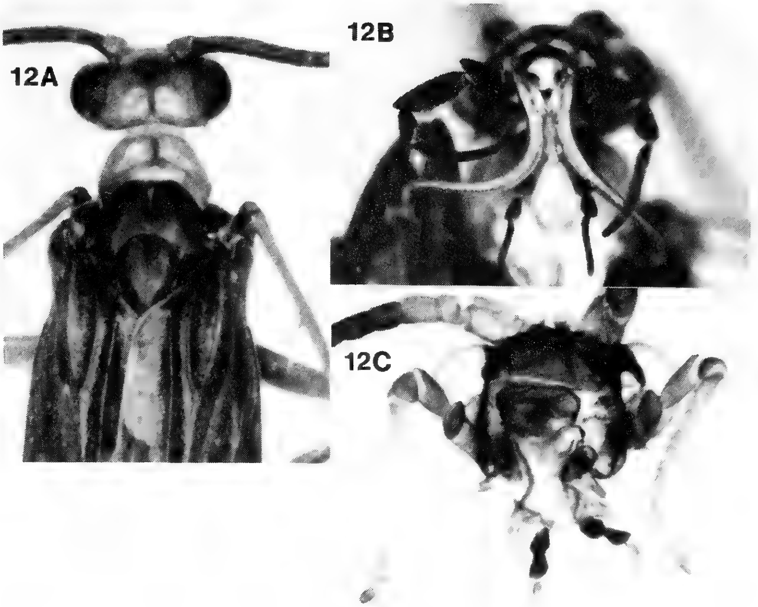
Dipseudopsis bicolorata Martynov, 1935: 165-166, figs. 68a-c, 69a-b, Type series: INDIA: '2♂, ♀. Castle Rock, North Kanara district, Bombay Pres. October 1916. S. W. Kemp ... ♂. Talewadi, Castle Rock, N. Kanara district, Bombay Pres. 3-10.1916. S. W. Kemp'. The type material present in the collection of the Zoological Survey of India is in poor condition and too delicate to send by mail (pers. comm. Dr. K. Rai). Syntype 1♀*: det. Martynov, Karnataka, N. Kanara dist., Castle Rock, in alcohol, X.1916, S. Kemp (ZRAS). – Fischer 1962: 5; Higler 1992: 80.

Specimens examined. – INDIA: Karnataka: 1♂, Shimoga Dist, Agumbe Ghat 2000ft, V.1974, Lucas (CLHM). Tamil Nadu: 4♂, Kattalaimala, 25-26.XII.1961, F. Schmid (-CNCI). 1♂, Ottakada, 5.I.1962, F. Schmid (CNCI).

Male. – Body and wings (fig. 1). Head dorsum and pronotum orangish brown, frontoclypeus mostly dark brown but dorsal margin orangish brown, genae yellowish, antennal scape orangish, pedicel and flagellum brown, palps dark brown, but stipes orangish brown, maxillary palps 3.2 mm, proboscis 1.7 mm, as long as first three segments of maxillary palps, labial palps 1.4 mm; cervical sclerites and mesonotum dark brown. Forewing 16-21 mm, almost unicoloured dark brown, but darker along anterior margin between C and R and posterior margin, only hyaline spots at m-cu and arculus. Front leg brown, middle and hind legs with coxae, trochanters and femora orangish brown, distal segments brown. Modified spur (fig. 20) having one apical point, curving in



Figures 3-11. – Fig. 3-4, *Dipseudopsis nervosa* Brauer: Fig. 3, male. Fig. 4, female. Fig. 5, *D. doehleri* Ulmer, male. Fig. 6, *D. nieuwenhuisi* Ulmer, male. Fig. 7, *D. nebulosa* Albarda, male. Fig. 8, *D. digitata* Ulmer, male. Fig. 9, *D. spectabilis* Banks, male wings. Fig. 10, *D. benardi* Navás, male forewing. Fig. 11, *D. flinti*, n. sp., male forewing.



Figures 12A-C. – Fig. 12A, *Dipseudopsis nebulosa* Albarda, male, head and thorax, dorsal. Fig. 12B, *D. doehleri* Ulmer, male, head with mouthparts, ventral. Fig. 12C, *Protodipseudopsis sjoestedti* Ulmer, male, head with mouthparts, anterior.

plane perpendicular to longitudinal axis of spur.

Genitalia (fig. 20): Tergum IX triangular with blunt apex in dorsal view, posterior margin only slightly overhanging segment X in lateral view. Segment X ellipsoidal with length 1½ × basal width in dorsal view, tapered distad and apex incised. Preanal appendages with dorsal margin irregular in lateral view, directed dorsad with apex obtuse or sometimes rounded and ventral margin broadly rounded. Inferior appendages with massive dorsal extension that doubles height at middle as compared to base in lateral view, with distinct apicomesal tooth in ventral view, and with curved apicolateral flanges.

Distribution. – India: Karnataka, Tamil Nadu.

Remarks. – This is the largest species of *Dipseudopsis* known from India and is easily recognized by its colouration of the males which superficially resemble ctenuchid moths. The orangish brown dorsum of the head and pronotum contrast strikingly with the unicoloured, dark brown mesonotum and forewings. The modified spur bears a single curved apical point that lies in a plane perpendicular to the longitudinal axis of the spur. The specimen in fig. 2 is possibly a female of this species.

Dipseudopsis collaris McLachlan, 1863

(fig. 21)

Dipseudopsis collaris McLachlan, 1863: 496, pl. 19: fig. 6, Lectotype ♂*, selected by Kimmins (1957: 101), Hong Kong: (BMNH). Cotype 1♂*: Hong Kong: Soochow (MCZC 11080). Weidner (1964): Paratype ♀, CHINA: Hong Kong (ZMUH). – Fischer 1962: 7; Weidner 1964: 73; Fischer 1972: 3.

Dipseudopsis stellata McLachlan, 1875: 16-17, pl. 2: fig. 11, Holotype ♂ (Kimmins, 1957: 101): [CHINA: Zhejiang:] Shanghai, McL. coll. (BMNH); 3♂* [possible syntypes]: Shanghai, McL. coll. (BMNH); 'Paratype' 1♀*: 'N China' McL. coll (BMNH). – Fischer 1962: 15. Fischer 1972: 7-8. Syn. n.

nec *Dipseudopsis stellata*. – Ulmer 1915: 73 (Sri Lanka); Lestage 1925: 65, 115 (Java); Banks 1931b: 401 (*stellatus*, Thailand); Tsuda 1942: 266 (Thailand); Schmid 1958: 35, 89 (Sri Lanka).

Dipseudopsis nebulosa. – Banks 1914: 178 (Luzon) [misdet.].

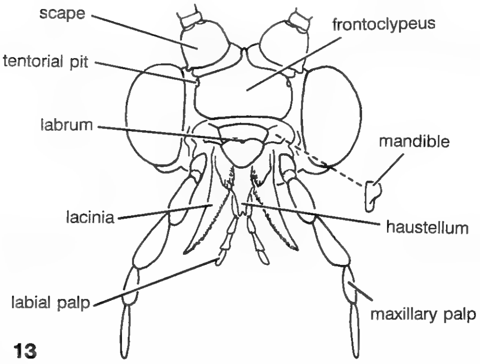
Dipseudopsis bakeri Banks, 1916: 215-216, pl. 2: figs. 20, 21, Type ♂*, PHILIPPINES: Luzon, Laguna, Mt Maquiling and Los Baños,Baker (MCZC 11768). Only 1♂ at the MCZC labelled as type, although several other specimens, not labelled as types, at the MCZC and USNM are part of the type series. – Fischer 1962: 5; Fischer 1972: 3. Syn. n.

Dipseudopsis discors Navás, 1924: 205. – Fischer 1962: 8. Syn. n.

Dipseudopsis morosa. – Banks 1924: 450 (pro parte). Syntype 1♂* is actually *D. collaris*: Luzon: Mt Maquiling, Baker (MCZC 14826).

Bathytinodes alba Iwata, 1927: 209-210, pl. 4: fig. 87-91.

Dipseudopsis alba (Iwata, 1927). – Fischer 1962: 217; Fischer 1972: 2.



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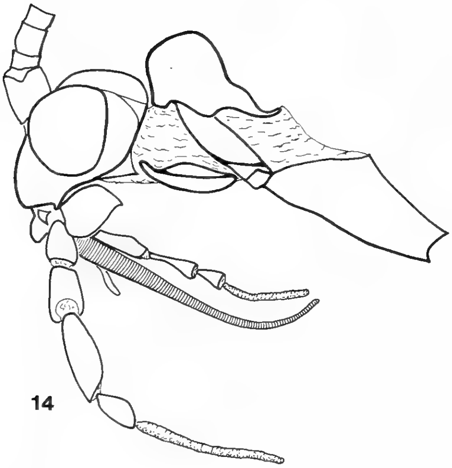

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Figures 13-14. – Fig. 13, *Dipseudopsis sp.*, male head, anterior, modified after (Crichton 1957). Fig. 14, *Dipseudopsis doehleri* Ulmer, male head and prothorax, lateral.

Specimens examined. – CHINA: Guangdong: 3♂, Hushan, 3.VI.1963, Tian (CLHM). Jiangxi: 1♂ 2♂, det. Ulmer (1905) as *D. stellata*, 'Kiang-si', 1869, A. David (MNHN). Hong Kong: 1♂, Foochow (MCZC). Jiangsu: 6♂, Fulin, 18.VIII.1987, Tian (CLHM). 8♂ 1♀, Jinhu, 22.VI.1987, Sun Changhai (USNM). Zhejiang: 1♂ 1♀, 'Chekiang Hangtchéou', Hangzhou, 1925, A. Pichon (MNHN). 2♂ 1♀, Shanghai, det. McLachlan as *D. stellata*, (BMNH). 2♂, Shuian, 20.VI.1957, Tian (CLHM). JAPAN: 1♂, Lewis, McL. coll (BMNH). PHILIPPINES: Luzon: 8♂ 1♀ Los Baños (MCZC), 27♂ (USNM), 1♂ (BMNH). 1♂, Manila (MCZC). 33♂ 6♀, Mt Maquiling, Baker (USNM), 2♂ (CNCI), 7♂ 4♀ (MCZC), 1♂ 1♂ (BMNH). 3♂ 1♀, Balinag, A. P. Ashby (USNM).

Male. – Head, thorax, wings and legs with colouration similar to *D. robustior*. Forewing 13-15 mm, with circular pattern of 5-7 small translucent spots around discal cell, having most spots distal to cord, and spot at arculus adjoining hyaline area at apex of Cu_2. Modified spur (fig. 21) apical ⅓ bifid, crescent-shaped, with two subequal curved points. Genitalia (fig. 21): Tergum IX triangular in dorsal view, slightly overhanging segment X in lateral view; sternum IX mesosuperior process ellipsoidal with blunt apex pointed posteriad, extending above basal ⅔ of phallus. Preanal appendages with posterior margin slightly incised in lateral view, dorsal margin at right angle to posterior margin, ventral margin at obtuse angle, sometimes varied with ventral margin continuous with posterior margin. Inferior appendages fingerlike with short basoventral shelf in lateral view.

Distribution. – China: Guangdong, Hong Kong, Jiangsu, Jiangxi, Zhejiang; Philippines: Luzon; Japan: Honshu.

Remarks. – This species is similar to *D. robustior*, but differs by having inferior appendages more broad and fingerlike in lateral view (although this is variable) and modified spur with two apical points both crescent-shaped and subequal in length. In *D. robustior* the inferior appendage is more slender and angled, its modified spur bears two points, one point slenderer, more curved and more than 2x longer than other. Previous records of *D. collaris*, as *D. stellata*, from Sri Lanka, Java and Thailand are probably in error.

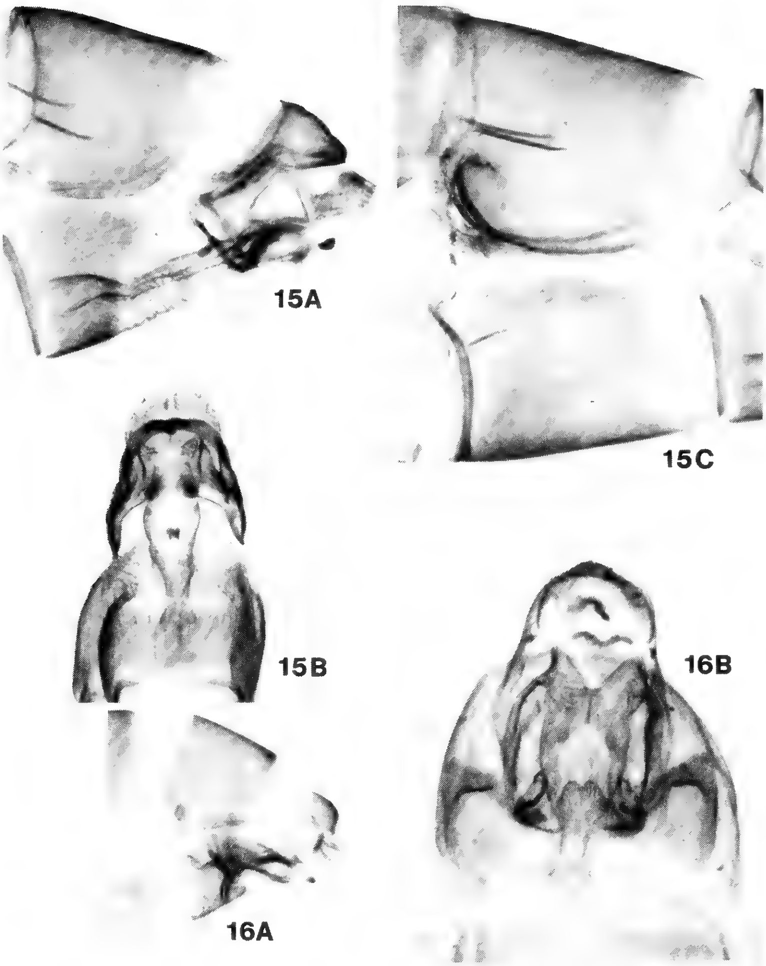
Dipseudopsis contorta Banks, 1931
(fig. 22)

Dipseudopsis sp. – Ulmer, 1905: 96, fig. 75c (not fig. 75e as listed by Fischer 1962).
Dipseudopsis infuscata. – Ulmer 1905: 96, fig. 75d; Ulmer 1951: 128 [prob. misdet.].
Dipseudopsis contorta Banks, 1931b: 400-401, fig. 20, lectotype by present designation ♂*: MALAYSIA: West Malaysia: Selangor, Kuala Lumpur, 29.I.1924, at light, H. M. Pendlebury (BMNH); paralectotype 1♂*, without hind legs: Pahang, Kuala Tahan, 300ft at light, 23.XI.1921, H. M. Pendlebury (MCZC 16480). – Fischer 1962: 8; Malicky & Weaver 1988: 3-4, fig. 3a-e.

Specimens examined. – 2♂, 'Borneo' det. Ulmer 1905 as *D. infuscata* (MNHN). INDONESIA: Kalimantan: 1♂, Pontianak, VII.1907, F. Muir (USNM). Java: 1♂, [Muller?] (RMNH). Sumatra: 1♂, Dolok Merangir, 19.VII-20.VII.1971, Diehl (CLHM). 1♂, same data, V-X.1980, Diehl (CLHM). 1♂, Ost-Aceh 26-30.VIII. 1972, Diehl (CLHM). 1♂, NE Sumatra, 16.I-18.II.1979, Diehl (CLHM).

Male. – Head dorsum dark brown, except posterior warts orangish brown, frontoclypeus dark brown, antennae orangish brown; cervical sclerites dark brown, pronotum light orangish brown and mesonotum dark brown. Maxillary palps 2.2 mm, brown;

Figures 15-16. – Fig. 15, *Dipseudopsis recta* Martynov, female: 15A, genitalia, lateral; 15B, genitalia, ventral; 15C, abdominal segment VII, lateral. Fig. 16, *Dipseudopsis sp.* female, 'Manipur Nungha' (CNC): 16A, genitalia, lateral; 16B, genitalia, ventral.



proboscis 1.6 mm, as long as first two segments of maxillary palps. Forewing 10-12.5 mm, brown with row of lighter spots from stigma to Cu_1 just distal to cord, and large translucent spot at arculus, hyaline spot at m-cu. Legs mostly light brown, except front and middle coxae dark brown. Modified spur (fig. 22) distal ⅓ branched into two subequal curved points, with points diverging basally but converging distally, sometimes with rounded subapical shelf. Genitalia (fig. 22): Tergum IX semicircular in dorsal view, with posterior margin having almost no extension overhanging segment X in lateral view; sternum IX with mesosuperior process short, slender, acuminate having apex curved dorsad in lateral view. Segment X ellipsoidal in dorsal view, long trapezoidal in lateral view, extended distad beyond apex of inferior appendage. Preanal appendages variable, either D-shaped with lobe extending distally as far as inferior appendages in lateral view, or with posterior margin incised and with short dorsoapical blunt point. Inferior appendages with basoventral notch and apicoventral obtuse angle in lateral view, apical ½ variable, either equal in height to base and truncate, or sometimes more expanded and clavate; with apex and apicolateral margin curved in ventral view, but bearing subapicomesal obtuse tooth.

Distribution. – Indonesia: Kalimantan, Sumatra, Java; Malaysia: West Malaysia.

Remarks. – This species is similar to *D. collaris*, but differs by having the inferior appendage capitate, with

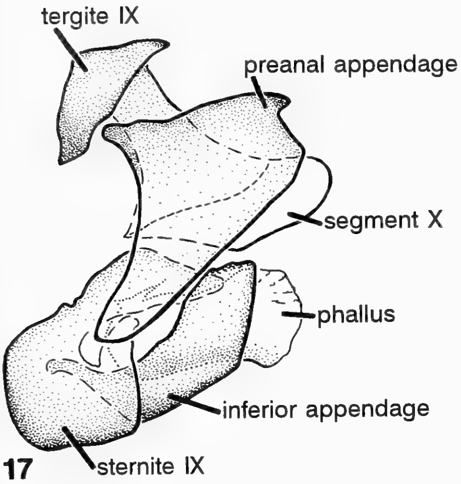


Figure 17. – Fig. 17, *Dipseudopsis sp.*, male genitalia, lateral.

a basodorsal notch and an apicoventral obtuse angle in lateral view, and the modified spur with apical points directed more laterally. Slight variation is noticeable in the male modified spur and genitalia (cf. Malicky & Weaver 1988).

Dipseudopsis diehli Malicky & Weaver, 1988
(fig. 23)

Dipseudopsis diehli Malicky & Weaver, 1988: 8, fig. 6a-f. Holotype ♂*: INDONESIA: Sumatra: Prapat, 1400m, Diehl (CLHM); paratypes 27♂: Prapat, Bukit Tinggi, Aek Tarum, Sitahoan, Dolok Merangir (CLHM, CLJW).

Specimens examined. – INDONESIA: Sumatra: Pematang Siantar: 5♂, 1.VII.84-13.IV.1985; 3♂, 1.VI-12.XII.1985; 3♂, 22.IV-11.VII.1986; 5♂, 1.IX.88-15.I.1989; 1♂, 9.III-10.X.1989, Diehl (CLHM).

Male. – Head dorsum yellowish brown with dark semicircular spot at anterior margin. Frontoclypeus brown. Scape yellowish brown, distal portion of antenna brown. Maxillary palps 3.0 mm, proboscis 2.4 mm, extending as far as 4½ segment of maxillary palp. Cervical sclerites and pronotum yellowish brown. Mesonotum and tegulae brown, with scutellum yellowish brown. Forewing 16-20 mm, brown with four translucent areas: 1) long stripe adjacent to costal margin; 2) ellipsoidal spot between stems of R and M; 3) transverse band distal to cord, between R_1 and M_4, with two V-shaped incisions along distal margin, and having narrow connection with anterior margin; 4) triangular spot at arculus. Hindwing unicoloured brown, but with hyaline comma at m-cu. Legs yellowish brown, with light brownish tibiae, apparently caused by more dense covering of fine brown setae. First segment of hind tarsi uniquely bent mesad about ⅓ of its length to permit free motion of broad modified spur. Modified spur (fig. 23) with apex bifid with two sinuate points nearly parallel and slightly unequal in length, both curved mesad, but apices curved distad. Genitalia (fig. 23): tergum IX with apical ⅓ hanging over base of segment X in lateral view; broad and short with posterior margin bilobed or slightly triangular in dorsal view, anterior margin slightly bilobed. Sternum IX mesosuperior process extending to end of phallus. Segment X ellipsoidal in dorsal view. Preanal appendages triangular in lateral view with dorsal margin slightly inclined dorsad and ventroposterior margin curved steeply dorsad. Inferior appendages fingerlike and with ventral margin slightly concave in lateral view, but dorsal margin serrate in middle; with U-shaped basomesal notch in ventral view, distal arms slightly diverging apically and each tapering into small apical lobe.

Distribution. – Indonesia: Sumatra.

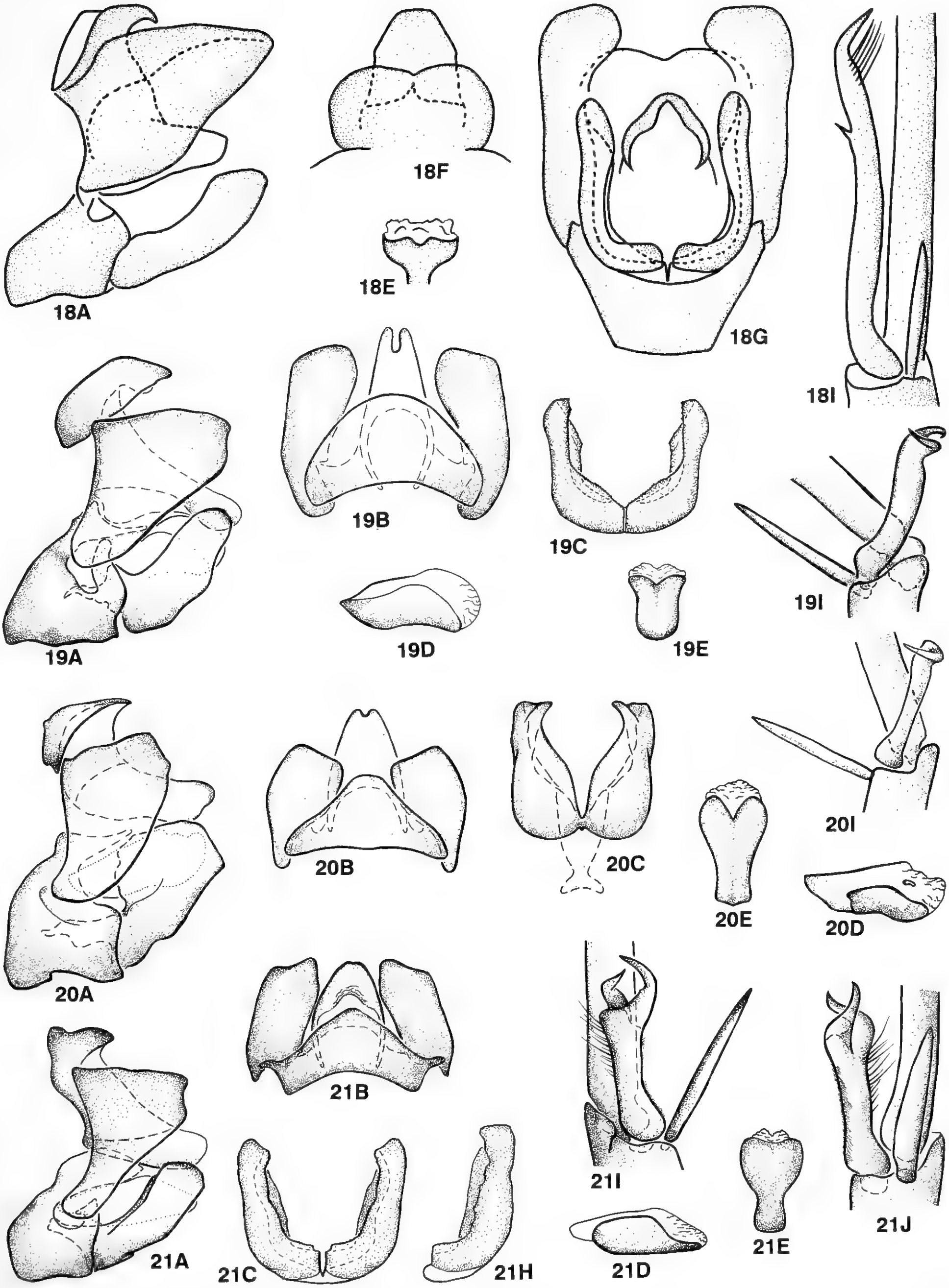
Remarks. – This species is easily recognized by having the male modified spur extremely broad and bifurcate, with points curved a wide whorl, and by having forewing with large translucent spots. Some specimens are darker brown, having brown parts that are usually yellowish brown in other species.

Dipseudopsis digitata Ulmer, 1907
(figs. 8, 24)

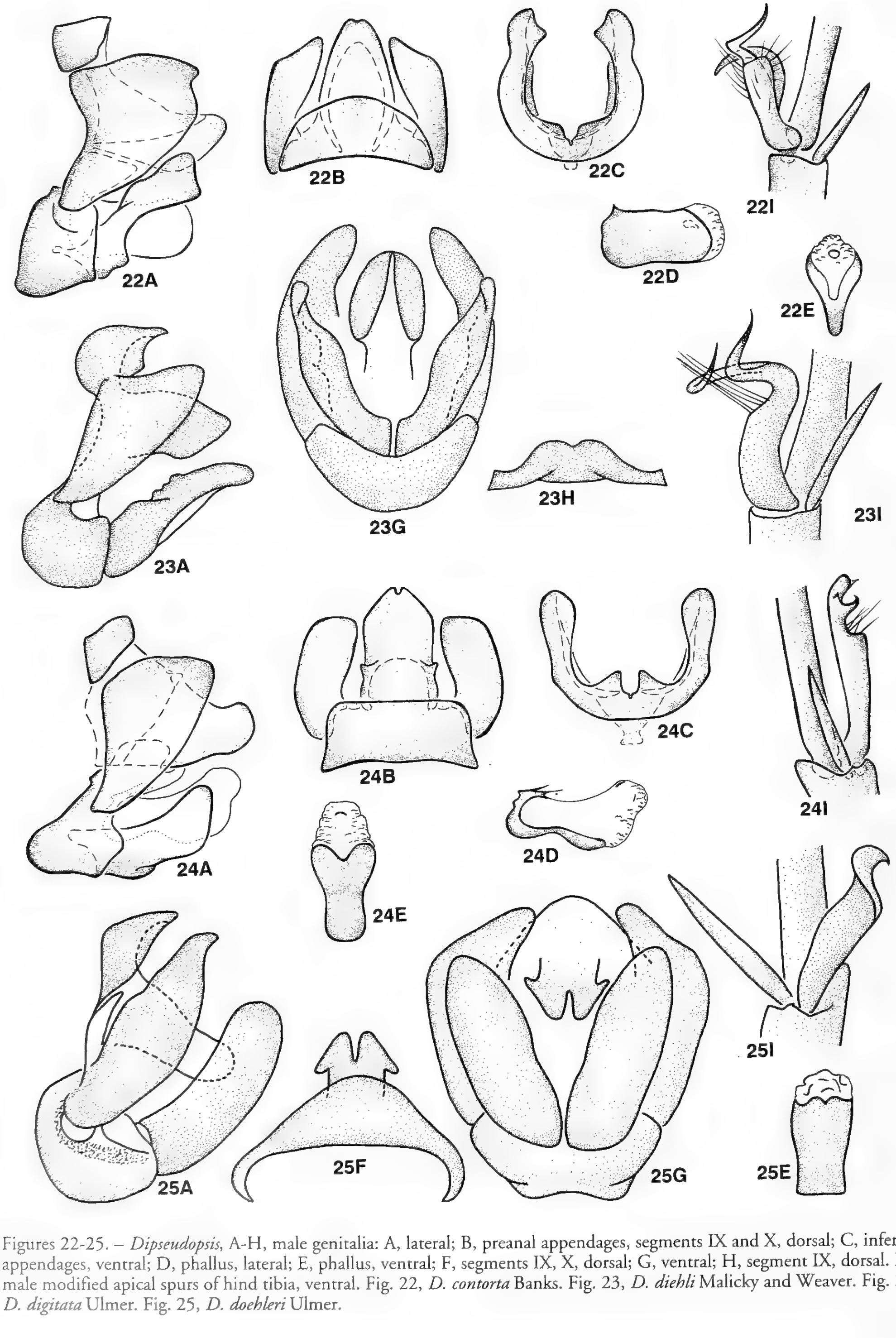
Dipseudopsis digitata Ulmer, 1907a: 39-40, figs. 56-57, Holotype ♂*: MALAYSIA: Banguey Is, Staudinger (ZMHB). – Fischer 1962: 8; Fischer 1972: 3.

Specimens examined. – PHILIPPINES: Balabac: 2♂, Dalawan Bay, 5.X.1961; 1♂, 9.X.1961; 3♂, 12.X.1961 (ZMUC). Busuanga: 5♂, 4 km N San Nicolas, 20-29.V.1962, H. Holtmann (BPBM). Culion: 6♂ 1♀, 6km W Culion, 7-11.VI.1962, light trap, H. Holtmann (BPBM). Palawan: 1♂, Brooke's Point, Macagua, 75m, 1-4.IV.1962 (BPBM). 19♂ 1♀, Tarumpitao Point, H. E. Milliron (BPBM). 17♂ 7♀, Irawan, 14km W Puerto Princessa, 5m, D. R. Davis (USNM). 1♂, Litso, Amoyan Ck., 57km N Puerto Princessa, 10m, 10.XII.1965, D. R. Davis (USNM). 1♂, Mainit, 11km NW Brooke's Point, 18.XI.1965, D. R. Davis (USNM). 1♂, Chromite Mine, 28km W Puerto Princessa, 400m, 1-7.XII.1965, D. R. Davis (USNM). 30♂, Brooke's Point, Uring Uring, 14-23.VIII.1961 (ZMUC).

Male. – Body and wings (fig. 8). Head, thorax and forewing with pattern of light and dark bands. Head dorsum with dark brown median band widening anteriad and narrowing posteriad, lateral areas light brown and posterior warts lighter. Frontoclypeus mostly dark brown, but with yellowish V-shaped band pointed dorsad. Antennae light brown. Maxillary palps 2.3 mm, proboscis 1.4 mm, as long as



Figures 18-21. – *Dipseudopsis*, A-H, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral; H, left inferior appendage, ventral. I-J, male modified apical spurs of hind tibia, ventral. Fig. 18, *D. adiaturix*, n. sp. Fig. 19, *D. benardi* Navás. Fig. 20, *D. bicolorata* Martynov. Fig. 21, *D. collaris* McLachlan, 21H, type of *D. stellata* McLachlan.



Figures 22-25. – *Dipseudopsis*, A-H, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral; H, segment IX, dorsal. I-J, male modified apical spurs of hind tibia, ventral. Fig. 22, *D. contorta* Banks. Fig. 23, *D. diehli* Malicky and Weaver. Fig. 24, *D. digitata* Ulmer. Fig. 25, *D. doehleri* Ulmer.

first three segments of maxillary palp. Cervical sclerites dark brown ventrally, light brown dorsally. Pronotum with raised areas light brown, median furrow and lateral sides dark brown. Mesonotum and tegula dark brown. Forewing 10-14 mm, with striped pattern of dark brown veins and lighter cells, noticeably darker along thicker veins, R_1 and Cu_1. Legs with coxae dark brown and trochanters and distal segments light brown, except front coxa bicoloured, dark brown ventrad and lighter dorsad. Modified spur (fig. 24) with three minute apical points and one long acuminate subapical point curved laterally, all points distal to blunt subapical shelf. Genitalia (fig. 24): Tergum IX short and truncate in lateral view, posterior margin not overhanging segment X, rectangular in dorsal view; sternum IX small, with massive mesosuperior process having large broad dorsal lobe and slender posteroventral process extending above basal ⅔ of phallus. Segment X with pair of minute basodorsal lateral lobes, dorsal margin angled obliquely ventrad in lateral view, but with apex turned dorsad, ventral margin straight but also turned dorsad apically; about ½ as wide as tergum IX and about twice as long as wide in dorsal view, lateral sides parallel but tapered into triangular apex, and apex slightly incised. Preanal appendages broad and not incised in lateral view, somewhat triangular with dorsal margin and ventral margin curved and converging at blunt dorsal apex. Inferior appendages capitate in lateral view, dorsal margin concave, ventral margin straight with short basal shelf, apex truncate with corners slightly curved, extended dorsad.

Distribution. – Malaysia: Banguey Is.; Philippines: Balabac, Busuanga, Culion, Palawan.

Remarks. – This species is easily recognized, having the male segment X with a pair of minute dorsolateral lobes at its base, and modified spur with three minute apical points, one long acuminate subapical point curved laterally, and all points distal to a squarish subapical shelf.

***Dipseudopsis doehleri* Ulmer, 1929**
(figs. 5, 12B, 14, 25)

Dipseudopsis döhleri Ulmer, 1929: 189-190, fig. 27, Holotype ♂*: INDIA: Meghalaya: Khasi Hills, McL. coll (BMNH). – Fischer 1962: 8.
Dipseudopsis doehleri Ulmer. – Fischer 1972: 4; Higler 1992: 80

Specimens examined. – BURMA: 1♂, Washaung, 20km E of Myitkyina, 200m, 4.VII.34, Malaise (NHRS). 1♂, Myitkyina, 175m, 1934, Malaise (BMNH). INDIA: Assam: 1♂, 8mi E Ledo, 125m, 27.34N 95.34E, 13.X.1961, Ross & Cavagnaro (CASC). 2♀, Abhoypur For., Naphuk, 360m, 12.X.1961, Ross & Cavagnaro (CASC). THAILAND: 9♂, Nakhon Nayok Prov., Khao Yai National Park, 700m, 29.IX-6.X.1984, Karsholt, Lomholdt & Nielsen (ZMUC). 7♂, Nam Nao, Pet Cha Boon, 5.V.1989, Allen (CLHM). 20♂, Puk Hieo, Chayapoom, 6.V.1989, Allen (CLHM).

Male. – Body and wings (fig. 5). Head and all of its appendages dark brown, except proboscis yellowish. Mouthparts (fig. 12B, 14): Maxillary palps 3.6 mm; proboscis 2.7 mm, extended to midlength of apical segment of maxillary palp; haustellum 0.8 mm; labial palps 1.7 mm. Cervical sclerites and prothorax ivory. Mesonotum, tegula and metanotum dark brown. Forewing 16-17 mm, dark brown with three distinct translucent spots: 1) basal triangle between R_1 and Cu_1 from base to fork I of Rs, 2) subapical spot distal to cord with apical margin incised at forks II, and III) ellipsoidal spot at arculus, similar as in *D. nebulosa* except for translucent spot at arculus. Legs dark brown, except front coxa with lateral side ivory. Hindwing with large translucent triangle as in front wing, apical region brown, anal region translucent, Cu_1 dark brown. Modified spur (fig. 25) similar to *D. immaculata*, unbranched, slightly longer than adjacent spur, basal ⅔ unmodified, apical ⅓ twisted 180° into short spiral, apical point directed mesad. Abdomen with anterior sternites II-V ivory, giving translucent triangles of forewings a white background so that contrasting pattern is displayed when wings are folded, sternites VI-VIII dark brown. Genitalia (fig. 25): Tergum IX triangular with posterior margin rounded in dorsal view, apical ½ overhanging segment X in lateral view. Segment X long slender in lateral view, with short base having parallel sides in dorsal view, and apical portion cordate and apex deeply incised. Preanal appendages abbreviated with slender dorsoapical point in lateral view, but truncate and triangular in dorsal view. Inferior appendages long and thumblike, without incisions or points, curved slightly dorsad in lateral view.

Distribution. – Burma; India: Assam, Meghalaya; Thailand.

Remarks. – This species is most similar to *D. nebulosa*, but differs by having the head entirely dark brown and pronotum ivory, forewing with translucent round spot at the arculus, and modified spur relatively shorter, with less than ½ of apical portion twisted. It also differs by having male genitalia with segment X and the preanal appendages more slender in lateral view, and segment X also bears a unique pair of basolateral humps in dorsal view. A teneral male specimen from Hainan Island, possibly an undescribed species near *D. doehleri*, was observed in the collection at the MCZC.

Dipseudopsis elongata Banks, 1920
(fig. 26)

Dipseudopsis elongata Banks, 1920: 361-362, pl. 1: fig. 13, Type ♂*: MALAYSIA: Sabah, Sandakan, Baker (MCZC 10882). – Fischer 1962: 8-9; Fischer 1972: 4.

Specimens examined. – MALAYSIA: Sabah: 1♂, Sandakan Bay, NW Sepilok For. Res., 1-10m, 26.X.1957, J. L. Gressitt (BPBM). 1♂, 'North Borneo' McL. coll (BMNH).

Male. – Head dorsum glossy dark brown, but posterior warts light brown, frontoclypeus glossy dark brown, genae yellowish. Cervical sclerites, pronotum, mesonotum tegula dull dark brown. Antenna brown, but scape light brown. Palps brown, maxillary palps 3.0 mm; proboscis 2.0 mm, as long as first 3½ segments of maxillaty palp. Forewing 16 mm, uniformly dark brown, with small hyaline spots at nygma and m-cu, and large translucent spot at arculus. Front and middle leg with coxa, trochanter and basal ½ of femur dark brown, and distal portion of leg light brown; hind leg light brown. Modified spur (fig. 26) long and truncate, about 3X longer than adjacent spur, with apex more than 2X as wide as base, and minute apical points curved mesad. Genitalia (fig. 26): Tergum IX short and slightly overhanging segment X in lateral view, posterior margin rectangular with lateral edges curved in dorsal view; sternum IX with elongate mesosuperior process, extending above ¾ of phallus in lateral view. Segment X acuminate with blunt apex in lateral view; broad ellipsoidal with apex slightly incised in dorsal view. Preanal appendages triangular with corners rounded and dorsal margin slightly concave in lateral view, ventroposterior margin curved dorsad, apex broad and blunt. Inferior appendages capitate with curved truncate apex in lateral view.

Distribution. – Malaysia: Sabah.

Remarks. – This species was previously only known from the unique type from Sabah. Two additional male specimens were found in the material borrowed from BPBM and BMNH. The male is distinguished by having modified spur long and truncate, about 3X longer than adjacent spur, with apex more than 2X wider than base, and with minute apical points curving mesad.

Dipseudopsis flavisignata (McLachlan, 1866)
(fig. 27)

Nesopsyche flavisignata McLachlan, 1866: 269, pl. 17: fig. 6, pl.: 19 fig. 6, Type ♂*: INDONESIA: Sulawesi: Ujung Pandang, 'Celebes Macassar', Wallace coll. (BMNH). The type was mounted on two separate slides by Mosely (1933), one slide with wings mounted dry, and the second slide with body mounted in balsam, but prothorax absent.

Dipseudopsis flavisignata (McLachlan, 1866). – Mosely 1933: 499-502, figs. 1-7. Fischer 1962: 9. Fischer 1972: 4.

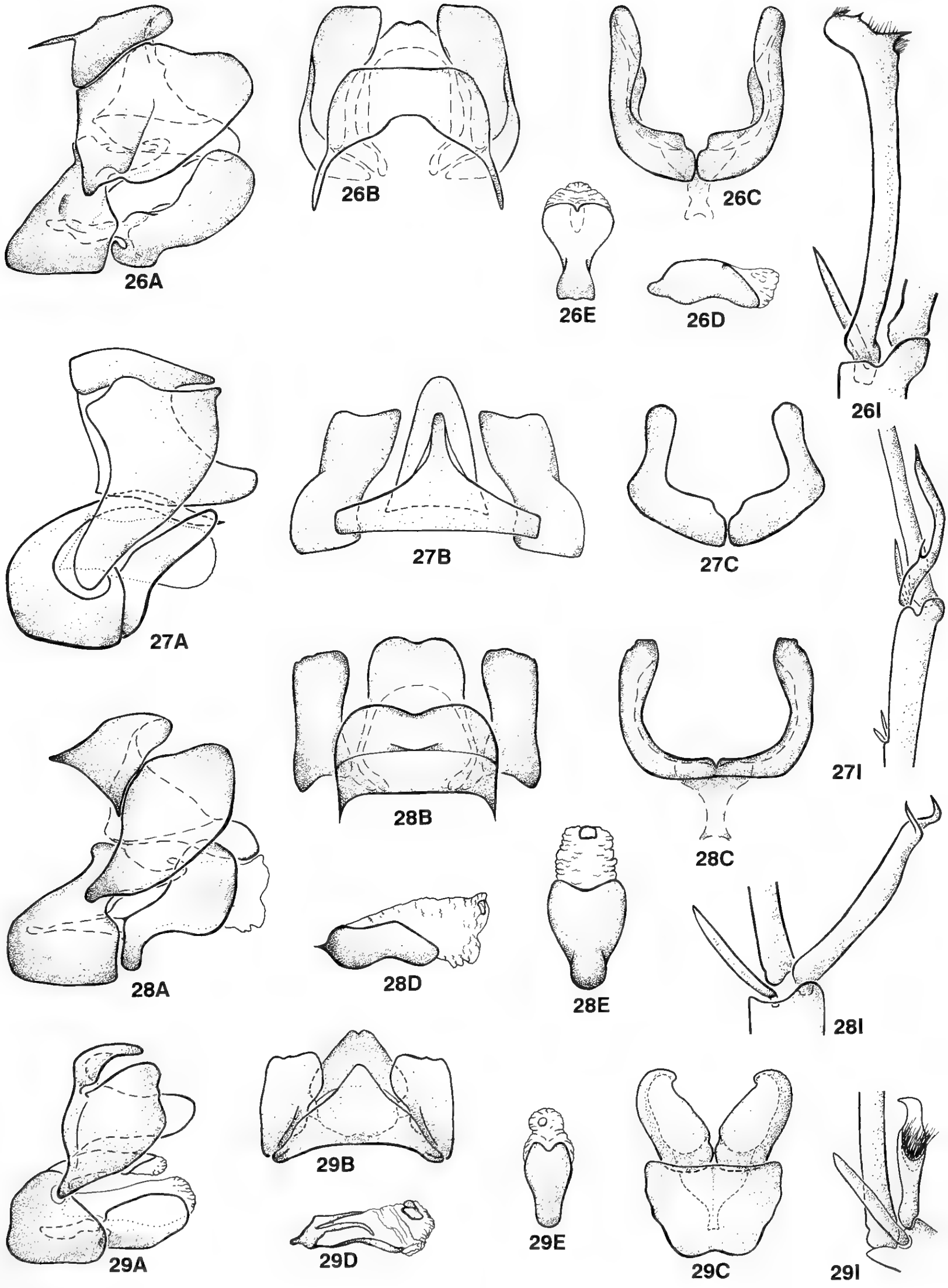
Male. – Head dorsum dark brown, yellowish brown between antenna, frontoclypeus dark brown. Antenna base of scape yellowish brown and remainder dark brown. Maxillary palps 2.3 mm dark brown, labial palps 0.8 mm yellowish. Proboscis 1.7 mm about as long as first four segments of maxillary palp. Mesothorax and abdomen black. Forewing 12 mm, similar to that of *D. spectabilis* (fig. 9), dark brown background with large yellowish spots: 1) irregular band on anterior margin tapering toward base, 2) subapical C-shaped spot having distal side open and filled with dark narrow stripe along M_1 (but in description by Mosely (1933: fig. 1) the latter is depicted as an irregular O-shaped spot), 3) semicircular irregular band through anal region, running from base, distad through anal loops and thyridial cell to arculus. Front leg with coxa, trochanter and basal portion of femur dark, apical portion yellowish; Middle and hind leg with similar colour pattern but lighter. Modified spur (fig. 27) nearly as long as first tarsal segment, basal ¼ unmodified, distal slender twisted blade, bearing a small tooth at base, a ridge at midlength and apical ½ flattened like a blade. Genitalia (fig. 27): Tergum IX posterior margin broad at base in dorsal view, but abruptly tapering into slender fingerlike extension, apical ½ overhanging segment X in lateral view. Segment X long ovoid projection tapering slightly posteriad in dorsal view. Preanal appendages with dorsal margin nearly horizontal, meeting curved ventroposterior margin at small dorsoapical lobe in lateral view. Inferior appendages similar as in *D. spectabilis*, heavily sclerotized, and darker brown than other appendages, basal ⅓ angled dorsally, and apical ⅔ fingerlike and angled more posteriorly in lateral view.

Distribution. – Indonesia: Sulawesi.

Remarks. – This species is only known from the unique type. It is a sibling species to *D. spectabilis*, but differs by having the forewing with a yellowish C-shaped subapical spot, almost closed except for a narrow dark strip along M_1, and by having the modified spur with one short subapical point distant from apical point.

Dipseudopsis flinti sp. n.
(figs. 11, 28)

Type material. – Holotype ♂: MALAYSIA: West Malaysia:



Figures 26-29. – *Dipseudopsis*, A-G, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral. I-J, male modified apical spurs of hind tibia, ventral. Fig. 26, *D. elongata* Banks. Fig. 27, *D. flavisignata* (McLachlan). Fig. 28, *D. flinti*, n. sp. Fig. 29, *D. immaculata* Ulmer.

Selangor, Kuala Lumpur, 21.IV.1931, H. M. Pendlebury, (MCZC 33382).

Male. – Head completely glossy dark brown, almost black, antennae and mouthparts dark brown. Maxillary palps 2.3 mm, proboscis 1.3 mm, as long as first three segments of maxillary palp. Pronotum dull dark brown, except anterior margin light, mesonotum and tegula dark brown and metanotum light brown. Forewing 12 mm, dark brown except for slender light brown stripe along posterior margin, running from cell 3A and expanded at arculus; cells below M_2 and Cu_1 light brown distally. Front leg with coxa, trochanter and basal ⅔ of femur dark brown, distal portions of leg light brown; middle leg with coxa dark brown and distal segments light brown; hind leg light brown. Modified spur (fig. 28) about 2X longer than adjacent spur, having less than apical ¼ bifid with two short apical points parallel and angled distad toward tarsus. Genitalia (fig. 28): Tergum IX posterior margin broadly bilobed in dorsal view; IX sternum base rectangular in lateral view, mesosuperior process with blunt dorsal lobe and slender posterior projection with apex curved anteriad. Preanal appendages trapezoidal with dorsal margin slightly inclined dorsad toward blunt distal apex in lateral view, ventral margin curved gradually into posterior margin. Segment X about ⅔ as wide as tergum IX in dorsal view, somewhat rectangular with posterior margin broadly bilobed. Inferior appendages capitate with apical ½ ellipsoidal and about 3X as thick as base in lateral view, lateral arms slender and fingerlike with truncate apex in ventral view.

Etymology. – Named after Oliver S. Flint, Jr.

Distribution. – Malaysia: West Malaysia.

Remarks. – This species is only known from the unique type. The modified spur of the male is similar to that of *D. stabatensis*, but it differs by having two apical points parallel and angled toward the tarsus, the adjacent spur is relatively shorter, about ½ as long as the modified spur; in *D. stabatensis* the apical points of the modified spur are not parallel but are directed in opposite directions, and the adjacent spur is relatively longer, ⅔ as long as the modified spur. Also, *D. flinti* differs by having the inferior appendage capitate in lateral view, with the apical ½ ellipsoidal and about 3X as broad as the base.

Dipseudopsis immaculata Ulmer, 1905

(fig. 29)

Dipseudopsis immaculata Ulmer, 1905: 92-93, 96, figs. 68b, 69, Type ♂, 'Borneo' in alcohol (MNHN). – Fischer 1962: 9; Weidner 1964: 73; Fischer 1972: 4; Malicky & Weaver 1988: 4, fig. 1a-e.

Dipseudopsis moesta Banks, 1931b: 400, 401, fig. 9, Type ♂*: MALAYSIA: West Malaysia: Johor, Lubok, Kedondong, NW Gunung Ledang (Mt Ophir), Lalang & Belukar, H. C. Abraham (MCZC 16481). – Fischer 1962: 11. Syn. n.

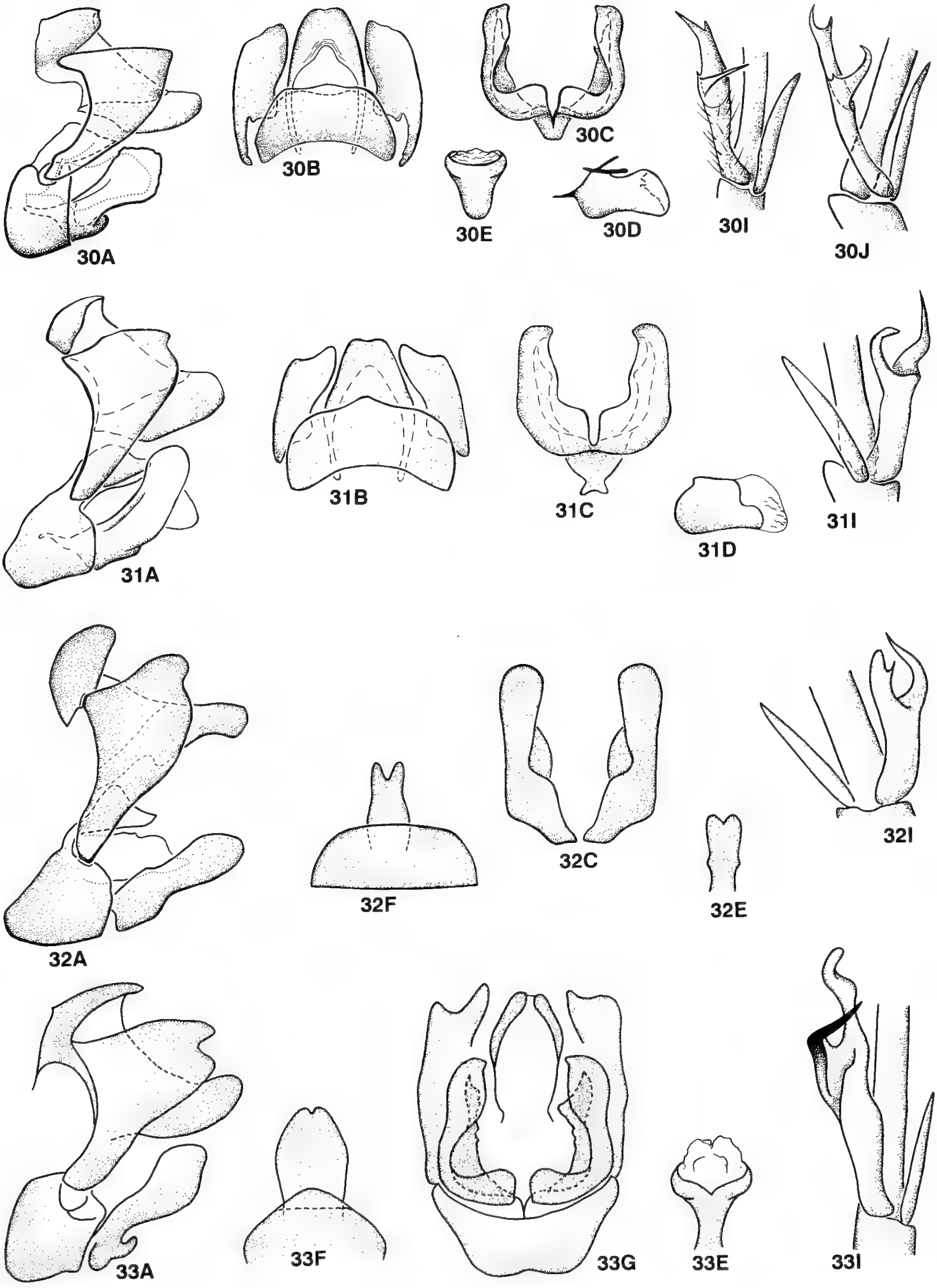
nec *Dipseudopsis moesta*. – Ulmer 1951: 128 [reidentification of Ulmer 1905, fig. 75b sub nom. *D. stellata*] [= *D. benardi*].

Specimens examined. – INDONESIA: Sumatra: 2♂, Karny, Pakan Baroe, at light, 23.X.1925 (RMNH). 1♂, Huta Padang, 20.I.1990, Diehl (CLHM). 1♂, Dolok Merangir, 15.VI.82-4.I.1983, Diehl (CLHM). MALAYSIA: Sarawak: 1♂, Merirai Valley near Kapft, 180m, 28.VII.-6.VIII.1958, T. C. Maa (BPBM). West Malaysia: 1♂ 1♀, Pahang, Rompin Mining Co., railway track, 31km, Petoh Swamp, 11.XII.1960 (BPBM).

Male. – Head dorsum, cervical sclerite and pronotum light orangish brown; frontoclypeus mostly dark brown, but lateral margins yellowish brown; genae yellowish brown except dark brown ventral spike. Antennae light brown. Mouthparts brown, maxillary palps 2.2 mm; proboscis 1.2 mm, about as long as first three segments of maxillary palps. Mesonotum and tegula dark brown, about as dark as eyes. Legs light brown. Modified spur (fig. 29) slightly longer than adjacent spur, apical ½ modified into twisted point with setose basal pocket; apex almost truncate, but lateral side curved and other side with short point directed toward tarsus. Tegula dark brown. Forewing 11-12 mm, almost uniformly brown, except for hyaline spots at m-cu and arculus. Genitalia (fig. 29): Tergum IX triangular in dorsal view, with about ¾ of posterior overhanging segment X in lateral view. Segment X thumblike in lateral view, extending posteriad as far as inferior appendage; broadly cordate in dorsal view with apex slightly incised. Preanal appendages rhomboidal or sometimes simply rounded in lateral view. Inferior appendages oblong and truncate in lateral view, ellipsoidal in ventral view, but apicomesal margin incised with blunt subapicomesal tooth.

Distribution. – Indonesia: Sumatra; Malaysia: Sarawak, West Malaysia.

Remarks. – The male of this species has a modified spur which is similar to that of *D. doehleri* and *D. nebulosa*, but can be distinguished from these by its almost uniformly dark brown forewing. It also differs by having the male genitalia with more than ⅔ of tergum IX overhanging segment X, and the inferior appendage with a blunt subapicomesal tooth in ventral view. A lighter phase is noted in male specimens from Borneo, having apical region of the forewing brown, remainder nearly translucent except for several dark



Figures 30-33. – *Dipseudopsis*, A-G, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral. I-J, male modified spurs apical spurs of hind tibia, ventral. Fig. 30, *D. indica* McLachlan. Fig. 31, *D. infuscata* McLachlan. Fig. 32, *D. knappi* Schmid and Denning. Fig. 33, *D. lamellata* Martynov.

veins. A slight variation also is observed in males from Sumatra, having forewing with narrow lighter strip along anterior margin and indistinct translucent area in outer ⅓ of wing, and preanal appendage more noticeably incised distally. Regarding specimen determined as *D. stellata* by Ulmer (1905: fig. 75b) and later determined as *D. moesta* by Ulmer (1951), cf. 'Remarks' of *D. benardi* above.

Dipseudopsis indica **McLachlan, 1875**

(fig. 30)

Dipseudopsis indica McLachlan, 1875: 18-20, pl. 2: figs. 13-14 (*indicus*), Type 'Habitus in India orientali.' Lectotype ♂: INDIA, designated by Kimmins (1957: 101). – Fischer 1962: 10; Fischer 1972: 4; Higler 1992: 80.

Dipseudopsis buddha Banks, 1913: 239, pl. 23: fig. 8, pl. 24: fig. 19, Type ♂*: INDIA: West Bengal, Chapra, Mackenzie, no date (MCZC 11757). – Fischer 1962: 5; Higler 1992: 80. **Syn. n.**

Dipseudopsis indica sindica Martynov, 1935: 159, 206, fig. 59a-b, Type: Pakistan: '♂. Bubak, Sind, from pools. 12.XI.1927. B. Prashad and B. N. Chopra.' – Fischer 1962: 10; Fischer 1972: 4. **Syn. n.**

Specimens examined. – BANGLADESH: 18♂ 36♀, Chicknagul, 10mi N Sylhet, 10m, 30.IX.61, Ross & Cavagnaro (CASC). 5♂ 6♀, Cormilla, 50ft, 23.IX.61, Ross & Cavagnaro (CASC). INDIA: Bihar: 1♂, Pusa, at light, 22.-VIII.08 (MCZC). 1♂, Pusa, IV.1919, M. A. Husain (BMNH). 1♂, Pusa, 2.VIII.1924, Mukerjee (BMNH). Orissa: 2♂, det. Martynov, Balighai, near Puri, 16-20.VIII.11 (ZRAS). 1♂, Cuttack, 6.III.1944, at light (BMNH). 2♂, Bhubaneswar, II.1983, J. Oláh (CLHM). West Bengal: 1♂, Chapra, Mackenzie (MCZC). 6♂ 32♀, Malda 110m, 28.X.61, Ross & Cavagnaro (CASC). 2♂ 2♀, 10mi SE Asansol 175m, 6.XI.61, Ross & Cavagnaro (CASC). Pakistan: Sind: 1♂, Makli, near Thatta, 22.IX.1976, Hevel & Dietz (USNM). 2♂ 1♀, Makli, near Hyderabad, 24.IX.1976, Hevel & Dietz (-USNM).

Male. – Colour dull brown, with eyes dark brown. Pronotum lighter brown than head and mesonotum. Maxillary palps 2.0 mm; proboscis 0.8 mm, as long as first 3½ segments of maxillary palp. Legs light brown. Modified spur (fig. 30) with apical ½ modified, subdivided into two acuminate branches, first branch bifid with apical points unequal and both directed distally, second branch curved, directed laterally with minute point at its base. Forewing 11-14 mm, mostly uniform dull brown, but costal margin lighter brown, with arc of faint translucent spots distad of cord, central spot at m-cu, and two translucent spots at arculus. Genitalia (fig. 30): Tergum IX only slightly overhanging segment X in lateral view, posterior margin broadly curved in dorsal view, but middle slightly protruding; sternum IX short, with mesosuperior process acuminate in lateral view, extending above basal ¾ of phallus. Segment X dorsal margin inclined ventrad with blunt apex lobiform in lateral view, ellipsoidal and long in dorsal view. Preanal appendages with dorsal margin straight and horizontal in lateral view, ventroposterior margin curved apicodorsal angle squarish. Inferior appendages capitate in lateral view, with short ventrobasal shelf, narrow middle section and broad squarish apex; lateral arms with apicomesal tooth in ventral view.

Distribution. – Bangladesh; India: Bihar, Orissa, West Bengal; Pakistan: Sind.

Remarks. – This species is easily recognized by the complex male modified spur, having two branches, one branch directed distally and bifid, and the other branch curved laterally and acuminate, but with a minute point at its base. Examination of the type of *D. buddha* revealed that it is identical to *D. indica.* Based on its original description, the subspecies *D. i. sindica* is recognized as a junior synonym of *D. indica.*

Dipseudopsis infuscata **McLachlan, 1875**

(fig. 31)

Dipseudopsis infuscata McLachlan, 1875: 15-16, pl. 2: figs. 6-10, Holotype ♂*: INDONESIA: Sulawesi, Ujung Pandang 'Piepers Celebes Macassar' (RMNH). – Fischer 1962: 10; Fischer 1972: 4; Malicky & Weaver 1988: 3, fig.4a-e.

nec *Dipseudopsis infuscata.* – Ulmer 1905: 96, fig. 75d; Ulmer 1951: 128; Malicky 1984: 214, 216

Specimens examined. – INDONESIA: Java, Jakarta 'Batavia': 1♂, II.1908; 1♂, VIII.1907; 1♂, IX.1907 (RMNH); 1♂, I.1908, Jacobson (ZMAN). Kalimantan: 1♂ 3♀, Telang X.1881 (MCZC). 1♂, West Java, [Piepers?], McL. coll (BMNH). Sumatra: 2♂, Palembang, 13.V.1972, Diehl (CLHM).

Male. – Head and antennae brown. Maxillary palps 1.6-1.8 mm, proboscis 0.5-1.0 mm as long as first two or three segments of maxillary palp. Antenna yellowish brown with fine brown setae that become less dense apically so that distal part appears more yellowish. Forewing 12 mm, brown with small translucent spot distal to r, hyaline spots at m-cu and arculus. Modified spur (fig. 31) slightly longer than adjacent spur, bifid with two acuminate apical points, longer point straight directed distally and almost ½ as long as long as spur, shorter point curved with apex directed mesad. Genitalia (fig. 31): Tergum IX with posterior margin rounded in dorsal view, with slight protrusion in middle, short and not extended over segment X in lateral view. Segment X with basal ⅔ of dorsal margin inclined ventrad apical portion directed posteriad, having apex truncate, in lateral view; dorsal and ventral margins narrowing toward apex, with apex truncate and slightly emarginate in dorsal view. Preanal appendages with posterior margin incised in lateral view. Inferior appendages with dorsal and ventral margins nearly parallel and curved dorsad in lateral view, having thumblike apex; base with mesal margin squarish in ventral view, distal portion long with mesal margin slightly convex, apicolateral margin rounded, and with apicomesal point.

Distribution. – Indonesia: Java, Kalimantan, Sulawesi, Sumatra.

Remarks. – This species is similar to *D. robustior*, but differs by having the two apical points of the modified spur with the longer point straight and slightly shorter than the unmodified base of the spur, and the shorter point curved with its apex directed mesad. All specimens determined as *D. infuscata* by Malicky (1984) from South Andaman Island are now considered to be *D. robustior andamanensis* Weaver & Malicky, n. ssp. The specimen referred to by Ulmer (1905: fig, 75d, 1951) is *D. contorta*, not *D. infuscata* (cf. *D. contorta* above).

***Dipseudopsis knappi* Schmid & Denning, 1979**
(fig. 32)

Dipseudopsis knappi Schmid & Denning, 1979: 246, 248, fig. 5a-e, Holotype ♂: THAILAND: Tha Phra, Khom Kaen, 17.V.1968, blacklight trap, F. W. Knapp (CASC).

Male. – Body brown. Forewing 13 mm, brown with scattered translucent spots. Modified spur (fig. 32) trifid with long curved acuminate point and slightly shorter fingerlike lobe bearing minute subapical point. Genitalia (fig. 32): Tergum IX broadly rounded in dorsal view, short in lateral view; sternum IX with mesosuperior process triangular in lateral view. Segment X slender with apex distinctly bilobed in dorsal view, lateral margins sinuate, base of dorsal margin slightly inclined dorsally distad in lateral view, apical ½ horizontal with ventral margin concave, apex slender and fingerlike. Preanal appendages trapezoidal with corners rounded and dorsal margin inclined dorsad in lateral view, having blunt apicodorsal lobe. Inferior appendages slightly clavate with basodorsal shelf in lateral view, middle portion constricted, and having clavate apex.

Distribution. – Thailand.

Remarks. – This species is only known from the type series from northeastern Thailand. The modified spur of *D. knappi* is trifid and somewhat similar to that of *D. spectabilis*, but differs by having second longest process of the spur lobiform, rather than pointed. The male genitalia differ by having segment X with a bilobed apex. The diagnosis of the male given above is based on the original species description (Schmid & Denning 1979).

***Dipseudopsis lamellata* Martynov, 1935**
(fig. 33)

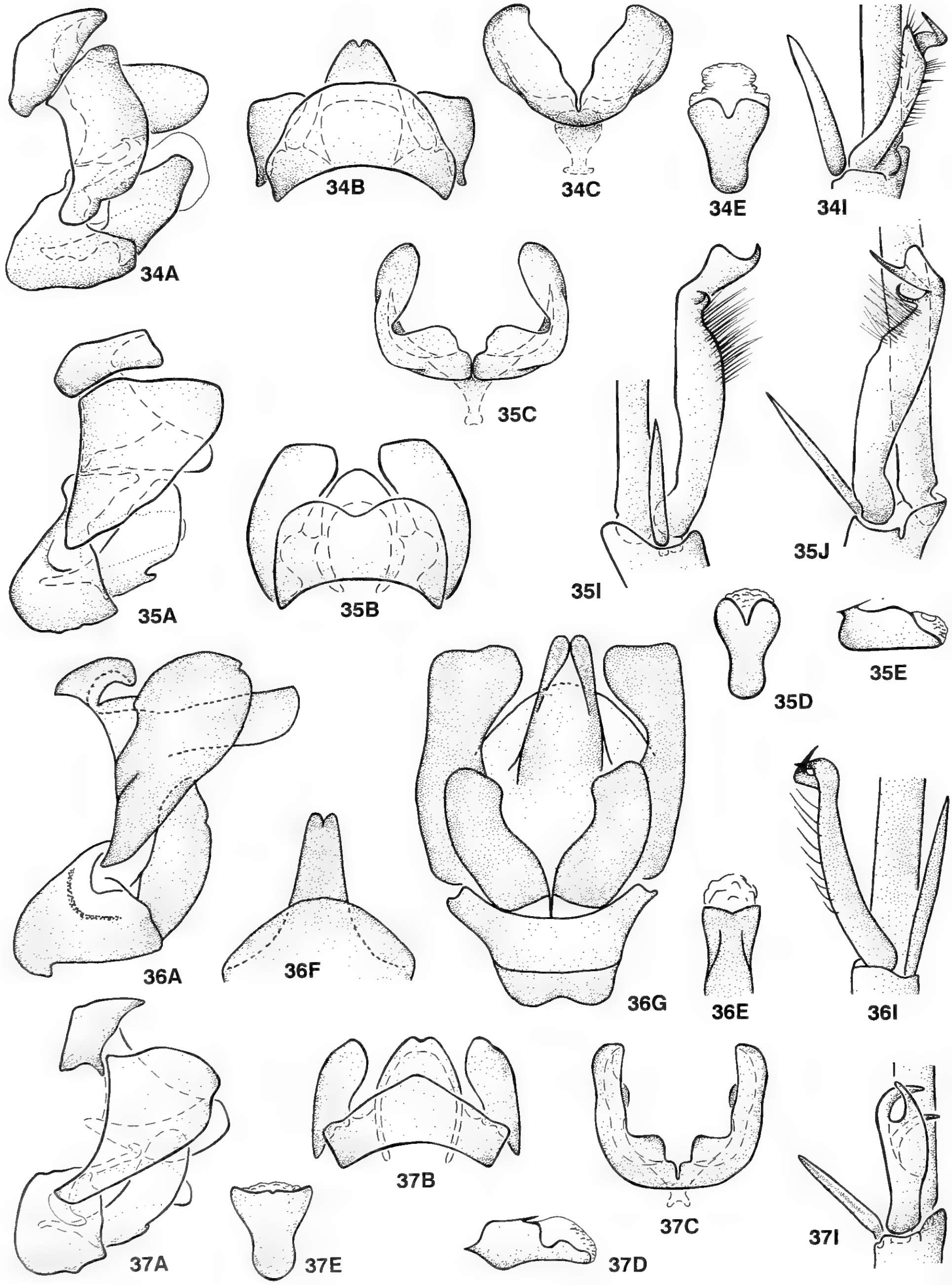
Dipseudopsis lamellata Martynov, 1935: 160-161, figs. 60a-b, 61, Type series: BURMA: Myitkyina Dist.: 1♂ 12♀, Lonton, W shores Indawgyi Lake, U. Burma, 18-31.X.1926, B. N. Chopra; Syntype 1♀*: Kamaing, U. Burma, X.1926, B. N. Chopra (NZSI); INDIA: Assam: Mangaldai, 26.26N 92.02E, 16-18.X.1910, S. W. Kemp. Fischer 1962: 10; Higler 1992: 80.

Specimens examined. – BANGLADESH: 1♂, Chicknagul, 10mi N Sylhet, 10m, 30.IX.61, Ross & Cavagnaro (CASC). 2♂ 4♀, Harbang For. 6mi N Chiringa, 50ft, 18.IX.61, Ross & Cavagnaro (CASC). 1♂, Umgebung Dacca, 1-15.V.1976, Dietz (CLHM). INDIA: Assam: 2♂ 3♀, Kohara, Kaziranga, 110m, 26.36N 93.28E, 7-16.X.61, Ross & Cavagnaro (CASC). Orissa: 2♂, Bhubaneswar, II.1983, J. Oláh (CLHM).

Male. – Colour brown. Forewing 13-15 mm, colouration similar as in *D. indica*, mostly brown, but with arc of five faint translucent spots distad of cord, central hyaline spot at m-cu, and broad translucent spot at arculus. Modified spur (fig. 33) 2x longer than adjacent spur, bearing two distal processes, longer process slender twisted and fingerlike, shorter process slender acuminate and bent laterad at right angle. Genitalia (fig. 33): Tergum IX broad triangular in dorsal view, apex slightly overhanging segment X in lateral view; sternum IX short, with mesosuperior process having blunt dorsal lobe and slender ventroposterior process in lateral view. Segment X dorsal margin concave, ventral margin convex, apical part narrow and curved dorsad in lateral view; lateral margins slightly convergent at basal ¼, distal portion elongate ellipsoidal, with apex slightly incised in dorsal view. Preanal appendages slender and somewhat trapezoidal in lateral view, with posterior margin strongly incised, bearing two blunt apical points. Inferior appendages capitate in lateral view, with base constricted, having short slender basal projection and widening into rhomboid apex; basomesal margin with deep curved incision in ventral view, distal portion widened, having apex with lateral margin curved and with short apicomesal point.

Distribution. – Bangladesh; Burma; India: Assam, Orissa.

Remarks. – This species differs from other species of *Dipseudopsis* by having a unique modified spur, bifid, with a long slender fingerlike twisted process, and with an acuminate process angled laterad.



Figures 34-37. – *Dipseudopsis*, A-G, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral. I-J, male modified spurs apical spurs of hind tibia, ventral. Fig. 34, *D. lucasi*, n. sp. Fig. 35, *D. maculata* Ulmer. Fig. 36, *D. malaisei*, n. sp. Fig. 37, *D. martynovi*, n. sp.

Dipseudopsis lucasi sp. n.
(fig. 34)

Type material. – Holotype ♂: INDIA: Karnataka: Shimoga Dist., Agumbe Ghat, 2000ft, 1974, Lucas (CLHM). Paratypes: 7♂ 3♀, Someshwar, 27.I.1959, F. Schmid (CNCI). 1♂, Nagodi, 28.I.1959, F. Schmid (CNCI). 1♂, Kerala: Sangalipalam, 20-21.XII.1961, F. Schmid (CNCI).

Male. – Head brown, eyes darker brown, frontoclypeus brown, antennae brown but ventral sides lighter brown, palps brown, maxillary palps 2.8 mm, labial palps 1.0 mm, proboscis 1.2 mm, almost as long as first three segments of maxillary palp. Pronotum dark brown, but lateral sides lighter, mesonotum and tegula dark brown. Forewing 14-17 mm unicoloured dark brown except small hyaline spots at m-cu and arculus. Legs with coxae dark brown, distal segments light brown. Modified spur (fig. 34) slightly longer than adjacent spur, apical ¼ modified with short curved subapical shelf, and long slender acuminate curved point directed distad. Genitalia (fig. 34): Tergum IX with posterior ¼ overhanging X in lateral view, posterior margin broadly rounded in dorsal view; sternum IX mesosuperior process with middle constricted and apex curved abruptly dorsad in lateral view. Segment X thumblike and directly posteriad in lateral view; elongate ovoid, with apex slightly incised in dorsal view. Preanal appendages short, extending to middle of segment X in lateral view, posterior margin broadly rounded, almost semicircular but with blunt apicodorsal angle. Inferior appendages basal ½ thick and broadened toward middle in lateral view, apical ½ tapered to truncate apex; lateral margin rounded and mesal margin almost straight in ventral view, but with obtuse apicomesal angle and minute basomesal angle.

Etymology. – Named after the collector J.A.W. Lucas.

Distribution. – India: Karnataka, Kerala.

Remarks. – The male genitalia of *D. lucasi* are similar to those of *D. doehleri* and *D. nebulosa*, having abbreviated preanal appendages. However, *D. lucasi* differs by having forewing almost unicoloured dark brown, and lacking the contrasting pattern, as in the forewings of *D. doehleri* and *D. nebulosa* (figs. 5, 7).

Dipseudopsis maculata Ulmer, 1907
(fig. 35)

Dipseudopsis maculata Ulmer, 1907a: 37-39, fig. 55a-b, Type ♂*: MALAYSIA: Sabah: Sandakan (BMNH). Fischer 1962: 11. Fischer 1972: 5.

Specimens examined. – MALAYSIA: Sabah: 1♂, Tawau, Quoin Hill, Cocoa Res. Sta., 1.X.1962, Y. Hirashima (BPBM). 1♂, Tawau, Quoin Hill, 15-20.VII.1962, Y. Hirashima (BPBM). 1♂, Sepilok For. Res., Sandakan Bay, 1-10m, 27.X.1957, J. L. Gressitt (BPBM).

Male. – Head dorsum with anterior ½ glossy dark brown, almost black, and posterior warts light brown, frontoclypeus glossy dark brown; antennal scape and pedicel light brown, flagellum darker, palps dark brown, maxillary palps 3.6 mm, proboscis 2.2 mm, as long as first four segments of maxillary palp. Pronotum, mesonotum and tegula dark brown, but metathorax and abdomen yellowish brown. Forewing 17-18 mm, veins dark brown against brown and translucent background, large translucent triangular spot between R_1 and Cu_1, also translucent spots at arculus, discal cell, and area distal to cord, and dark band distal to hyaline spot at m-cu. Fore leg coxa to basal ½ of femur dark brown, distal ½ of femur and other distal leg segments yellowish brown; mid leg coxa dark brown, distal leg segments yellowish brown; hind leg yellowish brown. Modified spur (fig. 35) 2X longer than adjacent spur, apical ⅓ modified, into two unequal short nearly parallel points curved laterally away from tarsus. Genitalia (fig. 35): Tergum IX distal ⅓ overhanging segment X and with broad apex in lateral view, posterior margin broadly rounded and bilobed in dorsal view. Sternum IX mesosuperior process triangular with blunt dorsal angle and acute posterior angle in lateral view. Segment X ventral margin straight and horizontal, dorsal margin slightly concave and inclined ventrad, apex rounded; ellipsoidal about ⅓ as wide as tergum IX in dorsal view. Preanal appendages broad and triangular with corners rounded in lateral view, dorsal and ventroposterior margins slightly irregular, apicodorsal apex blunt. Inferior appendages inclined dorsad and widening apically, having apex truncate with rounded corners in lateral view, dorsal margin straight and longer than ventral margin; ventral margin with basal ⅓ having protruding shelf extended as short free lobe, oblique angle at midlength, and distal ½ inclined dorsad; distal process thumblike in ventral view, mesal margin with deep narrow curved basolateral notch, and apex rounded.

Distribution. – Malaysia: Sabah.

Remarks. – The male of this species has a unique modified spur with a prominent apical point extending laterally from a blunt apical shelf, and a shorter subapical point curved laterally, having both points curved distad. *D. maculata* and *D. nieuwenhuisi* appear to be closely related based on similar colouration in the male forewing (cf. fig. 6 of *D. nieuwenhuisi*), and similar characteristics in the male genitalia. *D.*

maculata differs by being smaller in size, and by having male modified spur with only two apical points, rather than having three as in *D. nieuwenhuisi.*

Dipseudopsis malaisei sp. n.

(fig. 36)

Type material. – Holotype ♂: BURMA: Washaung, 600ft, 13.VII.1934, Malaise (NHRS). Paratypes: 3♂, same data, Malaise (NHRS).

Male. – Head dorsum and frontoclypeus dark brown, nearly black, posterior warts brown. Antennae, mouthparts, legs and sclerotized parts of thorax unicoloured brown. Maxillary palps 2.2-2.5 mm; proboscis 1.2-1.8 mm, as long as first four segments of maxillary palps. Forewing length 13-15 mm, dark brown except for small hyaline comma at m-cu. Modified spur (fig. 36) slender, slightly curved and longer than adjacent spur, with two small spiralling apical points. Abdomen yellowish brown. Genitalia (fig. 36): Tergum IX broadly rounded in dorsal view, with distal ⅔ overhanging segment X in lateral view; sternum IX with mesosuperior process fingerlike and ½ as long as segment X in lateral view. Segment X long and fingerlike, tapering slightly distad and apex incised in dorsal view. Preanal appendages oblong, with posterodorsal margin ellipsoidal in lateral view. Inferior appendages curved dorsad and broad in lateral view; broad with lateral and mesal margins parallel, and apices slightly bent mesad in ventral view.

Etymology. – Named after the collector R. Malaise.

Distribution. – Burma.

Remarks. – This species is only known from the type series. The male has segment X long and slender and modified spur with two small apical spiralling points similar as in *D. benardi.* However, *D. malaisei* differs by having male with preanal appendages oblong and ellipsoidal in lateral view, inferior appendages broad and flat, and dark brown forewings without large translucent spots, similar to *D. benardi* (fig. 10).

Dipseudopsis martynovi sp. n.

(fig. 37)

Type material. – Holotype ♂: PHILIPPINES: Sulu: Tarawakan NE, 12.II.1957 Yoshio Kondo (BPBM). Paratypes: Tawitawi, Tarawakan, north of Batu Batu, Noona Dan Exp. (ZMUC): 10♂, 21.X.1961; 4♂, 20.X.1961; 2♂, 13.XI.1961; 2♂: 14.XI.1961.

Male. – Head dark brown, but posterior warts light brown; frontoclypeus with ventral ½ light brown, dorsal ½ dark brown; antennae light brown, palps light brown, maxillary palps 2.3 mm, proboscis 1.2 mm, as long as first three segments of maxillary palp. Pronotum light brown. Mesonotum and tegula dark brown. Forewing 13 mm, dark brown with C and small light brown stigma and small hyaline spots at m-cu and arculus. Legs with coxae dark brown, distal segments light brown. Modified spur (fig. 37) short and stout, about 4x, as long as basal width apical ⅔ modified with three broad points clustered together. Genitalia (fig. 37): Tergum IX posterior ⅓ extended over segment X in lateral view, broad and triangular in dorsal view; sternum IX mesosuperior process straight rodlike with apex curved dorsad in lateral view. Segment X dorsal margin slightly concave and inclined ventrad in lateral view, ventral margin curved ventrad at middle and curved dorsad distad, apex blunt; ellipsoidal and about ½ as wide as tergum IX in dorsal view. Preanal appendages slightly shorter than segment X in lateral view, dorsal margin slightly sinuate at base, with broad dorsoapical curve, ventral margin nearly straight inclined dorsad, posterior margin with shallow incision. Inferior appendages fingerlike and inclined dorsad in lateral view, with narrow basoventral shelf, squarish with distal arms parallel and straight in ventral view, lateral apex rounded, basomesal margin with square-angled basal shelf, and lateral notch and apicomesal angle both square.

Etymology. – Named after Andrei Vasilievich Martynov.

Distribution. – Philippines: Sulu, Tawitawi.

Remarks. – This species is superficially similar to *D. recta* and *D. triclavata,* having modified spur trifid. However, it differs by having the spur short and stout, about 4x longer than basal width, with apical ⅔ of spur modified, and inferior appendage fingerlike in lateral view.

Dipseudopsis modesta Banks, 1911

(fig. 38)

Dipseudopsis modesta Banks, 1911: 105-106, pl. 6: fig. 2, Type ♂*: INDIA: Bihar: Pusa, 21.IX.08, T. N. J. (MCZC 11756). – Fischer 1962: 11; Fischer 1972: 5; Higler 1992: 80.

Dipseudopsis pallida Martynov, 1935: 166-167, fig. 70a-b, Type series: 1♂ 1♀ in copula, Pusa, 31.III.1911-4.IV, F. H. Gravely (probably NZSI). – Fischer 1962: 14; Higler 1992: 80. **Syn. n.**

Specimens examined. – INDIA: Assam: 3♂ 3♀, Kohara, Kaziranga, 110m, 26.36N 93.28E, 16.X.61, Ross & Cavagnaro (CASC). 1♂ 3♀, 13mi SW Kochugaon, 50m, 17.X.61, Ross & Cavagnaro (CASC). 2♂ 2♀, Meleng For., Mariani, 110m, 26.39N 94.18E, 10.X.61, Ross & Cavagnaro (CASC). 2♂ 3♀, Garampani Res. 10mi S Gologhat, 110m, 9.X.61, Ross & Cavagnaro (CASC). Assam: 1♂ 2♀, 'Doom Dooma' Dum Duma, 27.34N 95.34E, VI.1943, E. Hardy (USNM). 'U.D.M.N.C.H.' [United District of Mikir and North Cachae Hills]: 1♂, Kalanga, 1.V.1960, F. Schmid (CNCI). Bihar: 4♂ 2♀, Pusa (MCZC). 2♂, Pusa (BMNH). Orissa: 2♂, Bhubaneswar, 21.II.1985, J. Oláh (CLHM). West Bengal: 3♂, Chapra, Mackenzie (MCZC).

Male. – Head glossy dark brown; frontoclypeus, antennae and palps dark brown; maxillary palps 2.6 mm, proboscis 1.0 mm, almost as long as first three segments of maxillary palp. Pronotum, mesonotum and tegula dark brown. Forewing 12-15 mm, dark brown, except for hyaline lunula at m-cu and small translucent spot at arculus. Legs light brown slightly darker basad. Modified spur (fig. 38) slightly shorter than adjacent spur with two minute apical points (cf. 'Remarks' below). Genitalia (fig. 38): Tergum IX triangular with acute apex slightly inclined dorsad and distal ⅓ overhanging segment X in lateral view; posterior margin broadly rounded in dorsal view; sternum IX mesosuperior process with short broad dorsal triangle, posterior process narrow having dorsal margin irregular and slightly concave, and ventral margin curved dorsad in lateral view, extending above basal ½of phallus. Segment X long slender and apex bilobed with deep mesal notch in dorsal view; fingerlike and slightly tapered in middle, extending posteriad distal to inferior appendages in lateral view. Preanal appendages trapezoidal, posterior margin slightly incised in lateral view. Inferior appendages slender and long in lateral view, extending dorsad toward apex of preanal appendage, dorsal margin curved and concave, ventral margin irregular; lateral margins curved and apicomesal margin straight with apical point in ventral view, mesal margin with curved notch in basolateral corner.

Distribution. – India: Assam, Bihar, Orissa, West Bengal.

Remarks. – This species can be distinguished by its unique male modified spur, having a short inconspicuous apical point directed distally and a long slender point curving halfway around the apex; the straight point is minute and lightly sclerotized, and without clear magnification it appears to be a small lobe. This species is similar to *D. benardi*, but it differs by having male modified spur with smaller apical points and inferior appendages narrower in lateral view. We have observed some variation in the shape of the preanal appendages. Comparison of the type of *D. modesta* with the original description of *D. pallida*, reveals that these species are conspecific, and thus the latter is recognized as a junior synonym.

Dipseudopsis morosa Banks, 1924

(fig. 39)

Dipseudopsis morosa Banks, 1924: 450, pl. 3: fig. 31. – Fischer 1962: 11; Fischer 1972: 5.

nec *Dipseudopsis morosa*. – Schmid 1958: 13, 24, 27, 89, pl. 15: figs. 12-13.

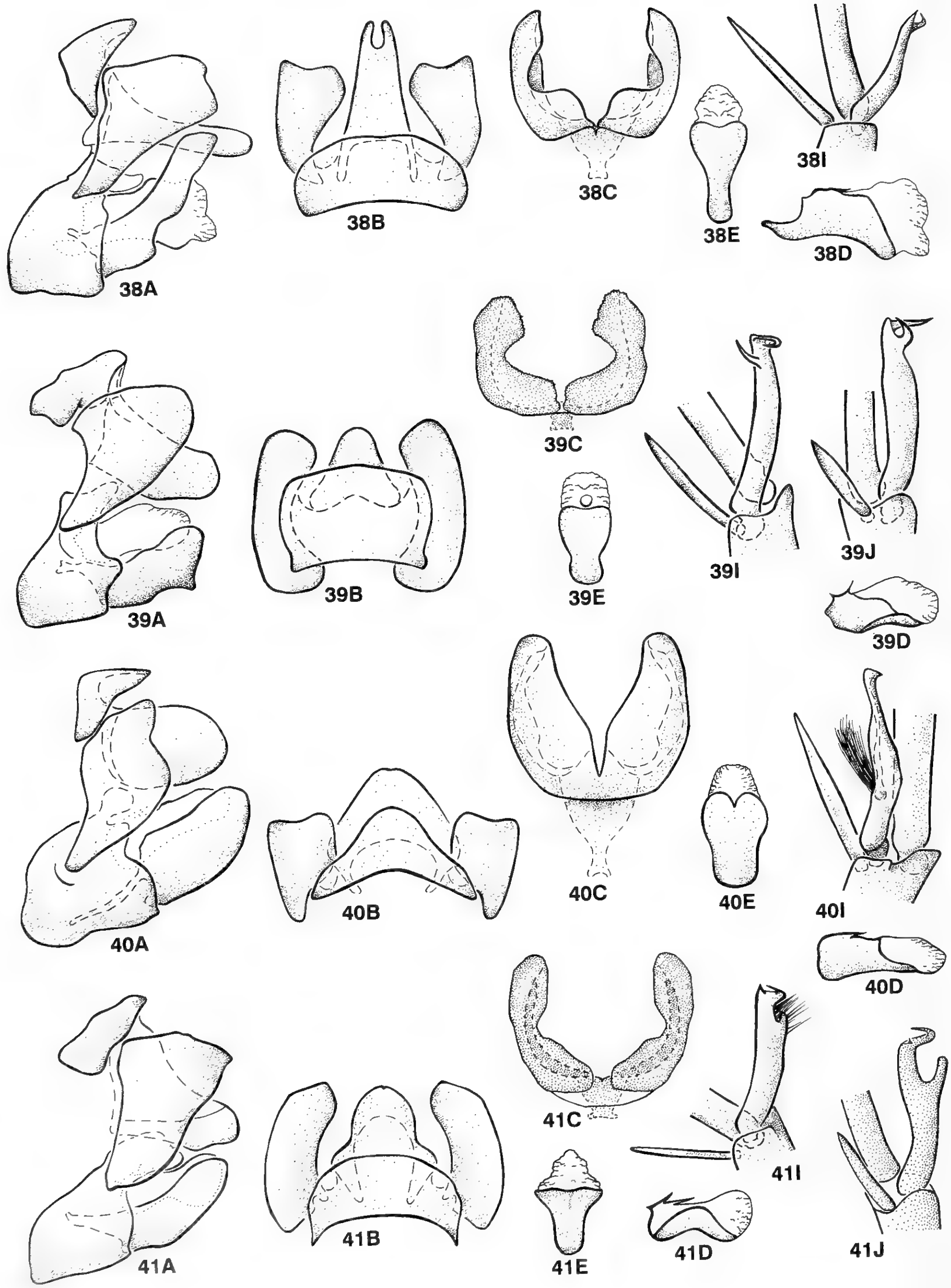
Lectotype designation. – ♂*: PHILIPPINES: Mindanao: Dapitan, Baker (MCZC 14826). 1♂*: Basilan: probably syntype but without type label, Baker (USNM). The type series: 3♂ (MCZC) is mixed and comprises three different species; in addition to the lectotype, the ♂* syntype from Luzon is *D. collaris*, and the ♂* syntype from 'Borneo' Kalimantan is *D. stabatensis*.

Specimens examined. – PHILIPPINES: Mindanao: 1♂, Lanao, 4.8 km E of Dansalan, 750m, 11.VI.1958, jungle along stream, H. E. Milliron (BPBM).

Male. – Head brown with black triangular median stripe, broad along anterior margin and tapering to middle of posterior margin, frontoclypeus glossy black and genae brown, antennae and palps brown, maxillary palps 2.3 mm, proboscis 1.0 mm, almost as long as first three segments of maxillary palp. Pronotum black with posterior dorsal margin brown, mesonotum and tegula almost black. Forewing 9-10 mm, uniformly dark brown, but small hyaline spots at m-cu and arculus. Legs with coxae of fore and mid legs dark brown and distal segments yellowish, hind leg yellowish. Modified spur (fig. 39) 1½x longer than adjacent spur, apex truncate with two apical points, both points curved and one point nearly in plane perpendicular to longitudinal axis of spur, and other longer point with apex directed more distad. Genitalia (fig. 39): Tergum IX not extended over base of segment X in lateral view, slightly inclined dorsad; sternum IX mesosuperior process short and blunt in lateral view, with square dorsoanterior angle, posterior lobe inclined dorsad and extended above basal ⅓ of phallus. Segment X dorsal and ventral margins nearly parallel and inclined ventrad in lateral view, but apical portion of ventral margin horizontal, apex rounded; triangular and with rounded posterior apex in dorsal view. Preanal appendages broad and somewhat D-shaped with apex extended dorsoposteriad in lateral view. Inferior appendages oblong with distinct subapical ventral tooth in lateral view, distal portion capitate in ventral view with apex and basomesal notch curved.

Distribution. – Philippines: Basilan, Mindanao.

Remarks. – *D. morosa* has been confused with *D. triclavata*, due to similarities of the male modified spurs. However, these species are not closely related and are distinguished from each other by characteris-



Figures 38-41. – *Dipseudopsis*, A-G, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral. I-J, male modified spurs apical spurs of hind tibia, ventral. Fig. 38, *D. modesta* Banks. Fig. 39, *D. morosa* Banks. Fig. 40, *D. nebulosa* Albarda. Fig. 41, *D. nervosa* Brauer.

tics of the male genitalia, *D. morosa* having the inferior appendage broader and with a distinct blunt ventral tooth in lateral view, and by having modified spur with only two apical points. The type series of *D. morosa* at the MCZC is mixed, comprising three syntypes, each a different species. Records of *D. morosa* from Sri Lanka by Schmid (1958) are actually *D. triclavata.*

Dipseudopsis nebulosa Albarda, 1881
(figs. 7, 12A, 40)

Dipseudopsis nebulosa Albarda, 1881: 19, pl. 5: fig. 4, Type ♀, INDONESIA: 'in insula Sumatra'. – Fischer 1962: 11-12; Fischer 1972: 6; Malicky & Weaver 1988: 4, fig. 2a-f.
nec *Dipseudopsis nebulosa.* – Banks 1914: 178 (Luzon).

Specimens examined. – BURMA: 2♂, Tenasserim, Sukli, 75km E of Moulmein, 600m, 27-31.X.1934, Malaise (BMNH). 1♂, Mekane, 20 km W Myawaddy, Amherst Dist, 700ft, 3.XI.1934, Malaise (NHRS). INDONESIA: Sumatra: 1♂, W Morton (CNCI). 1♂, Tandjong Morawa Serdang (RMNH). 1♂, Loeboek Sikaping, 450m (RMNH). 1♂, Pematang Siantar, 1.VI-12.XII.1985, Diehl (CLHM). 12♂, Huta Padang, Diehl (CLHM). MALAYSIA: West Malaysia: Pahang: 3♂, Kuala Tahan, at light, Pendlebury (BMNH). 1♂, Sungei Tembeling, 18.XI.1922, Pendlebury (MCZC). 1♂, Kuala Teku, 500ft, 5.XII.1921, Pendlebury (MCZC). Selangor: 12♂ 6♀, Kuala Lumpur, 15-31.XII.1958, Quate (BPBM). THAILAND: 3♂, upper Pran River, 13-15.IV.1926 (MCZC 1♂, BMNH 2♂). 2♂, det. Mosely as *D. doehleri*, same data, 15.IV.1927, Landell (BMNH). 1♂, Trang, 26.VI.1924, Evans (MCZC). 2♂ 1♀, Trang Prov., Khaophappha Khaochang, 200-400m, 12-13.I.1964, Samuelson (BPBM). 5♂, Krachong For. near Trang, 100m, 2.VII.62, Ross & Cavagnaro (CASC). 1♂, 20 km E of Krabi, 10-20.II.1962, Friedel (CLHM). 1♂, Trang, Banchang, 16.V.1924, at light, Evans (BMNH).

Male. – Body and wings (fig. 7). Head dorsum, antennae, cervical sclerites and pronotum orangish brown, and contrasting with dark brown mesonotum, tegula and forewings (fig. 12A). Frontoclypeus and mouthparts brown. Fore and mid legs with coxae and trochanters brown, femora with basal portions dark brown and apical portions orangish brown, tibiae and tarsi orangish; hind leg dark brown. Forewing 12-14 mm, dark brown with translucent spots: long triangular spot below R_1 above Cu_1 from base of Rs to hyaline lunula at m-cu, translucent oblong spot distal to cord with apical margin deeply incised, and small translucent spot at arculus. Modified spur (fig. 40) with twisted glabrous apical point, about ⅔ as long as spur. Genitalia (fig. 40) similar to *D. schmidi.* Tergum IX with posterior margin triangular with apex curved and lateral sides slightly depressed in dorsal view, apical ⅔ of dorsum overhanging segment X in lateral view. Sternum IX extended anteriad, with mesosuperior process globular in lateral view. Segment X short stout and ellipsoidal in lateral view, dorsal and ventral margins nearly parallel and horizontal, apex bluntly rounded, broad and cordate in dorsal view, length and width subequal, with apex slightly incised. Preanal appendages abbreviated in length, with posterior margin incised. Inferior appendages broad, somewhat ellipsoidal in lateral view, but dorsal margin slightly concave.

Distribution. – Burma; Indonesia: Java, Sumatra; Malaysia: West Malaysia; Thailand.

Remarks. – This species is similar to *D. doehleri*, but differs by having a translucent spot of forewing with faded edges, rather than a well defined oval-shaped spot at the arculus, and genitalia with sternum IX, segment X, and preanal appendages slightly broader in lateral view. The modified spur of *D. nebulosa* is similar to that of *D. immaculata* and *D. doehleri*, with a twisted glabrous apical point, having a setose pocket at its base, but it differs by having a longer glabrous point, about ⅔ as long as spur. We have accepted the description of the male provided by Ulmer (1951), who associated it with the female type from middle Sumatra. We have observed that a male specimen from Luzon was misidentified by Banks (1914) and actually is *D. collaris.*

Dipseudopsis nervosa Brauer, 1868
(figs. 3, 4, 41)

Dipseudopsis nervosa Brauer, 1868: 267-268, Type ♀: PHILIPPINES: (Semper) [cf. 'Remarks' below]. – Fischer 1962: 12; Fischer 1972: 6.
Dipseudopsis luctuosa Banks, 1913: 178, pl. 8: fig. 3, Type ♂*: Luzon: Los Baños, P. L. Baker (MCZC 11769). – Ulmer 1930: 380, as syn. – Fischer 1962: 12; Fischer 1972: 6.
Dipseudopsis venosa Navás, 1931: 86, Type ♀ 'Filipinas: Mindanao, Kolambogan, 11.VI.1914. Col. m.' [We were unable to locate the female type of *D. venosa* for examination, but are relatively certain that this species is synonymous with *D. nervosa*, because only two species of *Dipseudopsis* are known from Mindanao, *D. modesta* and *D. nervosa*, and the size of the female type of *D. venosa* only agrees with the female of *D. nervosa.*] – Fischer 1962: 16. **Syn. n.**

Specimens examined. – PHILIPPINES: Leyte: 3♂, Palo (-BPBM). 1♂, Tacloban (USNM). Luzon: 3♂ 3♀, Los Baños (-MCZC). 2♂ 5♀, Los Baños (USNM). 4♂ 3♀, Mt Maquiling (CNCI, USNM). 1♂, det. Ulmer (1905), bez. Bilneao, prov. Laguna, 1876, Laglaize (MNHN). Mindanao: 1♂, Kolambugan (BMNH). 1♂ ('Paratypus' see discussion above) Mindanao, 1867 (NHMW). 2♂, Agusan Los Arcos (BPBM). 1♀, Agusan Esperanza (BPBM). 3♂, Agusan Jabonga Mayogda (MCZC). 2♂, Bukidnon, Dalongdong, 40km NW Maramag, Talakag, Urwaldrand, 800m, 7°53'N 124°40'E (-ZMHB). 1♂ 2♀, Butuan (MCZC, USNM). 1♂, Cotabato, Kalaong (BPBM). 2♂, Sapamoro, Curnan dist. (ZMUC).

Mindoro: 1♂, Laguna de Nanjan Soldanski (CLHM). Negros: 2♂ 3♀, L. Balinsasayao (BPBM). 1♂, Sibulan (BPBM). 2♂ 1♀, Victorias (MCZC, USNM). Panay: 1♂, Pr. Capiz, Libacao (ZSMC). Sibuyan: 1♂, Magdiwang-Tampayan, Ga-ong, Pawala River (CLHM).

Male. – Body and wings (fig. 3). Head dorsum similar to *D. morosa*, having dark brown median acute triangle, tapering posteriad, and lateral sides yellowish brown; frontoclypeus with dark brown median stripe tapering dorsad and lateral sides yellowish brown; antennae and palps brown, maxillary palps 2.8 mm, proboscis 1.7 mm, as long as first 3½ segments of maxillary palp. Cervical sclerites mostly dark brown, but dorsal part yellowish brown. Pronotum yellowish brown, median furrow and lateral sides dark brown; propleuron yellowish brown. Mesonotum, metanotum and tegula dark brown. Mesothorax, metathorax and abdomen brown dorsad and yellowish brown ventrad. Forewing 14-17 mm, dark brown with three translucent spots: 1) basal stripe between R_1 and Cu_1, 2) triangular spot distal to cord, and 3) round spot at arculus. Fore leg coxa bicoloured, basal ½ dark brown and distal ½ yellowish brown. Pleuron bicoloured, cervical sclerites and side of thorax with lower portion dark brown and upper part yellowish brown. Modified spur (fig. 41) trifid, with long apical point spiraling distad, minute apical point, and subapical lobe. Genitalia (fig. 41): Tergum IX inclined dorsad in lateral view, minute portion of apex overhanging segment X, posterior margin broadly curved in dorsal view; sternum IX mesosuperior process oblong in lateral view, dorsal margin curved. Segment X dorsal margin slightly concave, strongly inclined ventrad to blunt apex in lateral view; base broad and narrowing toward oval-shaped apex in dorsal view. Preanal appendages irregular triangle, with dorsal margin irregular and curved in lateral view, ventroposterior margin steeply inclined dorsad, dorsoposterior apex squarish. Inferior appendages fingerlike and curved dorsad in lateral view, lateral margin curved in ventral view, extended arms fingerlike with middle of mesal margin having small semicircular incision.

Female. – Body and wings (fig. 4).

Distribution. – Philippines: Leyte, Luzon, Mindanao, Mindoro, Negros, Panay, Sibuyan.

Remarks. – This species is similar to *D. digitata*, but differs by having unique colouration of the male head and forewings, and by characteristics of the male hind spur and genitalia.

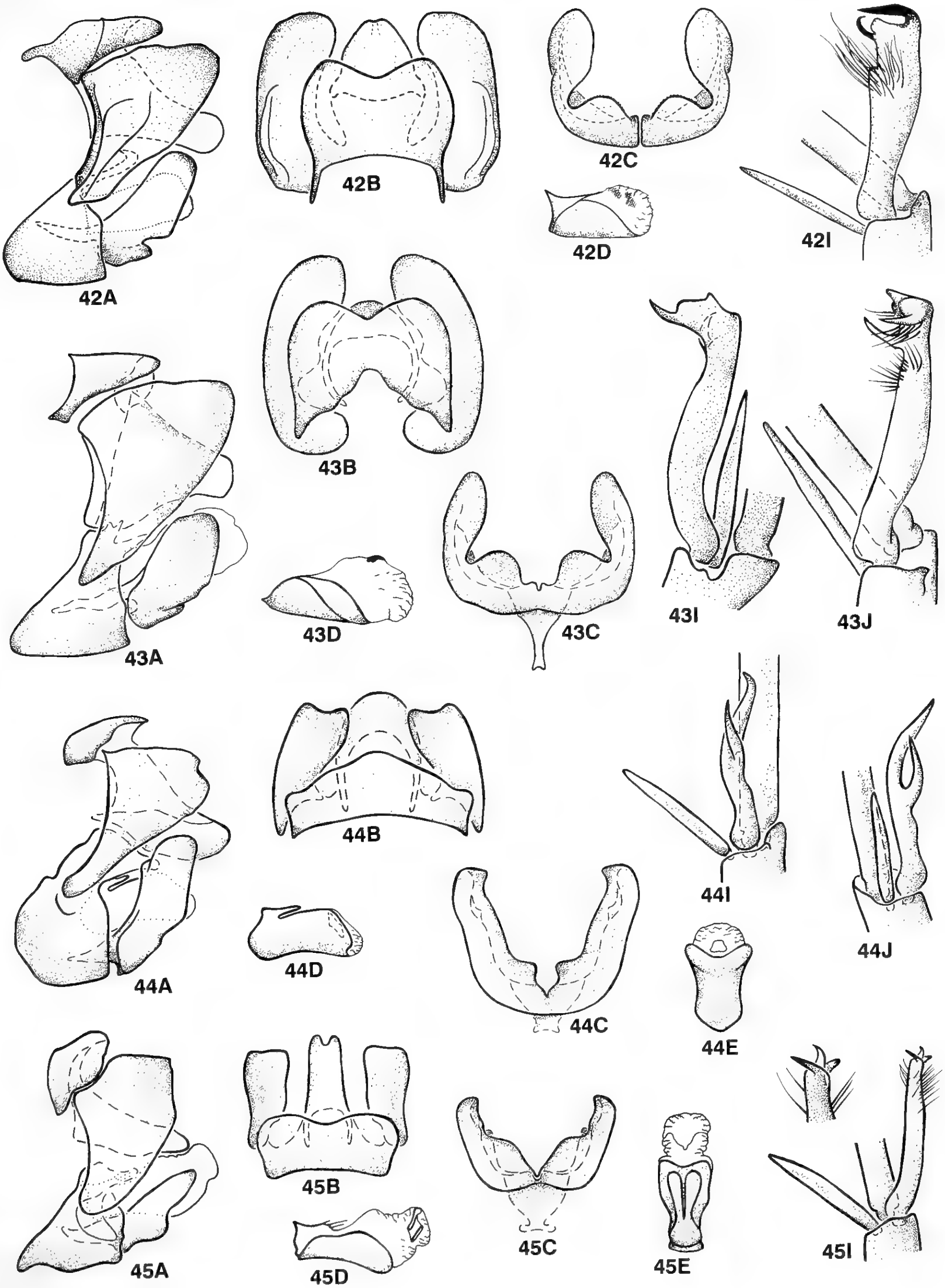
Brauer (1868) described this species after a female from the Philippines, and the species epithet, *nervosa*, was probably derived in references to the colouration pattern of the female forewing, having dark veins against a translucent background. The type which should be at the NHMW is missing. Instead a male specimen with a hand-written type label reading 'Paratypus' is present, but this specimen was not mentioned by Brauer and thus cannot be regarded as a syntype. The red 'paratype' label was probably added to this specimen after the species was described. This specimen cannot be the type because the type description was clearly based on a female specimen; also the forewing length of the type should be 19 mm, but that of the male 'paratype' is only 17 mm. Therefore, we conclude that the type is missing. We accept the male association of this species by Ulmer (1929). Furthermore, we are reasonably sure that the identity of this species is correct because there are no other species as large as *D. nervosa* known from the Philippines., i.e. the other four Philippine species, *D. collaris, D. digitata, D. martynovi,* and *D. morosa*, are much smaller.

***Dipseudopsis nervosella* Ulmer, 1905 stat. n.**
(fig. 42)

Dipseudopsis sp.– Ulmer, 1905: 96, fig. 75e.
Dipseudopsis morosa. – Ulmer 1951: 128 [misdet.].
Dipseudopsis morosa nervosella Ulmer, 1951: 141-143, pl. 7: figs. 140-142, Type ♂*: 'Borneo' 1886, F. Baczes (NHMW). – Fischer 1972: 5.

Specimens examined. – MALAYSIA: Sarawak: 1♂, at foot of Mt Dulit, junction of rivers Tinjar & Lejok, 19.VIII.1932 (BMNH). 1♀, same data, 30.VIII.1932 (BMNH). 1♂, R. Kapah trib. of R. Tinjar, 25.X.1932, Oxford Univ. Exp. (BMNH).

Male. – Dorsum of head with curved M-shaped pattern marked by division between glossy dark brown, almost black, anterior triangle pointed posteriad and dark brown lateral margins, and yellowish brown area, filling in two triangles of 'M' and with acute angle of each triangle pointed toward base of antenna. Frontoclypeus glossy, almost black, antennae yellowish brown, cervical sclerites dark brown. Maxillary palps 3.0 mm, dark brown; proboscis brown, 1.8 mm, almost a long as first four segments of maxillary palp; labial palps 1.2 mm. Pronotum dark brown with slender yellowish brown posterior edges along median fissure and lateral margins, propleuron light brown; mesonotum almost black, mesopleuron dark brown except epimeron light brown; metathorax and abdomen yellowish brown. Forewing 15-16 mm, dark brown with golden hairs, and three large translucent spots, similar to *D. nervosa* and *D. nebulosa* (cf. figs. 3, 7): 1) long band between R_1 and Cu_1, 2) equilateral triangle at arculus, and 3) subapical area distal to cord with six translucent gaps between



Figures 42-45. – *Dipseudopsis,* A-G, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral. I-J, male modified spurs apical spurs of hind tibia, ventral. Fig. 42, *D. nervosella* Ulmer. Fig. 43, *D. nieuwenhuisi* Ulmer. Fig. 44, *D. notata* (Fabricius). Fig. 45, *D. recta* Martynov.

dark apical veins, and in discal cell. Fore leg and middle leg with coxae, trochanter and basal portion of femur dark brown, distal portion of leg yellowish; hind leg yellowish. Modified spur (fig. 42) 1½x longer than adjacent spur, apex truncate with two apical points, both points curved in plane perpendicular to longitudinal axis of spur (cf. 'Remarks' below). Genitalia (fig. 42): Tergum IX with posterior ⅓ overhanging segment X in lateral view, posterior margin bilobed with two blunt lateral angles separated by a obtuse mesal notch in dorsal view; sternum IX dorsomesal process slender horizontal, with pointed apex curved dorsad in lateral view. Segment X dorsal margin slightly concave in lateral view, distal portion narrow; ellipsoidal and with apex slightly incised in dorsal view. Preanal appendages large lobate and extended dorsoposteriad in lateral view. Inferior appendages thumblike and inclined dorsad in lateral view, ventrobasal shelf with short free apical projection; distal arms ellipsoidal in ventral view, without sharp mesal tooth, mesal margin with deep narrow curved basolateral notch.

Distribution. – Malaysia: Sarawak.

Remarks. – This species was originally described as a subspecies of *D. morosa.* Comparison of the male type of *D. nervosella* with that of *D. morosa* reveals that each is a distinct species. The modified spur in *D. nervosella* is similar to that of *D. morosa,* but more robust and actually a mirror image of the other, having apical points curved in opposite directions. This species also differs by having the male forewing with a more contrasting colour pattern, and inferior appendage having mesal margin with deep curved basolateral notch in ventral view. Also, *D. nervosella* is only known from Sarawak, and *D. morosa* is only known from the islands of Mindanao and Basilan of the Philippines.

Dipseudopsis nieuwenhuisi Ulmer, 1909

(figs. 6, 43)

Dipseudopsis nieuwenhuisi Ulmer, 1909: 128-129, fig.4, Type ♂*: Borneo Exp., Dr. Nieuwenhuis, L. Dengay, 1.X.1894 (RMNH). – Fischer 1962: 12; Fischer 1972: 6.

Specimens examined. – MALAYSIA: Sarawak, Mt Dulit, 4000ft, moss forest, at light, Oxford Univ. Exp., B. M. Hobby & A. W. Morre (BMNH): 1♂, 22.IX.1932; 5♂, 19-29.X.1932; 1♂, 17.IX.1932.

Male. – Body and wings (fig. 6). Head dorsum with dark brown triangle along anterior margin extending to middle of posterior margin, posterior warts and lateral margins yellowish, frontoclypeus dark brown, antennae yellowish brown, palps dark brown. Maxillary palps 4.0 mm, proboscis 2.8 mm, labial palps 1.6 mm. Pronotum dark brown except posterior lateral corners light brown, propleuron light brown, mesonotum and tegula dark brown, metathorax light brown. Forewing 19-23 mm, dark brown, veins dark brown with several translucent stripes between veins, similar to that *D. digitata,* having three translucent areas, basal stripe in thyridial cell, round marginal spot at arculus and subapical translucent stripes distal to cord. Front and middle legs with coxae dark brown, trochanters to apex yellowish brown; hind leg mostly yellowish. Modified spur (fig. 43) 2x as long as adjacent spur and 2x as thick, with three apical points, one minute point, and two large points parallel and curved, one large point subapical. Genitalia (fig. 43): Tergum IX posterior margin broadly bilobed, having shallow mesal notch in dorsal view. Segment X originating from relatively shallow cavity of tergum IX in lateral view, apex blunt, ventral margin slightly concave; ellipsoidal and posterior margin broadly bilobed in dorsal view. Preanal appendages triangular and rounded with dorsal margin horizontal, broadly curved and slightly emarginate in lateral view, ventroposterior margin broadly curved and strongly inclined dorsad. Inferior appendages oblong with ventrobasal shelf in lateral view; angulate with distal arms thumblike in ventral view, mesal margin with deep narrow curved basolateral notch.

Distribution. – Malaysia: Sarawak.

Remarks. – This is the largest Asian species of *Dipseudopsis* known. It appears to be closely related to *D. digitata* and *D. nervosella,* but differs by its larger size and by characteristics of the male modified spur and genitalia.

Dipseudopsis notata (Fabricius, 1781)

(fig. 44)

Phryganea notata Fabricius, 1781: 390, Type ♂*: 'N. America' [mislabelled, cf. 'Remarks' below], (BMNH). – Fischer 1962: 13.

Dipseudopsis horni Ulmer, 1915: 46-47, fig. 13. Type series: SRI LANKA: '2♂, [N. Cen. Prov.: Mahl Iluppallama] Maha Illupalama, Ceylon, Juli 1912, J. C. F. Fryer leg., im Museum Cambridge [MCZC]; ferner 9 Exemplare (♂, ♀), [Cen. Prov.]: Kandy, resp. [E. Prov.: Kantalai?] Kanthaley, resp. [Cen. Prov.: Matale] Matala, Ceylon, Dr. W. Horn leg., im Deutsch. Entom. Museum Berlin-Dahlem' [ZMUH]. – Weidner (1964: 73): 'Ceylon, Matala, Paratypoid' of *D. horni,* (ZMUH). – Fischer 1962: 9; Weidner 1964: 73; Fischer 1972: 4. **Syn. n.**

Specimens examined. – INDIA: Karnataka: 8♂, Bhadravati (MCZC). 2♂, Shimoga, R. Tunga 1865ft (MCZC). Tamil Nadu: 3♂, Tanjore dist. 'Thanjavur', Nedungadu (MCZC). SRI LANKA: N. Prov.: 2♂, Marichchukkaddi (BMNH). N. Cen. Prov.: 6♂, Moradan Maduwa, Wilpattu Natl. Park, 23mi W of Anuradhapura, 80m (MZLU). 1♂, Kontalai, 60m (MZLU). Anuradhapura Dist: 7♂ 8♀, Wildlife Soc. Bungalow, Hunuwilagama, Wilpattu Natl. Park, 200ft (-USNM). 10♂ 10♀, Irrigation Bungalow, [Padawiya Tank] 'Padaviya', 180ft (USNM). 8♂ 2♀, Padaviya, 180ft (USNM). Polonnaruwa Dist: 2♂ 7♀, Pinburettawa, 13mi S Mannampitiya (USNM). 1♂, Polonnaruwa (SOFM). N. W. Prov.: 1♂ 2♀, Marai Villu (BMNH). 3♂, 5mi NNE of Puttalam, 5m (MZLU). S. Prov.: 1♂, Hikkaduwa, 11mi NW of Galle, 10m (MZLU). 2♂ 2♀, Badagiriya Tank, 6.5mi N Hambantota, 75ft (CLJW). 1♂ 1♀, Hambantota (BMNH). 1♂, Tangalla (MCZC). 1♂ 1♀, Weligama (BMNH). W. Prov.: 10♂ 11♀, Colombo (BMNH). 5♂, 18mi NE of Colombo, Dambuwa Estate, 30m (MZLU).

Male. – Head dorsum mostly brown, posterior margin lighter, frontoclypeus, antennae, and palps brown. Maxillary palps 2.3 mm; proboscis 0.9 mm, as long as first 2½ segments of maxillary palp. Pronotum brown, slightly lighter in colour than head and mesonotum. Mesonotum and tegula brown. Forewing 12-14 mm, mostly brown, similar to that of *D. robustior*, with arc of small translucent spots distad of cord, hyaline spot at m-cu and big spot at arculus. Legs with coxae brown and distal segments lighter. Modified spur (fig. 44) slightly longer than adjacent spur, bifid with two unequal sinuate points directed distally, longer point almost ½ as long as spur. Genitalia (fig. 44): Tergum IX apical ¼ overhanging segment X in lateral view, posterior margin with broad obtuse angle in dorsal view; sternum IX mesosuperior process triangular and extended above basal ⅔ of phallus in lateral view. Segment X dorsal margin slightly concave with blunt apex in lateral view, oval-shaped almost ½ as wide as IX in dorsal view. Preanal appendages trapezoidal with dorsal margin horizontal in lateral view, ventral margin inclined dorsad and posterior margin slightly incised. Inferior appendages angled dorsad in lateral view, dorsal margin concave and nearly parallel with ventral margin, middle of ventral margin with obtuse angle, apex rounded; distal arms diverging in ventral view, lateral margins with base and apex rounded, mesal margin with squarish basomesal angle, and short apicomesal point.

Distribution. – India: Karnataka, Tamil Nadu; Sri Lanka.

Remarks. – This species has male modified spur bifid and somewhat similar to that of *D. robustior*, but differs by having spur with the shorter point nearly straight and directed distad. Until now the identity of *D. notata* has been enigmatic, because the locality stated by Fabricius (1781) as 'America boreali' was very doubtful. McLachlan (1864) placed this species in *Dipseudopsis*, and suggested that the original locality information by Fabricius was in error, since at the time the genus was known only from South Africa and China. Our examination of the male type of *D. notata* reveals that it is identical to Ulmer's (1915) original description of *D. horni*, only known from southern India and Sri Lanka, and we therefore concur with McLachlan that the type of *D. notata* is mislabelled.

Dipseudopsis recta Martynov, 1935

(figs. 15, 45)

Dipseudopsis recta Martynov, 1935: 163-164, fig. 65a-b, Type, INDIA: '♂. Sanjai River, Chakradharpur, Chota Nagpur. 8-10.ii.1918. N. Annandale and F. H. Gravely' (probably NZSI). – Fischer 1962: 14; Higler 192: 80.

Dipseudopsis bombayana Martynov, 1935: 164-165, figs. 66a-b, 67, Type, INDIA: '♂. Gokak, Belgaum district, Bombay Presidency (at light). June 1928 B. Prashad and H. S. Rao.' [Type (NZSI) in poor condition; not able to borrow for examination, pers. comm. Dr. K. Rai]. – Fischer 1962: 5; Higler 1992: 80. Syn. n.

Specimens examined. – INDIA: Andhra Pradesh: 1♂, Lamnasinghi Ghats, 75km SW Vishak, 850m, 10.VII.1982, D. R. Davis (USNM). Bihar: 1♂ 5♀, Namkum Ranchi, 675m, 8.XI.61, Ross & Cavagnaro (CASC). Karnataka: 12♂ 1♀, Haveri, 2.XII.1961, F. Schmid (CNCI). 1♂, Jannapura, 22.I.1959, F. Schmid (CNCI). 2♂, Kakankote, 10.I.1959, F. Schmid (CNCI). 4♂ 8♀, Yellapur, 30.I.1959, F. Schmid (CNCI). 2♂, Shimoga, R. Tunga, 1865ft, III-12.VIII, P.S. Nathan (MCZC). Madhya Pradesh: Satanwara, 37♂ 17♀, 28.XI.1961; 1♂ 3♀, 29.XI.1961, F. Schmid (CNCI). 16♂, Phalghat, 6.II.1959, F. Schmid (CNCI). Maharashtra: 3♂ 1♀, (Bombay) Sykes, 5.II.1959, F. Schmid (CNCI). Tamil Nadu: 3♂, Varaiyattu Tittu, 21.XII.1958, F. Schmid (CNCI). 2♂, Maraiyur, 19.XII.1958, F. Schmid (CNCI). 1♂, Sathuparai, 1.XII.1958, F. Schmid (CNCI). NEPAL: 1♂, Chitwan Dist., Sauraha S.I. Camp, 31.X.1985, W. N. Mathis (USNM).

Male. – Head brown, occipital margin light brown, frontoclypeus light brown except dorsal margin with dark band, antennae with dorsal portions brown, and ventral areas light brown, palps light brown, maxillary palps 3.7 mm, proboscis 1.5 mm, almost as long as first three segments of maxillary palp. Pronotum brown, hind margin light brown, lateral sides light brown; mesonotum brown, with tegula and forewings light brown. Forewing 10-12 mm long, faded area distal to cord, small hyaline spots at m-cu and arculus. Legs light brown. Modified spur (fig. 45) about 1.5x long as adjacent spur, apical ⅛ with crown of three minute points, having two larger exterior points spiraling around minute middle point, middle point slightly curved, directed distad, inconspicuous and more lightly sclerotized than other points. Genitalia (fig. 45): IX tergum with apical ½ overhanging X in lateral view, posterior margin slightly incised in dorsal view; IX sternum mesosuperior process with blunt dorsal extension and slender posterior lobe overhanging basal ⅓ of phallus in lateral view. Segment X slightly longer than preanal appendage, with lateral margins parallel and apex deeply bilobed in dorsal view. Preanal appendages dorsal margin straight in lateral view, ventral margin curved dorsad, posterior margin truncate, apicodorsal angle square, ventroposterior angle obtuse. Inferior appendages similar as in *D. triclavata*, basal ½ twice as thick as apical portion in lateral view, with dorsal margin almost straight, ventral margin having distal ½ incised, distal ½ fingerlike but slightly acuminate; basal shelves separated by V-shaped notch in ventral view, posterior arms with blunt apicomesal point, lateral margin straight with curved apical and basal angles.

Female. – Tergite of abdominal segment VIII (fig. 15) with ventral submarginal recessed groove. Genitalia (fig. 15).

Distribution. – India: Andhra Pradesh, Bihar, Karnataka, Madhya Pradesh, Maharashtra, Tamil Nadu; Nepal.

Remarks. – *D. recta* is a sibling species to *D. triclavata*, but differs by having male modified spur with smaller apical points. The specific differences shown in the original species descriptions of *D. recta* and *D. bombayana* can be observed by rotating the modified spur. Hence, *D. bombayana* is considered to be a junior synonym of *D. recta*.

***Dipseudopsis robustior robustior* Ulmer, 1929 stat. n.** (fig. 46)

Dipseudopsis robustior Ulmer, 1929: 185-186, fig. 22, Type series: MALAYSIA: West Malaysia: 'Material in Coll. McLachlan: 1♂, Perak (etwas verletzt).' Cotype ♂*: abdomen missing, Perak (BMNH). – Fischer 1962: 14.

Dipseudopsis akhila Schmid & Denning, 1979: 243-244, fig. 2, Holotype ♂*: THAILAND: Chiang Mai Prov., Mae Ping, Chiang Mai, 1000ft, 10.XI.1964, Peters (CLDD); Paratypes*, Tha Phra, Khon Kaen. **Syn. n.**

Dipseudopsis thailandica Schmid & Denning, 1979: 246, fig. 4, Holotype ♂*: Tha Phra, Khon Kaen, 24.XII.1968, Knapp; Paratypes*, Nong Pora Kit bamroog, Roi-et, and Kalasin. **Syn. n.**

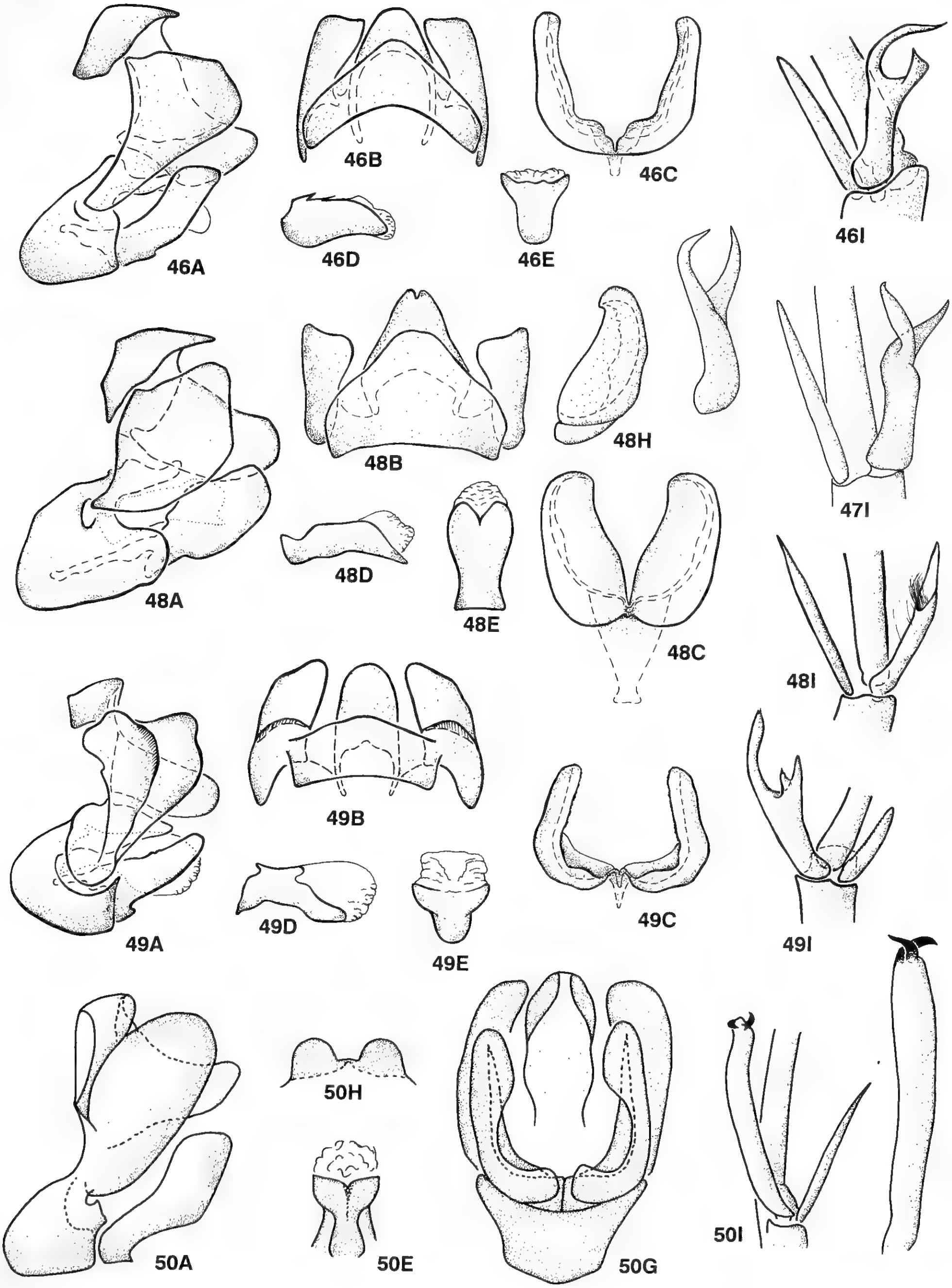
Dipseudopsis junki Marlier, 1979: 1-10, figs. 1-7, Type series: 2♂ 7♀, 4 larvae, 1 pupa, Bung Borapet, lake in central Thailand, 5.IX.1971, Dr. W. Junk. **Syn. n.**

Specimens examined. – BURMA: 1♂, Rangoon, McL. coll (BMNH). CAMBODIA: 6♂ 4♀, Phnom Penh (USNM, ZMHB). MALAYSIA: West Malaysia: Kedah: 1♂, Kuala Ketil (BMNH). 4♂, Bumbong Lima, light trap (USNM). THAILAND: 2♂ 1♀, Bangkok (USNM, MCZC). Chiang Mai: 25♂ 16♀ (USNM); 1♂ 1♀ (MCZC); 5♂ 1♀, Chiang Mai, Ban-tin-doi, 310m (BPBM). 4♂, Klong Rang Sit, at light (BMNH, NHMW). 1♂, Payao (USNM). 2♂, Bung Borapet (USNM). 4♂, det. Banks (1931b) as *D. stellata*, 'Penin. Siam', Patalung, 1.V.1924, I. H. N. Evans (MCZC, BMNH). 1♂, Patalung, Paknam Lampam (BMNH). 8♂, Tha Phra, Khon Kaen (CLDD). 7♂, Chiang Mai, River Ping (CLHM, ZMUC). 10♂, Chiang Mai Zoo, light trap (CLHM). 27♂, Tap-Tan (CLHM). 1♂, Chantaburi, Khao Soi Dao, 400m (UOPJ). 1♂, Kanchanaburi Dist., Sai Yok Natl. Park, 400m (CLHM). 1♂, Nam Nao Natl. Park (CLHM). 3♂, Puk Hieo, Chayapoom (CLHM). 5♂, Ayutthaya (CLHM). 2♂, Bangsaen (CLHM). 1♂, Tham Than Lod Natl. Park (CLHM). 1♂, Phuket, Kao Prataew Natl. Park (CLHM). VIETNAM: 1♂, Long Xuyen (MNHN). 2♂, Hue (MNHN).

Male. – Head mostly brown, posterior warts light brown, frontoclypeus with ventral ½ light brown and dorsal part brown, antennae mostly yellowish brown but dorsal surface dark brown, palps yellowish brown, maxillary palps 2.1 mm, proboscis 1.1 mm, as long as first three segments of maxillary palp. Pronotum and tegula light brown, mesonotum dark brown. Forewing 11-12 mm, similar as in *D. collaris*, with 5-7 small translucent spots in circular pattern around discal cell, having most spots distal to cord. Legs with coxae dark brown, distal segments yellowish brown. Modified spur (fig. 46) bifid, with two apical points, shorter point stout and angular, longer point slender, semicircular, and distant from other point. Genitalia (fig. 46): Tergum IX with short apical lobe extending over X in lateral view, posterior margin triangular in dorsal view; sternum IX mesosuperior process with short rounded dorsal lobe and long slender fingerlike posterior lobe in lateral view. Segment X dorsum inclined steeply ventrad toward blunt acuminate apex in lateral view, apex directed posteriad, having middle of ventral margin curved ventrad, and apicoventral margin slanted dorsad, ellipsoidal in dorsal view. Preanal appendages trapezoidal in lateral view, dorsal margin straight, ventral margin slanted dorsoposteriad, apicodorsal angle obtuse, apicoventral apex curved and extended more posteriad than apicodorsal angle. Inferior appendages with dorsal and ventral margins parallel and apical ½ bent dorsad in lateral view, basal ¼ with thin basal shelf, and apical ½ trapezoidal with apex slighted rounded, distal arms almost fingerlike in ventral view, lateral margins with apical and basal ends curved, basoventral shelf short, and mesal margin with squarish basal angle.

Distribution. – Burma; Cambodia; Malaysia: West Malaysia; Thailand; Vietnam.

Remarks. – *D. robustior* is the most common species of *Dipseudopsis* in Thailand, and is somewhat difficult to distinguish from *D. collaris* and *D. infuscata*. Possibly these species are merely variants of a widely distributed species.



Figures 46-50. – *Dipseudopsis*, A-G, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral. H, see specific descriptions below. I-J, male modified apical spurs of hind tibia, ventral. Fig. 46, *D. robustior* Ulmer. Fig. 47, *D. robustor andamanensis,* n. ssp. 47 I, modified spur, isolated spur depicted at left. Fig. 48, *D. schmidi,* n. sp., 48H. left inferior appendage, ventral, variation with apicomesal tooth. Fig. 49, *D. spectabilis* Banks. Fig. 50, *D. stabatensis* Malicky & Weaver; 50H, segment IX, dorsal.

Dipseudopsis robustior andamanensis ssp. n.
(fig. 47)

Dipseudopsis infuscata. – Malicky 1984: 214, 216 [misdet.].

Type data. – Holotype ♂: INDIA: South Andaman Island: Mongelutonge, 20.XII.1976, Starmühlner (CLHM). – Paratypes: 1♂ 5♀, same data (CLHM); 2♂ 15♀, Bimblton, 22.XII.1976, Starmühlner (CLHM).

Male. – Head, body, wings and genitalia similar to *D. robustior*. Modified spur (fig. 47) with two apical subequal in length and size.

Remarks. – This subspecies of *D. robustior* has unique, pincher-like modified spur (fig. 47) with two subequal points, but in *D. robustior* (fig. 46) the apical points of the modified spur are unequal, having a long slender curved point and a short broad point. It differs from *D. infuscata* (fig. 41) which has the modified spur with a long straight point directed distad and a shorter curved point. In *D. collaris* the points are shorter, only ⅓ as long as the spur. This subspecies represents the only member of the genus known from the Andaman Islands. All previous records of *D. infuscata* from South Andaman Island (Malicky 1984) are now recognized as this subspecies.

Etymology. – This subspecies is named after the Andaman Islands.

Distribution. – India: South Andaman Island.

Dipseudopsis schmidi sp. n.
(fig. 48)

Type material. – Holotype ♂: INDIA: Manipur: Kaiphundai, 20.V.1960, F. Schmid (CNCI). Paratypes: 9♂, same data, F. Schmid (CNCI). 1♂, Kambiron, 24.V.1960, F. Schmid (CNCI). Assam: 6♂ 2♀, Garampani Res., 10mi S Golaghat, 110m, 9.X.61, E. S. Ross & D. Cavagnaro (-CASC). 1♂, Kaziranga, 75m, 26.36N 93.28E, 7-9.V.1976, Wittmer (CLHM). 'U.D.M.N.C.H' [United District of Mikir and North Cachae Hills]: 1♂, Langtrang, 30.IV.1960, F. Schmid (CNCI). BANGLADESH: 1♂ 2♀, Lawa Chera For., Srimangal, 110m, 27.IX.61, E. S. Ross & D. Cavagnaro (CASC).

Male. – Head dorsum, pronotum and cervical sclerites light orangish brown, but head slightly darker. Frontoclypeus dark brown except for small orangish brown triangular area between bases of antennae; genae yellowish brown except ventral sides dark brown. Scape mostly orangish brown, but apical portion and remainder of antenna dark brown. Mouthparts, with palps dark brown, maxillary palps 2.5 mm, proboscis 1.5 mm, as long as first four segments of maxillary palp. Mesonotum and tegula dark brown. Forewing 11-13 mm, dark brown with indistinct translucent spots, large basal triangular translucent spot bordered by Sc, Cu_1 and first branches of Rs and M, another translucent spot distal to cord. Hindwing lighter brown than forewing, with translucent basal triangular area between Sc and Cu_1. Legs with colouration similar as in *D. nebulosa*, mostly dark brown, but apical ½ of front and middle femora lighter brown, as well as tibiae and tarsi. Hind leg mostly dark brown, tarsi slightly lighter. Modified spur (fig. 48) with basal ⅔ unmodified, distal ⅓ with setose pocket at base of straight acuminate apex pointed distad. Genitalia (fig. 48): Tergum IX broad and triangular in dorsal view, long with apical ⅓ overhanging segment X in lateral view. Segment X broad, extending distad slightly further than inferior appendages in lateral view, almost twice as long as broad and somewhat ellipsoidal, with dorsal and ventral margins inclined ventrad but extended posteriad at apex, apex broadly curved; elongate and cordate in dorsal view, with lateral margins tapered distad and apex slightly incised. Preanal appendages broad and rhomboid in lateral view. Inferior appendages broad and somewhat rectangular with curved ventral margin in lateral view, dorsal margin with short broad basal hump, maximum height about ⅔ total length.

Etymology. – Named after its collector Fernand Schmid.

Distribution. – Bangladesh; India: Assam, Manipur.

Remarks. – This species is easily recognized by having the male modified spur acuminate and nearly straight. The male is somewhat similar to *D. nebulosa*, but differs by having light areas of forewing with faded borders and less distinct, and sternum IX with mesosuperior process not short and globular, but long and slender, extending above basal ⅔ of phallus.

Dipseudopsis spectabilis Banks, 1931
(figs. 9, 49)

Dipseudopsis spectabilis Banks, 1931a: 69, pl. 5: fig. 1, Type ♂*: MALAYSIA: Sabah: Sandakan, Baker (MCZC 16421). – Fischer 1962: 15.

Male. – Head dorsum with anterior portion dark brown, posterior warts and lateral margins yellowish brown, frontoclypeus dark brown, genae and antennal scape yellowish brown, but flagellum dark brown, palps dark brown; maxillary palps 1.8 mm, labial palps 0.6 mm, proboscis 1.4 mm, longer than first four segments of maxillary palp. Pronotum, mesonotum and tegula dark brown. Wings (fig. 9): Forewing 11 mm, fork I absent, conspicuous pattern of lighter bands on dark brown background, similar as in *D. flavisignata*, with five translucent spots: 1) long slender stripe along anterior margin, ⅔ as long as Sc; 2) small oval-shaped spot at base of Rs; 3) cordate spot in discal and medial cells; 4) truncate V-shaped band running basad from subapex to crossvein r-m, then distal to cord to base of M_4, and to submargin through fork IV including $M_{4,}$ 5) long irregular semicircular band running from base of anal margin, tapering at m-cu, and widening toward margin at arculus. Modified spur (fig. 49): trifid, with three apical points, first point longest, slightly curved at base and ½ as long as spur, second point ¼ as long as spur, and third point minute and adjacent to second point and located in curved notch between first and second points. Genitalia (fig. 49): Tergum IX with posterior margin slightly extended over segment X in lateral view, posterior margin broadly rounded in dorsal view; sternum IX mesosuperior process acuminate, dorsal margin irregular, ventral margin nearly straight, extending above basal ¾ of phallus. Segment X dorsal and ventral margins nearly parallel in lateral view; thumblike with lateral margins parallel in dorsal view. Preanal appendages trapezoidal in lateral view, posterior margin slightly incised and lateral side with ridge parallel to anterior margin. Inferior appendages heavily sclerotized, fingerlike with dorsal and ventral margins tapering slightly distad in lateral view, having short ventrobasal shelf, and dorsal margin with some minute bumps; squarish in ventral view, with lateral arms fingerlike with lateral margins converging slightly distad and mesal margin finely serrate.

Distribution. – Malaysia: Sabah.

Remarks. – This species is only known from the unique type; it is a sibling species to *D. flavisignata* and differs from it in having the male forewing with a translucent subapical truncated V-shaped band. It also differs by characteristics of the male modified spur and genitalia.

Dipseudopsis stabatensis Malicky & Weaver, 1988
(fig. 50)

Dipseudopsis stabatensis Malicky & Weaver, 1988: 4-5, fig. 5a-e, Holotype ♂*: INDONESIA: Sumatra: Dolok Merangir, 2-18.V.1971, Diehl (CLHM). Paratype ♂*: Stabat 23.VI.1974 (CLJW).

Dipseudopsis morosa. – Banks 1924: 450 (pro parte) [misdet. syntype 1♂*: INDONESIA, Kalimantan, 'Borneo', Telang, X.1881 (MCZC)].

Male. – Head dorsum with dark brown median stripe tapering posteriad, lateral sides and posterior warts yellowish brown, frontoclypeus dark brown, genae light brown, antennae light brown, palps light brown, maxillary palps 2.4 mm, proboscis 1.2 mm, as long as first three segments of maxillary palp. Pronotum with raised areas yellowish brown, but deep median furrow and lateral sides dark brown. Mesonotum and tegula dark brown. Metanotum light brown. Forewing 13 mm, brown with translucent apical and anal spots, hyaline spots at m-cu and arculus. Fore and mid legs with coxae dark brown and distal segments yellowish brown, hind leg yellowish brown. Modified spur (fig. 50) 1⅓X longer than adjacent spur, apex bifid with two minute curved apical points, each about ⅛ length of spur. Genitalia (fig. 50): Tergum IX posterior margin bilobed, with lobes separated by squarish mesal notch in dorsal view, minute portion of posterior margin overhanging segment X in lateral view; sternum IX mesosuperior process similar to that of *D. flinti*, but slightly slenderer in lateral view. Segment X thumblike with lateral sides parallel and sinuate in dorsal view. Preanal appendages ellipsoidal and extended dorsoposteriad in lateral view. Inferior appendages capitate with trapezoid apex extended dorsad in lateral view; lateral arms fingerlike with lateral margins straight and parallel in ventral view, and mesal margins with broad curved basolateral incisions.

Distribution. – Indonesia: Kalimantan, Sumatra.

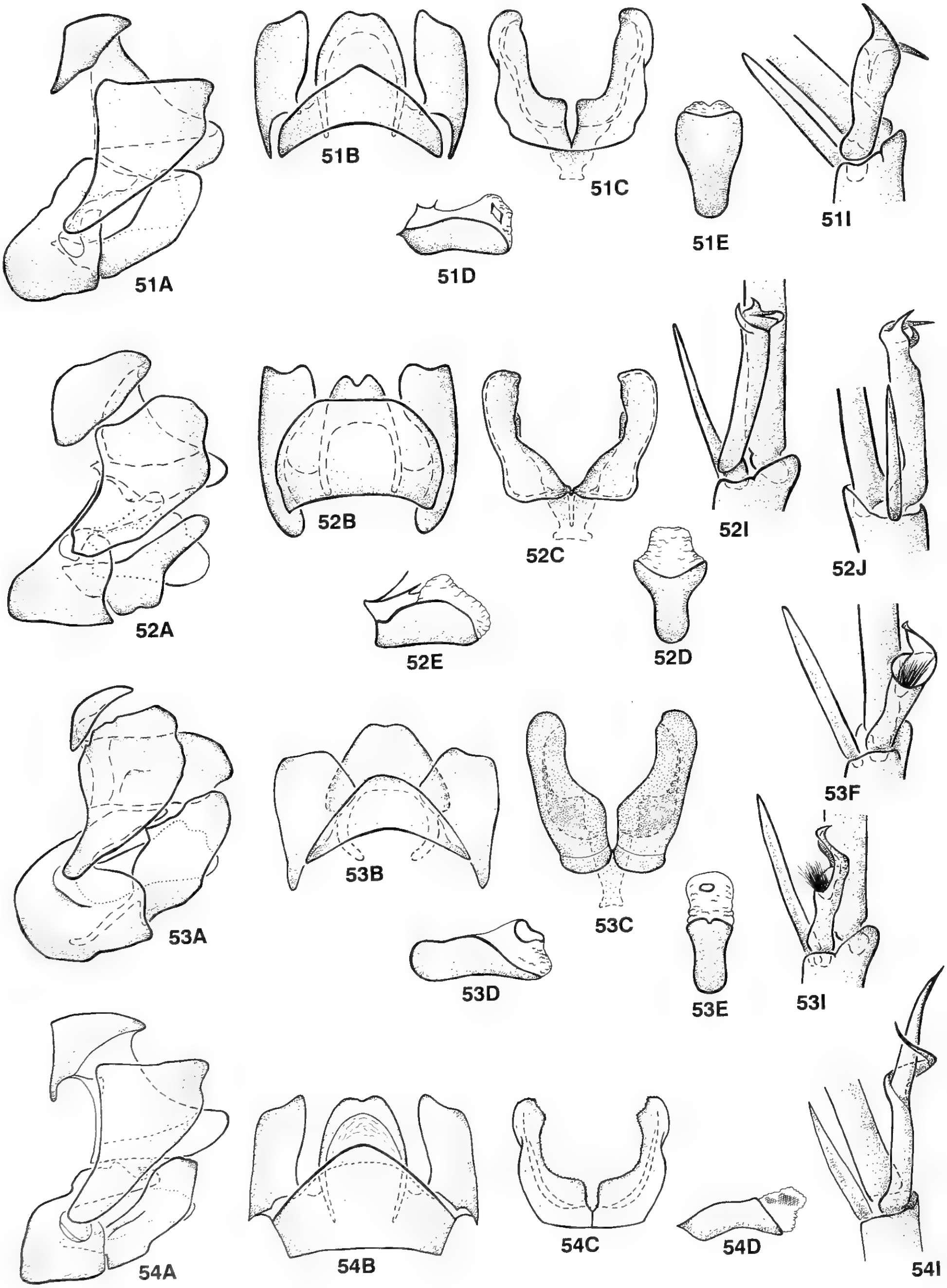
Remarks. – This species is similar to *D. flinti*, but differs by having inferior appendage slenderer in lateral view, and the modified spur with apical points shorter.

Dipseudopsis tonkinensis Navás, 1921
(fig. 51)

Dipseudopsis tonkinensis Navás, 1921: 79-80, Holotype ♂*: VIETNAM: 'Tonkin, Chogahn, 1919, P. de Joannis' (-MZBS). – Fischer 1962: 16; Fischer 1972: 8.

Specimens examined. – CHINA: Hainan: 1♂, Ta Hau, 4.VII.35, J. L. Gressitt (MCZC).

Male. – Head dorsum brown, posterior margin lighter brown, frontoclypeus brown, antennae brown but ventral side lighter brown, palps brown, maxillary palps 2.2 mm, proboscis 1.0 mm, as long as first three segments of maxillary palp. Pronotum brown, but posterior margin and lateral sides yellowish brown. Mesonotum and tegula brown. Forewing 12.5 mm, faded brown with small hyaline spots at m-cu and arculus. Legs with coxae brown and distal segments yellowish. Modified spur (fig. 51) bifid, with two robust acuminate points, first point directed obliquely distad and second point curved mesad. Genitalia (fig. 51): Tergum IX posterior margin only slightly overhanging segment X in lateral view, posterior margin



Figures 51-54. – *Dipseudopsis*, A-G, male genitalia: A, lateral; B, preanal appendages, segments IX and X, dorsal; C, inferior appendages, ventral; D, phallus, lateral; E, phallus, ventral; F, segments IX, X, dorsal; G, ventral. I-J, male modified spurs apical spurs of hind tibia, ventral. Fig. 51, *D. tonkinensis* Navás. Fig. 52, *D. triclavata* Martynov. Fig. 53, *D. varians* Ulmer. Fig. 54, *D. voluta* Ulmer.

broad triangular in dorsal view; sternum IX mesosuperior process in lateral view with blunt dorsal projection and acuminate posterior process extended above basal ½ of phallus. Segment X dorsal margin slightly concave and slanted ventrad having blunt apex in lateral view, ellipsoidal with apex slightly incised in dorsal view. Preanal appendages dorsal margin straight and ventral margin inclined dorsad distad with posterior margin broadly incised in lateral view. Inferior appendages, clavate, being slightly broadened in lateral view, bent dorsad with oblique angle in middle, dorsal and ventral margins parallel, apex truncate; apical arms with apicolateral margins rounded and slightly broadened in ventral view, apicomesal angles squarish, mesal margins with square basolateral notch and square basomesal shelf.

Distribution. – China: Hainan; Vietnam.

Remarks. – This species is similar to *D. collaris*, but differs by having male modified spur with apical points shorter, and by having the male genitalia with segment X broader in dorsal view.

***Dipseudopsis triclavata* Martynov, 1935**
(fig. 52)

Dipseudopsis triclavata Martynov, 1935: 161-162, figs. 62a-b, 63a-b, 64. New Lectotype ♂*: INDIA: Maharashtra: Khanapur, Belgaum dist., Bombay Presidency, 18-19.XI.1928, B. P. & H. S. R. (NZSI). Remainder of type series: 1♀, same data as lectotype. 1♂ [doubtful det.], Meghalaya: The Peak, Shillong, 8,400ft, 25.34N 91.53, 12.X.1914. S. W. Kemp. – Fischer 1962: 16; Higler 1992: 80.

Dipseudopsis morosa. – Schmid 1958: 13, 24, 27, 89, pl. 15: figs. 12-13 [misdet.].

Specimens examined. – INDIA: Karnataka: 3♂, Uppinangadi (CNCI). 1♂, Patan (CNCI). 14♂ 4♀, Shimoga, R. Tunga, 1865ft (MCZC). 2♂ 10♀, Bhadravati (MCZC). 8♂ 4♀, Kakankote (CNCI). SRI LANKA: E. Prov.: Amparai Dist.: 1♂, Inginiyagala, 250ft (USNM). Cen. Prov.: 1♂ det. Ulmer as *D. stellata*, Peradeniya (BMNH). Kandy Dist.: 11♂ 6♀, Hasalaka, Dam Spillway, 300ft (USNM). Matale Dist.: 2♂ 2♀, Sigiriya, 800ft (USNM). Nuwara Eliya Dist.: 2♂, Milk Board Dairy, 4.2mi SW Nuwara Eliya, 6200ft (USNM). N. Prov.: Vavuniya Dist.: 8♂ 2♀, Parayanalankulam Irrigation Canal, 25mi NW of Medawachchiya, 100ft (USNM). N. Cen. Prov.: Anuradhapura Dist.: 4♂ 2♀, Wildlife Soc. Bungalow, Hunuwilagama, Wilpattu Natl. Park, 200ft (USNM). NW. Prov.: Puttulam Dist.: 1♂, Wilpattu Natl. Park, 100ft, Tala Wila (USNM). Sabaragamuwa Prov.: 1♂, Niriella (USNM). Ratnapura Dist.: 15♂, Walawe Ganga, Embilipitiya, 100ft (USNM). S. Prov.: Galle Dist.: 1♂ 1♀, Hiniduma (USNM). Hambantota Dist.: 1♂, Palatupana, 10ft (USNM). Uva Prov.: Badulla Dist.: 1♂ 1♀, Dunhinda Falls, 1300ft (USNM). Monaragala Dist.: 9♂, Sella Karagama, Menik Ganga, 150ft (USNM). W. Prov.: Colombo Dist.: 1♂, Malewana (USNM).

Male. – Head dorsum brown, except narrow yellowish brown posterior margin; frontoclypeus mostly yellowish brown with brown stripe along dorsal margin, antennae dorsum brown and ventral sides yellowish brown; palps light brown, maxillary palps 2.5 mm, proboscis 1.3 mm, as long as first three segments of maxillary palp. Pronotum mostly brown, but lateral sides yellowish brown, propleuron and cervical sclerites yellowish brown. Mesonotum and tegula brown. Forewing 11-14 mm, dark brown with translucent stigma and hyaline spots at m-cu and arculus. Fore and mid legs with coxae to mid femora dark brown and apical ½ of femora and distal leg segments light brown; hind leg yellowish brown. Modified spur (fig. 52) trifid, apex of spur appears truncate, but with three distinct apical points spiraling in plane perpendicular to longitudinal axis of spur, having one minute point and two longer points, long points each ¼ as long as spur. Genitalia (fig. 52): Tergum IX with minute portion of apex overhanging segment X in lateral view, posterior margin truncate with broadly rounded lateral corners in dorsal view. Sternum IX mesosuperior process with rounded triangular dorsal process and smaller posterior lobe extended above basal ⅔ of phallus in lateral view. Segment X dorsal margin slightly concave and inclined steeply ventrad in lateral view, apex acuminate with rounded end, ellipsoidal with apex incised in dorsal view. Preanal appendages trapezoidal with dorsoposterior apex broadly rounded and dorsal and posterior margins concave in lateral view. Inferior appendages similar to *D. recta*, base 2X as thick as fingerlike apical ½ in lateral view, ventral margin of apical portion incised; basal shelves with broad V-shaped medial notch in ventral view, apical arms with middle of mesal margin having oblique incision, lateral apical margin rounded, basolateral margin squarish and apicomesal angle squarish with short blunt tooth.

Distribution. – India: Karnataka, Maharashtra; Sri Lanka.

Remarks. – This species is closely related to *D. recta*, but it differs by having male modified spur with longer apical points. There has been some confusion regarding the identity of this species, due to an erroneous redescription of 'D. morosa' by Schmid (1958), based on a specimen from Sri Lanka that was actually *D. triclavata. D. morosa* is only known from the southern islands of the Philippines. The male modified spurs of these species are similar, however the spur of *D. triclavata* (fig. 52) differs by being trifid, but that of *D. morosa* (fig. 39) is bifid. The record of the male syntype from Shillong, Meghalaya by Martynov (1935) is doubtful and should be confirmed.

Dipseudopsis varians Ulmer, 1929
(fig. 53)

Dipseudopsis varians Ulmer, 1929: 191-192, figs. 28-30, Type series: MALAYSIA: West Malaysia: 'Material in Coll. McLachlan: 3♂, Perak.' Type 1♂*: Perak (BMNH), condition poor, abdomen and hind legs absent, no other type material available at Mus. (pers. comm. P. C. Barnard). – Fischer 1962: 16.

Dipseudopsis petersorum Schmid & Denning, 1979: 345, fig. 3a-e, Holotype ♂, THAILAND: Chiang Mai Prov., east fork, Mae Ping at junction of small stream, 59 km north Chiang Mai, 1350ft, at light, 30.XI.1964, W. L. & J. G. Peters. **Syn. n.**

Specimens examined. – BURMA: Tenasserim: 1♂, Mekane, 90km E Moulmein, 200m (NHRS). MALAYSIA: West Malaysia: 1♂ 2♀?, Melaka, det. Ulmer 1905 as *Dipseudopsis* sp., 'de Malacca' Presqu'ile, 1899, Errington de la Croix et P. Chapé (MNHN). 1♂, Johor: Kota Tinggi (BMNH). 1♂, Negeri Sembilan: Kuala Pilah, at light (BMNH). 3♂, Pahang: Kuala Tahan, at light, (MCZC, BMNH, BPBM). 2♂, Kedah: Bumbong Lima, light trap (USNM). 1♂, Selangor: Kuala Lumpur (BMNH). THAILAND: 1♂, Trang (MCZC). 1♂ 1♀, 40mi SE Prachuab, 75m (CASC). 1♂, det. Denning as *D. petersorum*, Krabinburi, Thung Pho, 5.X.1970, Balmer (CLDD). 1♂, Phuket, Tonesai waterfall (SOFM). 1♂, Khao Soy Dan (CLHM). 1♂, Chantaburi, Phliu, 100m (UOPJ). 2♂, Loei, Phu Rua, 800m (UOPJ). 1♂, Nakorn Nayok Prov., Khao Yai Natl. Park, 700m (ZMUC). 23♂ 7♀, Chiang Mai Zoo, light trap (CLHM).

Male. – Head, cervical sclerites, and pronotum orangish brown. Mesonotum, tegula, frontoclypeus, palps and antennae dark brown, but genae lighter brown. Maxillary palps 2.4 mm, proboscis 1.3 mm, as long as first three segments of maxillary palps. Forewing 12 mm, colouration similar to that of *D. nebulosa* but borders of translucent spots more indistinct, dark brown background, large triangular spot between bases of R_1 and Cu_1 and translucent subapical spot proximal to fork I, similar to bilobed spot of *D. nebulosa* but second lobe below R_4 less distinct. Legs with coxae dark brown, distal segments light brown. Modified spur (fig. 53) shorter than adjacent spur, with modified apical portion ½ as long as spur, having spiraling point with tuft of setae in basal pocket. Genitalia (fig. 53): Tergum IX with apical ¾ or more overhanging segment X in lateral view, triangular with posterior margin rounded in dorsal view; sternum IX mesosuperior process slender and acuminate in lateral view. Segment X oblong with dorsal and ventral margins parallel in lateral view, apex broadly rounded with venter slightly incised; cordate and broad with lateral sides tapering distad in dorsal view, apex blunt and slightly incised. Preanal appendages D-shaped with obtuse dorsal angle in lateral view. Inferior appendages oblong with irregular dorsal and ventral margins in lateral view, ventral margin curved with obtuse basal bump, dorsal margin irregular with conspicuous tooth in middle, distal arms fingerlike in ventral view, with lateral margins diverging slightly distad and basal shelves broad.

Distribution. – Burma; Malaysia: West Malaysia; Thailand.

Remarks. – This species is somewhat similar to *D. immaculata*, but differs by having male with modified spur shorter and twisted like a short corkscrew, and by having the male genitalia with inferior appendages with a mid dorsal tooth in lateral view and without an apicomesal tooth in ventral view.

Dipseudopsis voluta Ulmer, 1906
(fig. 54)

Dipseudopsis voluta Ulmer, 1906: 87-88, 110, fig. 89, Type ♂*: INDONESIA: Sulawesi, 'Makassar', McL. coll, without abdomen and hind legs (BMNH). – Fischer 1962: 17; Fischer 1972: 8.

Specimens examined. – INDONESIA: Sulawesi: 1♂, without hind legs, 'Makassar', McL. coll (BMNH). Tenggara: 1♂, Desa Aopa, 50m, 27.X.1989, at light, R. de Jong & J. Huisman (RMNH). 1♂, Moramo, Sg Sena, 50m, 15.XI.1989, at light, R. de Jong & J. Huisman (RMNH).

Male. – Head dorsum mostly dark brown, posterior warts light brown; frontoclypeus brown with dorsal portion dark brown, genae light brown, antennal scape dark dorsad and light brown ventrad. Maxillary palps 2.3 mm, apical segments 1-3 yellowish brown, but basal segments 4-5 dark brown; proboscis 1.1 mm, as long as first three segments of maxillary palps, labial palps 0.5 mm, second and third segments minute. Pronotum mostly brown, posterior margin light brown with a few darker muscle scars, and propleuron yellowish brown. Mesothorax with notum and tegula dark brown, epimeron dark brown, episternum and sternum yellowish brown. Forewing 14-15 mm, dark brown with golden setae, and some translucent spots between R_{2+3} and R_{4+5}, M_{1+2} and $M_{3,}$ and hyaline spots at m-cu and arculus. Front leg with anterior portion of coxa dark brown, remainder of leg yellowish brown, mid and hind legs yellowish brown, but hind tibia with brown ring at subapical spur. Modified spur (fig. 54) 2 longer than adjacent spur, bifid with long subapical point spiraling around longer straight point, about ⅔ as long as spur. Genitalia (fig. 54): Tergum IX broad with posterior margin blunt triangular in dorsal view; sternum IX dorsomesal process with blunt posterior lobe in lateral view. Segment X similar as in *D. tonkinensis*, but base of ventral margin nearly straight and apex curved dorsad in lateral view. Inferior appendages basal ⅓ with slender squarish ventral shelf, distal ⅔ of ventral margin bent dorsad, dorsal margin slightly concave, apex broadened slightly and obtuse.

Distribution. – Indonesia: Sulawesi.

Remarks. – This species is easily recognized by having the modified spur with a long straight apical point and another more slender point spiraling completely around its base. The genitalia of *D. voluta* are similar as in *D. tonkinensis*, but differs by having inferior appendages with short obtuse subapical mesal tooth in ventral view, and with apical portion slightly tapered in lateral view. This species was previously only known from the male type which lacks the abdomen and is in rather poor condition. Two male specimens were collected recently, making it possible to provide a description of the male genitalia for the first time.

NOMINA DUBIA

Dipseudopsis onychophora Navás, 1935 nomen dubium

Dipseudopsis onychophora Navás, 1935: 104-105, Type ♂: INDIA: 'Lonawla (Bombay), 9-X-1934. H. Benavent, S. J.' [location of type unknown]. – Fischer 1962: 14; Higler 1992: 80.

Remarks. – The distributional data of other species of *Dipseudopsis* in India and the figure provided in the original description of *D. onychophora* by Navás (1935) of the modified spur of the male type, suggests that this species is probably synonymous with *D. triclavata*. However, since we are unable to locate and examine the type, the status of this species remains uncertain.

Dipseudopsis orientalis (Navás, 1913) nomen dubium

Esperona orientalis Navás, 1913: 12-13, fig. 2a-c, Type, sex unknown: VIETNAM: 'Hanoï (Tonkin). Un échantillon envoyé et cédé généreusement pour ma collection par M. Laboissière.' [location of type unknown]. – Fischer 1962: 14.

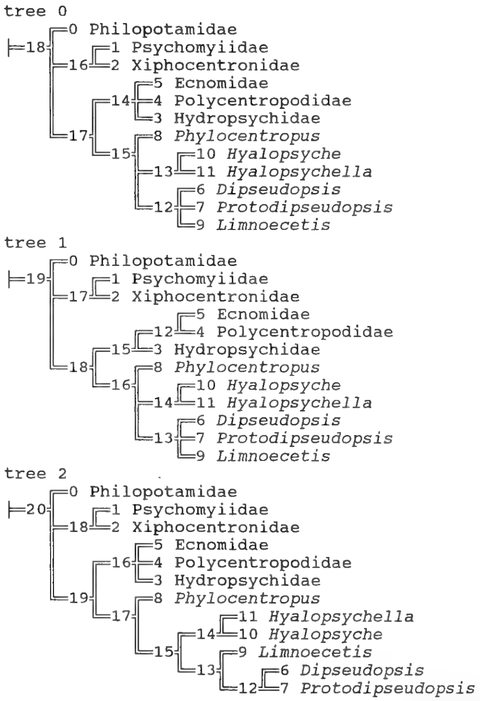
Remarks. – We were not able to locate and examine the type of this species, hence its identity remains uncertain. *D. orientalis* could be synonymous with one of the three species of *Dipseudopsis* known from Vietnam, *D. benardi*, *D. robustior*, and *D. tonkinensis*. According to the original species description (Navás 1913) the forewing of the type of *D. orientalis* is 12.4 mm, suggesting that this species is probably synonymous with either D. *robustior* or *D. tonkinensis*.

POLYCENTROPODIDAE ULMER

***Eodipseudopsis* Marlier 1959** nomen dubium

Eodipseudopsis Marlier 1959: 117. Type species: *Eodipseudopsis tomensis* Marlier (original designation).

The genus *Eodipseudopsis* is removed from the Dipseudopsidae and is provisionally placed in the Polycentropodidae. Three of its characteristics support its removal from Dipseudopsidae: 1) Female genitalia as figured in the original description have sternum VIII bearing a pair of ventrolateral processes (Marlier 1957: fig. 10A). 2) The antennae (cf. Marlier 1959: fig. 48A) are slender with their bases distant from each other. 3) The long slender lobe of the sent gland of sternum V (Marlier 1962: fig 10B) is uncharacteristic of dipseudopsid females examined, i.e. *Dipseudopsis, Hyalopsyche, Phylocentropus.*



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tree 0
    ╔═0 Philopotamidae
╞═18╣   ╔═1 Psychomyiidae
    ╠═16╩═2 Xiphocentronidae
    ║       ╔═5 Ecnomidae
    ║   ╔═14╬═4 Polycentropodidae
    ║   ║   ╚═3 Hydropsychidae
    ╚═17╣   ╔═8 Phylocentropus
        ╚═15╣   ╔═10 Hyalopsyche
            ╠═13╩═11 Hyalopsychella
            ║   ╔═6 Dipseudopsis
            ╚═12╬═7 Protodipseudopsis
                ╚═9 Limnoecetis
tree 1
    ╔═0 Philopotamidae
╞═19╣   ╔═1 Psychomyiidae
    ╠═17╩═2 Xiphocentronidae
    ║           ╔═5 Ecnomidae
    ║       ╔═12╩═4 Polycentropodidae
    ║   ╔═15╩═3 Hydropsychidae
    ╚═18╣   ╔═8 Phylocentropus
        ╚═16╣   ╔═10 Hyalopsyche
            ╠═14╩═11 Hyalopsychella
            ║   ╔═6 Dipseudopsis
            ╚═13╬═7 Protodipseudopsis
                ╚═9 Limnoecetis
tree 2
    ╔═0 Philopotamidae
╞═20╣   ╔═1 Psychomyiidae
    ╠═18╩═2 Xiphocentronidae
    ║       ╔═5 Ecnomidae
    ║   ╔═16╬═4 Polycentropodidae
    ║   ║   ╚═3 Hydropsychidae
    ╚═19╣   ╔═8 Phylocentropus
        ╚═17╣       ╔═11 Hyalopsychella
            ║   ╔═14╩═10 Hyalopsyche
            ╚═15╣   ╔═9 Limnoecetis
                ╚═13╣   ╔═6 Dipseudopsis
                    ╚═12╩═7 Protodipseudopsis
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Figure 55. Total tree output calculated by Hennig 86 for Hydropsychoidea, including outgroup and genera of Dipseudopsidae.

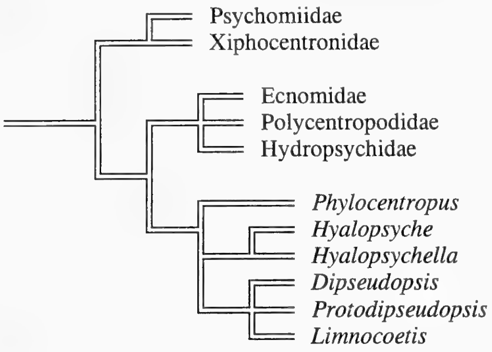

Figure 56. Consensus tree of the families of the Hydropsychoidea *s. str.* Weaver, showing phylogenetic relationships of the genera of Dipseudopsidae.

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REVIEW OF THE SOUTHERN PALAEARCTIC AND PALAEOTROPICAL LEAFHOPPER GENUS *HENGCHUNIA* VILBASTE (HOMOPTERA, CICADELLIDAE)

Asche, M. & M. D. Webb, 1994. Review of the southern Palaearctic and Palaeotropical leafhopper genus *Hengchunia* Vilbaste (Homoptera, Cicadellidae). – Tijdschrift voor Entomologie 137: 143-154, figs. 1-63 (ISSN 0040-7496). Published 15 December 1994.

The leafhopper genus *Pseupalus* Remane & Asche (Deltocephalinae: Paralimnini) is synonymized with *Hengchunia* Vilbaste syn. n. Four new species are described: *H. helleri* sp. n. from Cameroun and Zaire, *H. indica* sp. n. from India, *H. pakistanica* sp. n. from Pakistan and *H. javana* sp. n. from Indonesia: Java. *Hengchunia* now contains nine species which are probably all associated with the grass genus *Imperata*. The zoogeographical distribution of the species and their potential phylogenetic relationships are briefly discussed. Additions and amendments to Webb & Heller's (1990) check-list of Afrotropical and Oriental Paralimnini are made and include *Paralimnellus* Emeljanov (1972), oldest available name for *Bubulcus* Dlabola (1961) (junior homonym of *Bubulcus* Bonaparte 1854, Aves) and *Paralimnellus vittata* (Matsumura) comb. n. from *Henschia*.

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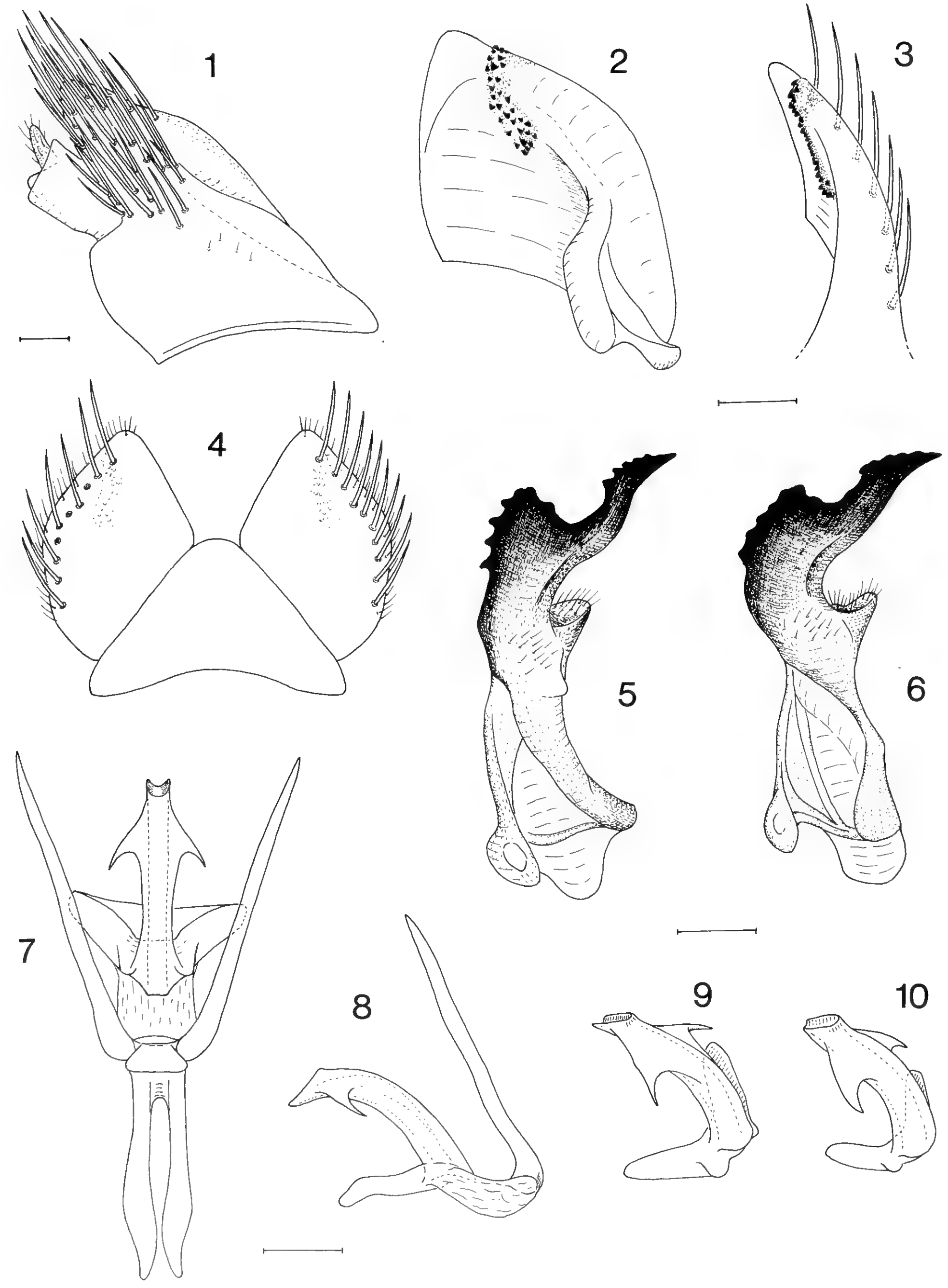
Key words. – Homoptera; Auchenorrhyncha; Cicadellidae; Paralimnini; *Hengchunia; Pseupalus;* review; new species; South Palaearctic and Palaeotropical Region.

This paper concerns a group of paralimnine leafhoppers (Cicadellidae: Deltocephalinae) apparently associated with the Palaeotropical grass *Imperata*, especially the species *I. cylindrica.* This association was reported by Remane & Asche (1980) who erected the genus *Pseupalus* for a single paralimnine species, *P. graecanarus* from the Canary Islands (type locality) and Greece. Recently, *Pseupalus* and related taxa were reviewed by Webb & Heller (1990) who added three more species: *P. gaiseri* from Ivory Coast, *P. digitus* from Thailand, and *P. murtus* from the Philippines: Luzon. Webb & Heller (l.c.) discussed the validity of the tribe Paralimnini sensu Emeljanov (1962), Remane & Asche (1980), Ossiannilsson (1983), and Emeljanov & Kirilova (1989) and Hamilton's 'Deltocephalina' (Hamilton 1975), and confirmed the tribal placement of *Pseupalus.* In addition, Webb & Heller (l.c.) provided a check-list of Afrotropical and Oriental paralimnine genera. Since then, the second author has examined specimens of a species from Taiwan, described as *Thamnotettix koshunensis* Matsumura, for which Vilbaste (1969) had established the genus *Hengchunia.* A comparison revealed not only the placement of *Hengchunia* in the Oriental Paralimnini, but also its generic synonymy with *Pseupalus.* Moreover, four new species of this genus were discovered in samples from Africa, India, and Indonesia, described below, together with an unidentifiable female specimen from Australia. The genus *Hengchunia* now contains nine species: one in the Southwestern Palaearctic, two in the Afrotropical Region, and 6 in the Oriental Region.

The following amendments and additions apply to the Afrotropical and Oriental paralimnine check-list (Webb & Heller 1990), noted above: *Paralimnellus* Emeljanov (1972) (type species: *cingulatus* Dlabola) oldest available name for *Bubulcus* Dlabola (1961) (type species: *cingulatus* Dlabola) (junior homonym of *Bubulcus* Bonaparte, 1854, Aves); *Paralimnellus vittata* Matsumura comb. n. (*Henschia*); *Pteropyx acutus* (Singh) (*Jassargus)* Emeljanov, 1972: 66; *Pteropyx maculatus* Emeljanov, 1972: 67 (Mali); *Khasia prima* Rao, 1989: 82 (India).

Depositories

Abbreviations for depositories of material used in this paper: M. Asche & H. Hoch, Marburg, private collection (AH); Agricultural University Wageningen, The Netherlands (AUWN); The Natural History Museum, London, United Kingdom (BMNH); Musée



Figs. 1-10. *Hengchunia gaiseri* (Webb & Heller), paratype ♂ from Ivory Coast; Figs. 6, 10: ♂ from Sierra Leone. – 1, male pygophore, left lateral view; 2, left subgenital plate, dorsal view; 3, same, dorsolateral view; 4, subgenital plates, ventral view; 5, 6, left style, dorsal view; 7, aedeagus and connective, ventrocaudal view; 8, aedeagus, left lateral view; 9, 10, same, left lateral view, slightly bent to left side. Scales: 0.1 mm.

Royal de l'Afrique Centrale, Tervuren, Belgium (MRAC); Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium (ISNB); Entomological Institute, Hokkaido University, Sapporo, Japan (EIHU); Staatliches Museum für Naturkunde Stuttgart, Germany (SMNS); University of Agricultural Sciences, Bangalore, India (UASB).

TAXONOMY

Hengchunia Vilbaste

Hengchunia Vilbaste, 1969: 8. – Type species by original designation: *Thamnotettix koshunensis* Matsumura.
Pseupalus Remane & Asche, 1980: 88, **syn. n.** - Type species by original designation: *Pseupalus graecanarus* Remane & Asche.

For relationship and diagnosis of *Hengchunia* see the corresponding paragraphs for *Pseupalus* in Webb & Heller (1990: 2, 3).

Key to the species of *Hengchunia* (males)
(after Webb & Heller 1990, modified and supplemented)

1. Preatrium of aedeagus with a pair of long and slender processes (e.g., figs. 7, 8) 2
– Preatrium of aedeagus without a pair of processes (fig. 46) .... *H. pakistanica* sp. n.
2. Aedeagal shaft with four spinose processes apically (fig. 63) .... *H. koshunensis* (Matsumura)
– Aedeagal shaft with two or less spinose processes apically or subapically (e.g., fig. 7) 3
3. Aedeagal shaft with a single spinose process or lateral flanges subapically 4
– Aedeagal shaft with two spinose processes apically or subapically 5
4. Aedeagal shaft with a horn-shaped subapical process directed ventrad, dorsal side of shaft at midlength with a bifurcate process and shortly basad of it with a single short process (figs. 32-34) .... *H. indica* sp.n.
– Aedeagal shaft with a subapical flange on each side, devoid of spinose processes (see Webb & Heller, 1990: 5, fig. 13) .... *H. graecanarus* (Remane & Asche)
5. Subgenital plates with distal margin slightly concave (fig. 14); aedeagal shaft medially on dorsal side with a group of 3 short spines (fig. 18) 6
– Subgenital plates with distal margin convex (e.g., figs. 2, 22); aedeagal shaft medially on dorsal side devoid of short spines (e.g., figs. 8, 26, 61) 8
7. Aedeagal shaft with apical processes almost directed laterad; mediodorsal processes comparatively distant from each other; style almost evenly tapering to apex without a subapical lobe (see Webb & Heller, 1990: 6 figs. 14, 15) .... *H. digitus* Webb & Heller
– Aedeagal shaft with apical processes directed ventrobasad; mediodorsal processes near to each other (fig. 18); style with a subapical lobe (fig. 16) .. ..*H. murtus* Webb & Heller
8. Aedeagal shaft with processes apically, directed dorsocaudad, not reflected (figs. 60-62) .... *H. javana* sp. n.
– Aedeagal shaft with processes subapically or medially, directed laterobasad (e.g., figs. 7, 25) 9
9. Aedeagal shaft with processes located subapically (figs. 7-10) .... *H. gaiseri* Webb & Heller
– Aedeagal shaft with processes located mediolateral (figs. 25, 26) .... *H. helleri* sp. n.

1. *Hengchunia koshunensis* (Matsumura)
(fig. 60)

Thamnotettix koshunensis Matsumura, 1914: 178. Lectotype ♂, Taiwan (EIHU), here designated [examined].
Hengchunia koshunensis: Vilbaste 1969: 8, fig. 6: A-J.

Material examined. – Lectotype ♂, 'Formosa/Matsumura' and '5.vii.1906/Koshun' on reverse; 1♀, 1 ? (sex unknown). – Paralectotypes, originally on same mount as lectotype (re-mounted) (EIHU).

11

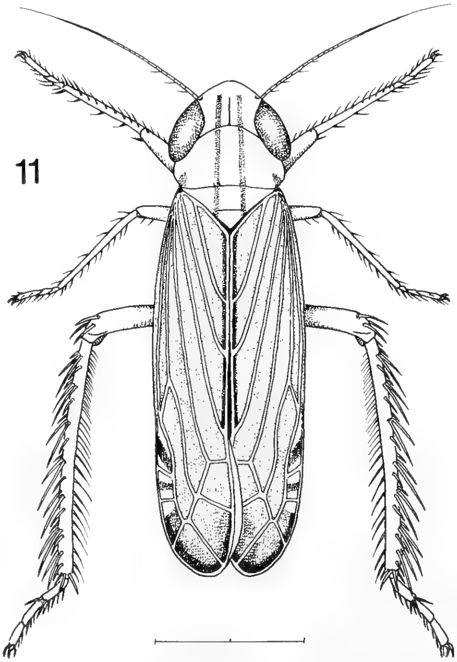
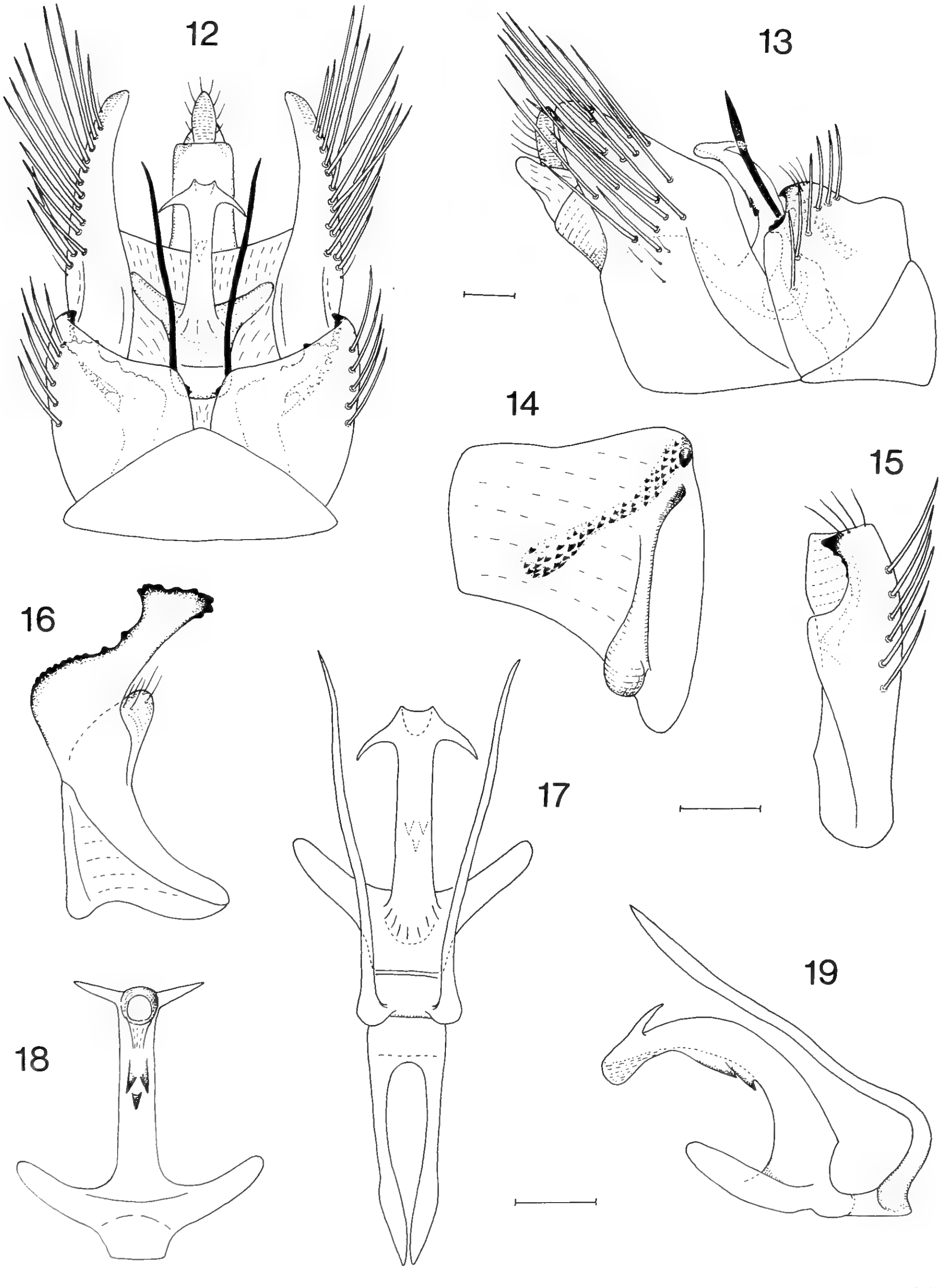


Fig. 11. Hengchunia murtus (Webb & Heller), ♂ from Sulawesi. – 11, habitus. Scale: 1.0 mm.



Figs. 12-19. *Hengchunia murtus* (Webb & Heller), ♂ from Sulawesi. – 12, male genitalia, ventral view; 13, same, left lateral view; 14, left subgenital plate, dorsal view; 15, same, dorsolateral view; 16, left style, dorsal view; 17, aedeagus and connective, ventrocaudal view; 18, aedeagus, dorsal view; 19, same, left lateral view. Scales: 0.1 mm.

Remarks. – *H. koshunensis* can be separated from the other *Hengchunia* species by the crown-shaped apex of the aedeagal shaft consisting of two pairs of spines: a pair of longer spines directed ventrad and a pair of shorter spines directed dorsad (not vice versa as noted in Vilbaste 1969: 8).

Distribution. – This species is only known from Taiwan (Matsumura 1914; Vilbaste 1969).

2. *Hengchunia graecanarus* (Remane & Asche) **comb. n.**

Pseupalus graecanarus Remane & Asche, 1980: 90, fig. 16 a-l. Holotype ♂, Canary Is, (Remane coll.) [examined]. – Webb & Heller 1990: 5, fig. 13. .

Material examined (additional to the type material of Remane & Asche 1980). – 2♂, 5♀, S Greece, Peloponnessos, Skala nr Gythion, on *Imperata cylindrica,* 6.x.1981, M. Asche & H. Hoch. - 9♂, 26♀, NW Greece, Corfu I., Aghios Stephanos, coastal biotopes with *Imperata cylindrica,* 14.x.1981, M. Asche & H. Hoch. - 3♂, 1♀, NW Greece, 27 km S. Igoumenitsa, S. Kastri, on *Imperata cylindrica,* 10.viii.1983, M. Asche & H. Hoch (AH).

Remarks. – Within the genus, *H. graecanarus* displays a unique configuration of the aedeagus with subapical flanges at the shaft instead of spinose processes.

Distribution. – This species is known from the type-locality in the Canary Islands: Gran Canaria, and from several localities in Greece (Remane & Asche 1980). According to the distribution of its host plant, *Imperata cylindrica,* a wider distribution at least in the Mediterranean Region is possible.

3. *Hengchunia digitus* (Webb & Heller) **comb. n.**

Pseupalus digitus Webb & Heller, 1990: 4, figs. 14-18. Holotype ♂, Thailand (BMNH) [examined].

Remarks. – No material additional to the type material has been examined.

H. digitus closely resembles *H. murtus* in the shape of the subgenital plates (including the toothed area) and aedeagus but the aedeagal shaft is straighter and has the three mediodorsal spines less closely adjacent and the style apex narrower.

Distribution. – This species has been reported only from Thailand (Webb & Heller 1990).

4. *Hengchunia gaiseri* (Webb & Heller) **comb. n.**
(figs. 1-10)

Pseupalus gaiseri Webb & Heller, 1990: 4, figs. 1-12. Holotype ♂, Ivory Coast (SMNS) [examined].

Remarks. – No material additional to the type material has been examined.

H. gaiseri is similar (and probably closely related) to *H. helleri* (see below). It differs from this species in the distally more pointed subgenital plates and in the position of the lateral spinose aedeagal processes which are located subapically in *H. gaiseri* and in midlength of shaft in *H. helleri.*

Distribution. – Although this species was described from Ivory Coast it is likely that a similar male specimen from Sierra Leone is conspecific (Webb & Heller 1990: 4).

5. *Hengchunia murtus* (Webb & Heller) **comb. n.**
(figs. 11-19)

Pseupalus murtus Webb & Heller, 1990: 6. Holotype ♂, Philippines (BMNH) [examined].

Material examined (additional to the type material of Webb & Heller 1990). – Indonesia: Sulawesi: 1♂, Sulawesi Utara, Dumoga Bone National Park, rainforest near basecamp Toraut, 19.x.1985; 1♂, ibid., banks of Toraut river; 1♂, ibid., light trap near basecamp, 7.xii.1985; 1♂, 2♀, ibid., trail to Tumpah river, 23.xi.1985; 1♂, ibid., trail to Tumpah river uphill to ca. 400 m, 20.x.1985; 1♀, ibid. banks of Tumpah river; 1♂, Molosso I., opposite Lolok (N.-coast), 11.xi.1985; all: on *Imperata* grass, Project Wallace Expedition, M. Asche & H. Hoch (AH, BMNH).

Remarks. – *H. murtus* closely resembles *H. digitus* in the shape of the male genitalia (see under *H. digitus).*

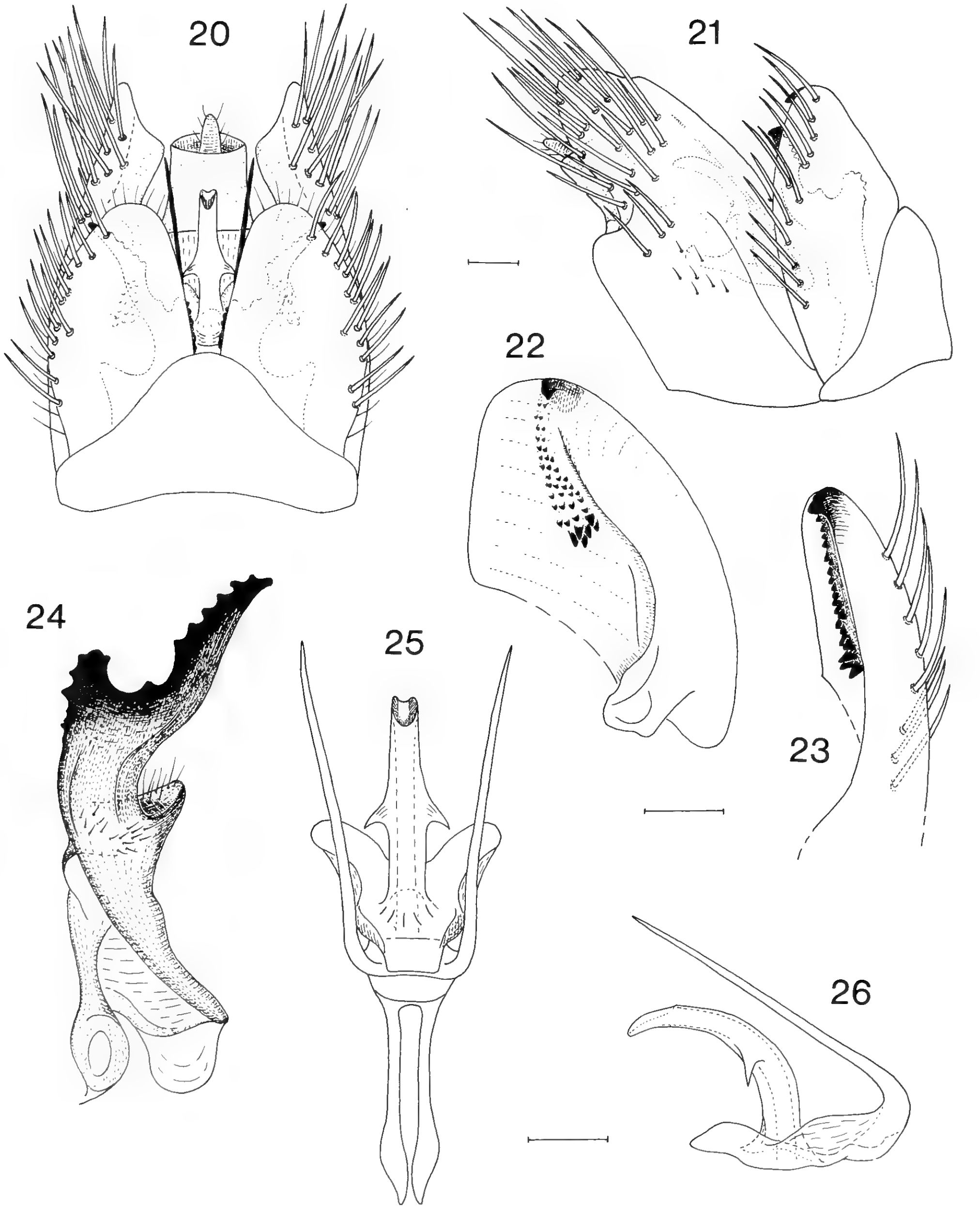
Distribution. – This species was originally described from Luzon I. in the Philippines (Webb & Heller 1990). Its occurrence in Sulawesi extends its range to the south.

6. *Hengchunia helleri* **sp. n.**
(figs. 20-26)

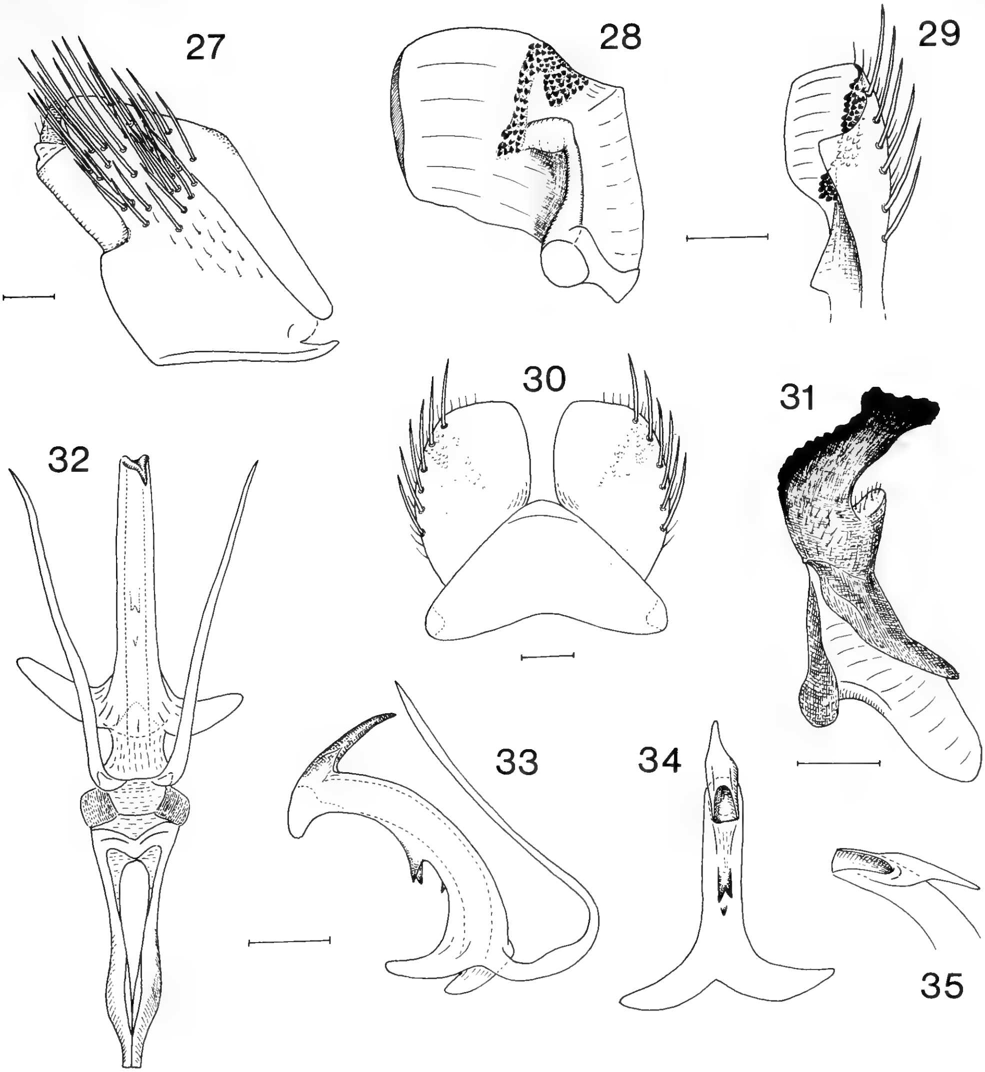
Type material. – Holotype ♂: Zaire, Lubumbasha (= Elisabethville), 30.iii.1939, at light, H.-J. Brédo (ISNB). – Paratypes: Zaire: 19♂, 43♀, 2 ? (sex unknown), same data as holotype (various dates) (ISNB, MRAC, BMNH); 3♂, 3♀, Libenge, Savane Liki-Bembe, 23-28.ii.1948 (one without date) (R. Cremer & M. Neuman, (ISNB); 1♀, Kivu, Kayimvira (Uvira), ii-iii.1955, G. Marlier (MRAC); 2♂, Kinchassa, Waelbroeck, 24.ii and 3.iv.1899 (ISNB); 1♂, 1♀, Maka, Lualaba, 25.i.1939, H.-J. Bredo (ISNB). - Cameroun: 1♂, Bertoua, 14.ix.1960, F.J. Breteler (AUWN).

Description. – Habitus, bodily proportions and colouration as in generic description (see Webb & Heller 1990).

Male genitalia: Subgenital plate (figs. 20-23) distally broadly rounded; toothed area rather long, extending from apex to about half of the length of the subgenital plate mediobasad, apical tooth and basal teeth



Figs. 20-26. *Hengchunia helleri* sp.n., paratype ♂ from Cameroun. – 20, male genitalia, ventral view; 21, same, left lateral view; 22, left subgenital plate, dorsal view; 23, same, dorsolateral view; 24, left style, dorsal view; 25, aedeagus and connective, ventrocaudal view; 26, aedeagus, left lateral view. Scales: 0.1 mm.



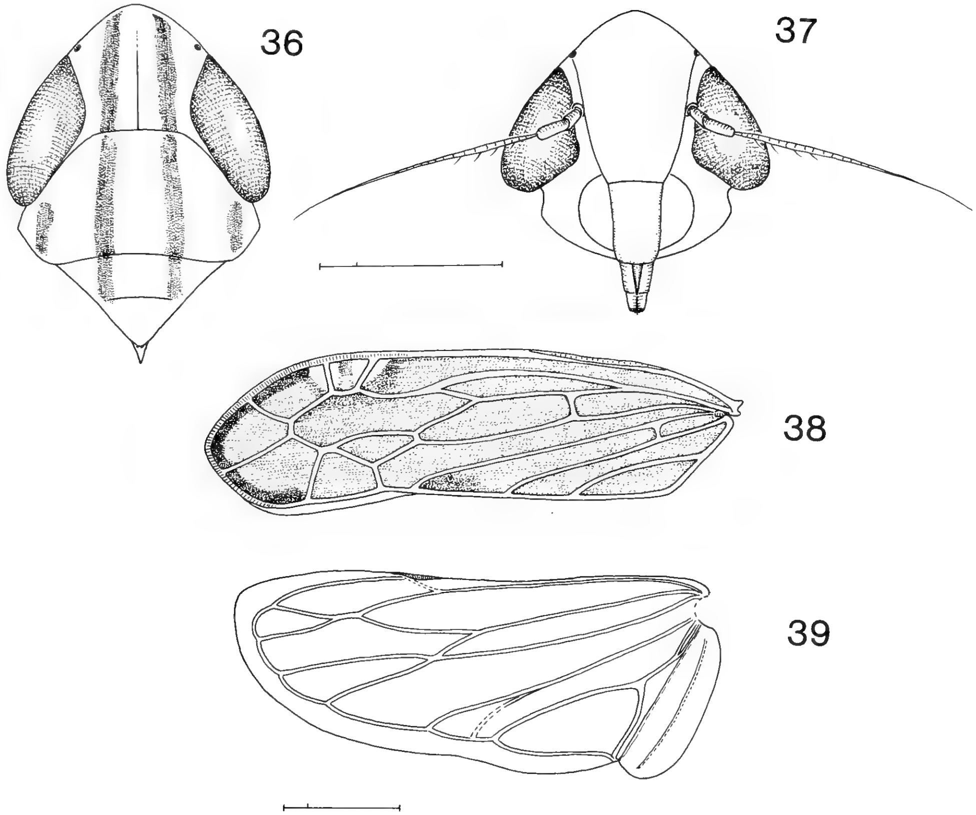
Figs. 27-35. *Hengchunia indica* sp.n., holotype ♂ from India. – 27, male pygophore, left lateral view; 28, left subgenital plate, dorsal view; 29, same, dorsolateral view; 30, subgenital plates, ventral view; 31, left style, dorsal view; 32, aedeagus and connective, ventrocaudal view; 33, aedeagus, left lateral view; 34, same, dorsal view; 35, apex of aedeagus, left dorsocaudal view. Scales: 0.1 mm.

strongest. Style (fig. 24) with short inner and long outer apophysis, the latter continuously tapering to apex, distal margin with about 7 tooth-like projections. Aedeagus (figs. 25, 26) with shaft short, evenly curved dorsad, on both sides at midlength a spinose process which is directed basad; phallotreme apically, exposed to the ventrocaudal side; processes of preatrium long and slender, straight.

Length: ♂: 3.5-3.6 mm, ♀: 3.8 mm.

Remarks. – *H. helleri* is similar (and probably closely related) to *H. gaiseri;* it can be distinguished mainly by the shape of the subgenital plates which are apically less pointed than in *H. gaiseri* and which bear a more extended toothed area, as well as by the position of the aedeagal processes which arise at midlength of the shaft (not subapically as in *H. gaiseri).*

Distribution. – The occurrence of *H. helleri* in Zaire and Cameroun may indicate a wider distribution, at least in Central- and West Africa.



Figs. 36-39. *Hengchunia pakistanica* sp.n., holotype ♂ from NE Pakistan. – 36, head and thorax, dorsal view; 37, head, frontal view; 38, left tegmen; 39, left hind wing. Scales: 0.5 mm.

7. *Hengchunia indica* sp. n.
(figs. 27-35)

Type material. – Holotype ♂: India, Bihar, Pusa, 14.v.1931, T. B. Fletcher (BMNH).

Description. – Habitus, bodily proportions, and colouration as in generic description (see Webb & Heller 1990).

Male genitalia: Subgenital plate (figs. 27-30) rather stout with distal margin very little convex, almost truncate; toothed area with a triangular portion at margin and an arm-like extension directed mediobasad. Style (fig. 31) comparatively short and stout, devoid of a mediodistal apophysis, subapically with a short lobe-like projection. Aedeagus (figs. 32-35) with shaft evenly curved dorsad; ventrobasad of the apical phallotreme with a gently curved horn-shaped process which arises on a broad base; medially on dorsal side of shaft a longer, apically bifurcate process, and basad of it a shorter single process; processes of preatrium slender, slightly curved ventrad.

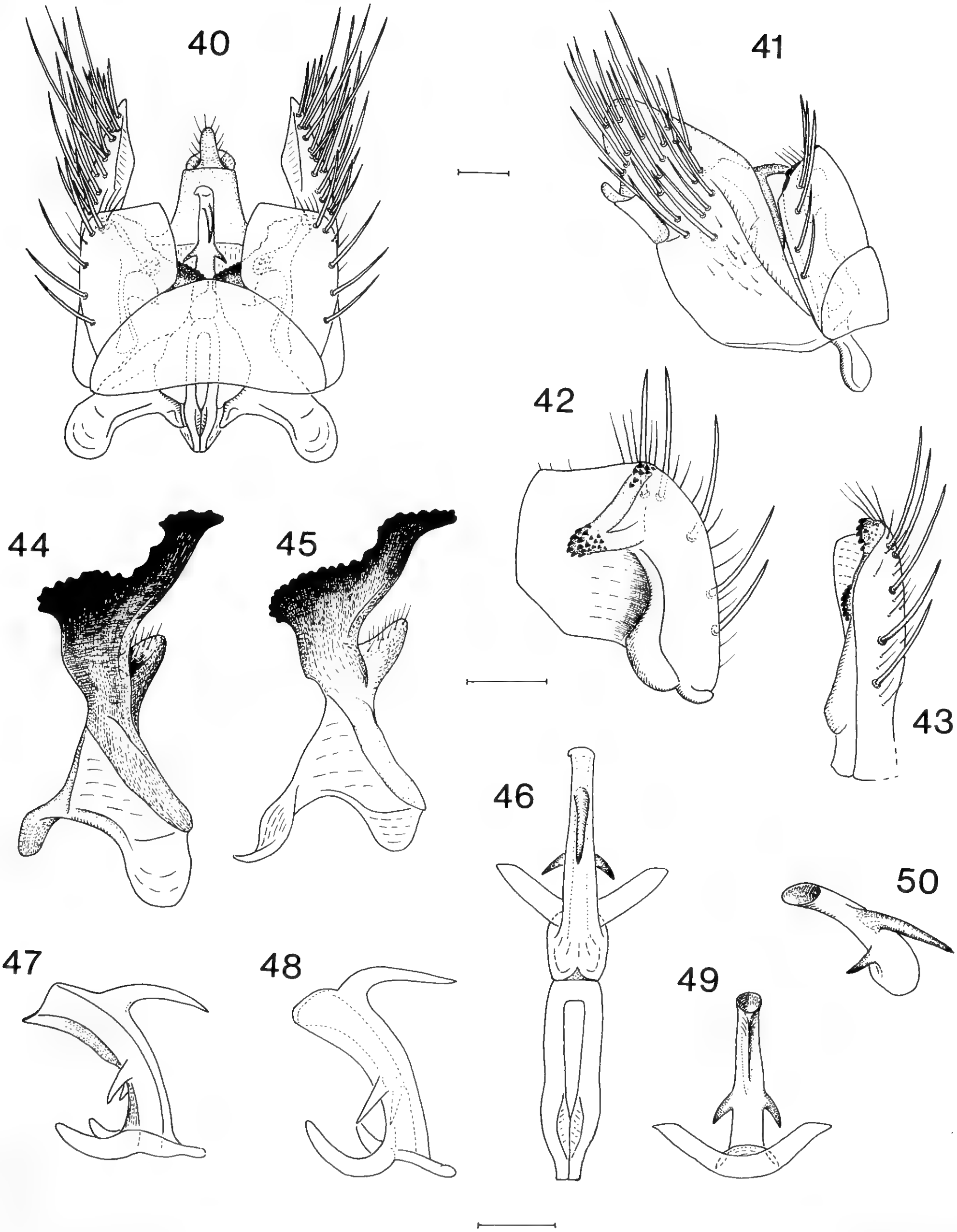
Length: ♂: 3.0 mm.

Remarks. – Within the genus, *H. indica* is most similar to *H. pakistanica* (see below) with which it shares the short and distally truncate subgenital plates and a single horn-shaped aedeagal process basad of the phallotreme on the ventral side. However, it differs considerably from this species in the shape of the toothed area of the subgenital plates and in details of the aedeagus, especially by the presence of paired processes of the preatrium which are entirely missing (probably reduced) in *H. pakistanica*.

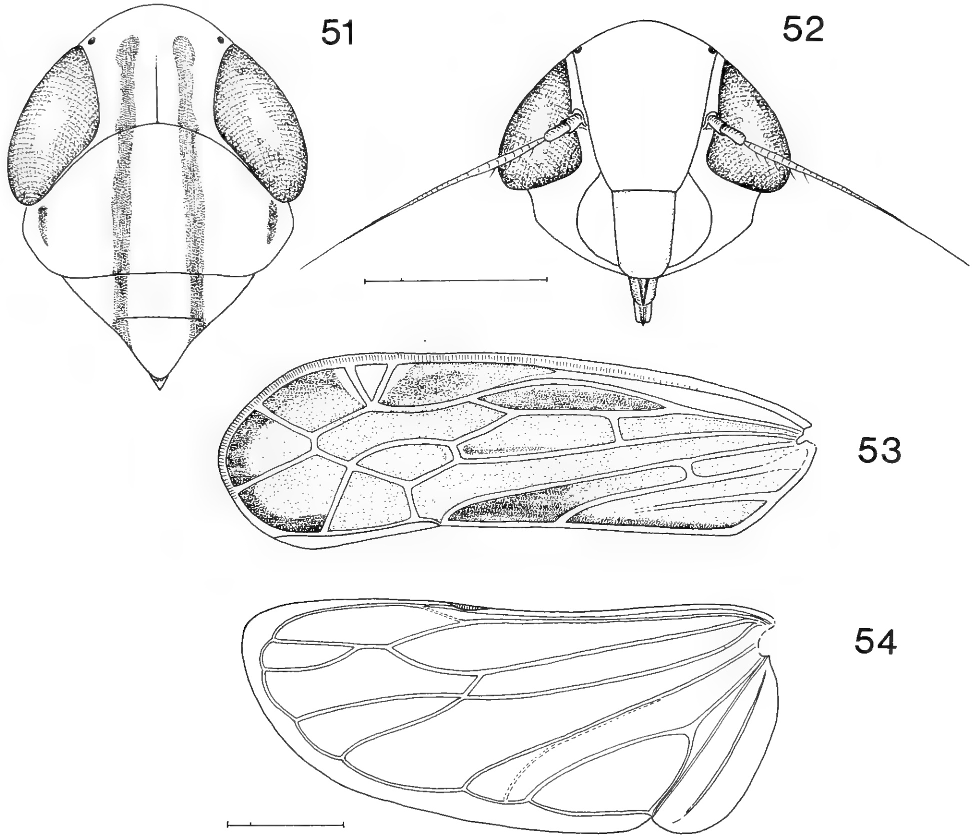
Distribution. – Only known from the Bihar-Region in North India.

8. *Hengchunia pakistanica* sp. n.
(figs. 36-50)

Type material. – Holotype ♂: Pakistan, Gujrat (= Guja-



Figs. 40-50. *Hengchunia pakistanica* sp.n., holotype ♂ from NE Pakistan; Figs. 45, 48: paratype ♂ from SE Pakistan. – 40, male genitalia, ventrocaudal view; 41, same, left lateral view; 42, left subgenital plate, dorsal view; 43, same, dorsolateral view; 44, 45, left style, dorsal view; 46, aedeagus and connective, ventrocaudal view; 47, 48, aedeagus, left lateral view; 49, same, dorsal view; 50, apex of aedeagus, left dorsocaudal view. Scales: 0.1 mm.



Figs. 51-54. *Hengchunia javana* sp.n., holotype ♂ from Java. – 51, head and thorax, dorsal view; 52, head, frontal view; 53, left tegmen; 54, left hind wing. Scales: 0.5 mm.

rat), Nausari, 16.i.1981, C.A. Viraktamath (BMNH). - Paratypes: 4♀, same data as holotype (UASB, BMNH); 1♂, 1♀, Pakistan, Hyderabad, Patanduru, vii-ix.1980, Bernays & Woodhead (BMNH).

Description. – Habitus, bodily proportions, and colouration as in generic description (see Webb & Heller 1990).

Male genitalia: Subgenital plate (figs. 40- 43) short, distally truncate, toothed area separated in an apical and a median field of teeth which are connected by a ridge. Style (figs. 44, 45) distally with a short median edge and a long outer apophysis with a short subapical lobe. Aedeagus (figs. 46-50) with shaft short, slightly curved dorsad; a single long, horn-shaped, ventrobasad directed process arising basad of phallotreme on the ventral side; shaft submedially with a pair of lateral processes; preatrium devoid of elongate paired processes.

Length: ♂: 3.0 mm, ♀: 3.1-3.3 mm.

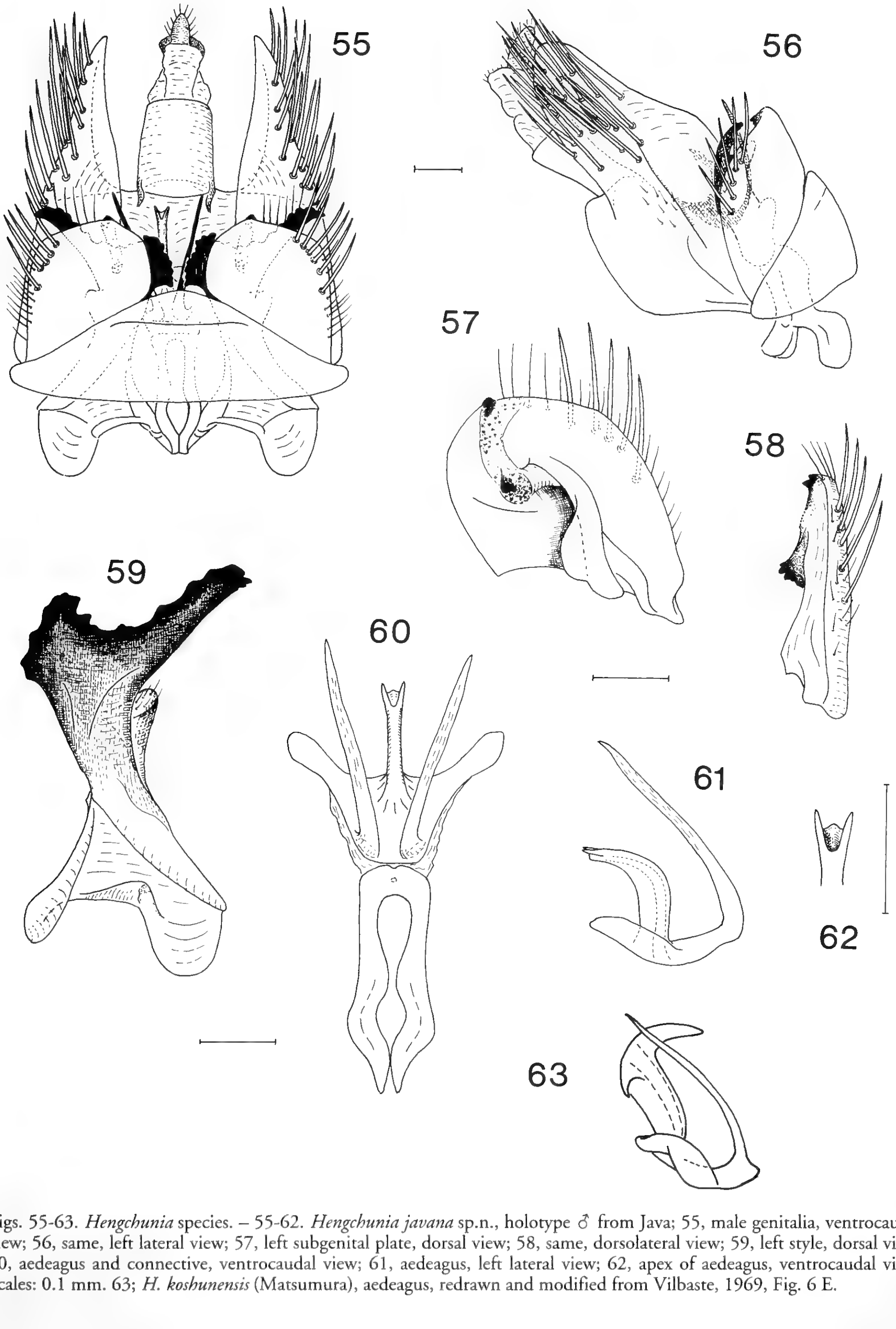
Remarks. – *H. pakistanica* can readily be distinguished from all other congeners by the lack of processes of the aedeagal preatrium. The aedeagal shaft with its single horn-shaped process on the ventral side is similar to that of *H. indica* but it differs in other genital characters, as noted above. Slight differences could by found in the genital structures (especially aedeagal spines and styles) between the males from North and South Pakistan but they seem too small to warrant species or even subspecific status.

Distribution. – Only known from the Gujrat-Region in the North-East and from the Sind-Region in the South-East of Pakistan.

9. *Hengchunia javana* sp. n.

(figs. 51-62)

Type material. – Holotype ♂: Indonesia: Java, Bogor, on *Imperata*, 24.xi.1989, M.R. Wilson (BMNH). - Paratype: 1♀, same data as holotype (BMNH).



Figs. 55-63. *Hengchunia* species. – 55-62. *Hengchunia javana* sp.n., holotype ♂ from Java; 55, male genitalia, ventrocaudal view; 56, same, left lateral view; 57, left subgenital plate, dorsal view; 58, same, dorsolateral view; 59, left style, dorsal view; 60, aedeagus and connective, ventrocaudal view; 61, aedeagus, left lateral view; 62, apex of aedeagus, ventrocaudal view. Scales: 0.1 mm. 63; *H. koshunensis* (Matsumura), aedeagus, redrawn and modified from Vilbaste, 1969, Fig. 6 E.

Description. – Habitus, bodily proportions, and colouration as in generic description (see Webb & Heller 1990).

Male genitalia: Subgenital plate (figs. 55-58) distally convex, toothed area devided in an apical and a median portion, both portions with prominent teeth. Style (fig. 59) with a short inner edge and an elongate outer apophysis with undulate margin. Aedeagus (figs. 60-62) with shaft short, in middle almost rectangularly bent dorsad; phallotreme apically, dorsally on each side flanked by a pair of short, fork-like spinose processes directed dorsocaudad; paired processes of the preatrium conspicuously surpassing the aedeagal shaft, almost straight.

Length: ♂: 3.4 mm; ♀: 3.6 mm.

Remarks. – Within the genus, *H. javana* is rather isolated. It can readily be separated from the other congeners by the configuration of the aedeagal shaft with its fork-like, dorsocaudad directed (not reflected) spinose processes at apex.

Distribution. – Only known from Bogor in West Java.

10. ***Hengchunia*** sp.

We have examined one female from Australia, Queensland, Cairns (ridge at Edge Hill, rainforest), collected on *Imperata* grass, on 10.vi.1987 by M. Asche & H. Hoch (AH). Externally, this specimen resembles *H. murtus,* but its specific identity can only be clarified after a corresponding male becomes available; however, this finding extends the geographic range of the genus *Hengchunia* to NE Australia.

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A NEW GENUS OF NOMADINE BEES FROM NORTH AFRICA (HYMENOPTERA: APOIDEA, ANTHOPHORIDAE)

Baker, D. B., 1994. A new genus of nomadine bees from North Africa (Hymenoptera: Apoidea, Anthoporidae). – Tijdschrift voor Entomologie 137: 155-159, figs. 1-4. [ISSN 0040-7496]. Published 15 December 1994.

Aethammobates prionogaster gen. et sp. n. Anthophoridae: Nomadinae) is described from a unique male collected in Egypt. The new genus is referred to the Holcopasitini and its relationships with other holcopasitine bees are discussed.

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Keywords. – Hymenoptera; Anthophoridae: Holcopasitini; *Aethammobates prionogaster*, new genus; new species; North Africa.

Among a number of epeoline bees received many years ago from the late Prof. Dr. H. Priesner was a single male of a strange nomadine bee that could not be referred to any described genus. A description and figures were prepared, and the specimen was then set aside in the expectation that further specimens, including possibly the female, would sooner or later come to light. After more than 40 years, this expectation has not been fulfilled, although the locality where the bee was obtained (Gebel el Asfar, near Cairo) was one much visited by both pre-War and more recent local collectors. Since the locality is now being devastated by construction works (C.G. Roche, in litt., 6 September, 1992), making the recovery of further material less likely, and since also the systematics of the Nomadinae have recently come under review by several authors, notably Alexander (1990) and Roig-Alsina (1991), it seems desirable to place the new genus and species on record.

Aethammobates gen. nov.

Description. – Head in frontal aspect transverse, the eyes rather small, separated by 1.2 times their length, their inner margins convex, subparallel; clypeus short, carinate laterally along epistomal suture, paraocular area adjacent to carina slightly concave and narrowly impunctate; labrum elongate (length to breadth ration 1.44 : 1), apically entire, lacking discal tubercles; antennal sockets at mid-level of eyes; interantennal carina divided, forming a V-shaped protuberance, the open end of the V upward; facial foveae absent; vertex longer than inter-ocellar distance; preoccipital ridge carinate; malar area rudimentary. Antennae 13-segmented, scape long (length to breadth ratio 3 : 1); pedicel free; first flagellar segment long (length to breadth ratio 3 : 1), equal to segments 2+3; segments 2-10 passing from transverse to quadrate. Mandibles simple, with weak basal protuberance opposed to lateral termination of clypeal carina; only posterior articulation in contact with eye. Stipital comb absent; maxillary palpi 5-segmented; blade of galea moderately, uniformly sclerotized, acuminate, extreme apex very narrowly rounded.

Mesosoma broad, dorso-ventrally compressed. Pronotum with well developed dorsal surface limited anteriorly by an uninterrupted carina; anterior surface broad, flat, rounded abruptly into collum. Mesoscutum little convex; parapsidal lines well marked, about as long as tegula; axillae not protuberant; scutellum extending laterad slightly beyond axillae, with distinct dorsal and posterior vertical surfaces separated by a weak, irregular (interrupted by punctation) carina, slightly overhanging subvertical, coplanar surfaces of metanotum and propodeum; omaulus continuous across mesepisternum, forming prominent angles on either side of a median, semicircular inflexion; mesepisternum anterior to intermediate coxae strongly transverse, transversely concave. Metanotum with prominent lateral lobes. Wings (fig. 4) short, forewing about 0.6 body length. Forewing bare basally, becoming pubescent apically, especially beyond cells; marginal cell broad, rather broadly rounded at apex, apex separated from wing-tip by less than cell length; distal abscissa of Rs absent; two submarginal cells, the second much shorter than the first, the first receiving 1 m-cu near its apex, the second 2 m-cu beyond the middle. Hindwing with jugal lobe very short; second abscissa of M + Cu about 1,5 times longer than cu-v, not quite half as long as M. Legs of normal proportions. Anterior coxae proximate, transverse, the trochanters widely separated; tarsus sub-bipectinate, basitarsus and segments two to four apically each with a few strong setae on either side; basitarsus flattened and slightly expanded apicad. Intermediate coxae widely separated, short, much shorter than distance from their summits to posterior wing bases; femur broad; tibia without anterior setose area, coarsely spiculate. Posterior coxae large, broad, inwardly weakly, externally strongly carinate; tibiae coarsely spiculate. Arolia present, normally developed.

Metasoma broad, depressed, greatest width at apex of segment 2. Tergum 1 with vertical anterior and horizontal dorsal surfaces separated by a deeply arcuate carina, in dorsal aspect with prominent lateral angles; marginal areas of terga abruptly and progressively more strongly depressed caudad, the margins of the discal areas passing from subserrate on tergum 1 to strongly denticulate on terga 4-6; pygidial plate strong, rostriform, rounded apically, not constricted basally, considerably exceeding apical margin of segment; sternum 6 laterally dentate.

Vestiture generally squamiform, on the terga forming basal and marginal fasciae, not maculae; simple, erect hairs largely confined to mandibles and disc of labrum; anterior angles of malar areas not penicillate; eyes bare; sterna without subapical fimbriae of modified hairs, but sterna 5 and 6 mesially with fine, dense, erect pubescence, on 6, towards the lateral teeth, becoming longer and directed mesad.

Integument black with extensive pale areas, the appendages and metasoma predominantly pale; moderately strongly, moderately densely to subreticulately punctate, microsculpture not evident at 37,53.

Distribution. – N.E. Africa.

Host. – Not known.

Type species. – *Aethammobates prionogaster*, sp. n.

Derivatio nominis. – Gr. ἀήθης, strange, + *Ammobates*, nom. propr. Hymenoptera

Aethammobates is separated from other nomadines by a variety of autapomorphies, but for purposes of recognition its general habitus and the modifications of the pronotum and first metasomal tergum are immediately diagnostic (see Discussion).

Aethammobates prionogaster sp. n.

(figs. 1-4)

Type material. – Holotype ♂: 'Coll. A. Mochi / 27.V.37 / Geb. Asfar / Egitto' (in coll. Baker)

Description

Male. – Structural characters: See generic description. POL = OOL. Hamuli 8. Length 7.5 mm, forewing 4.75 mm.

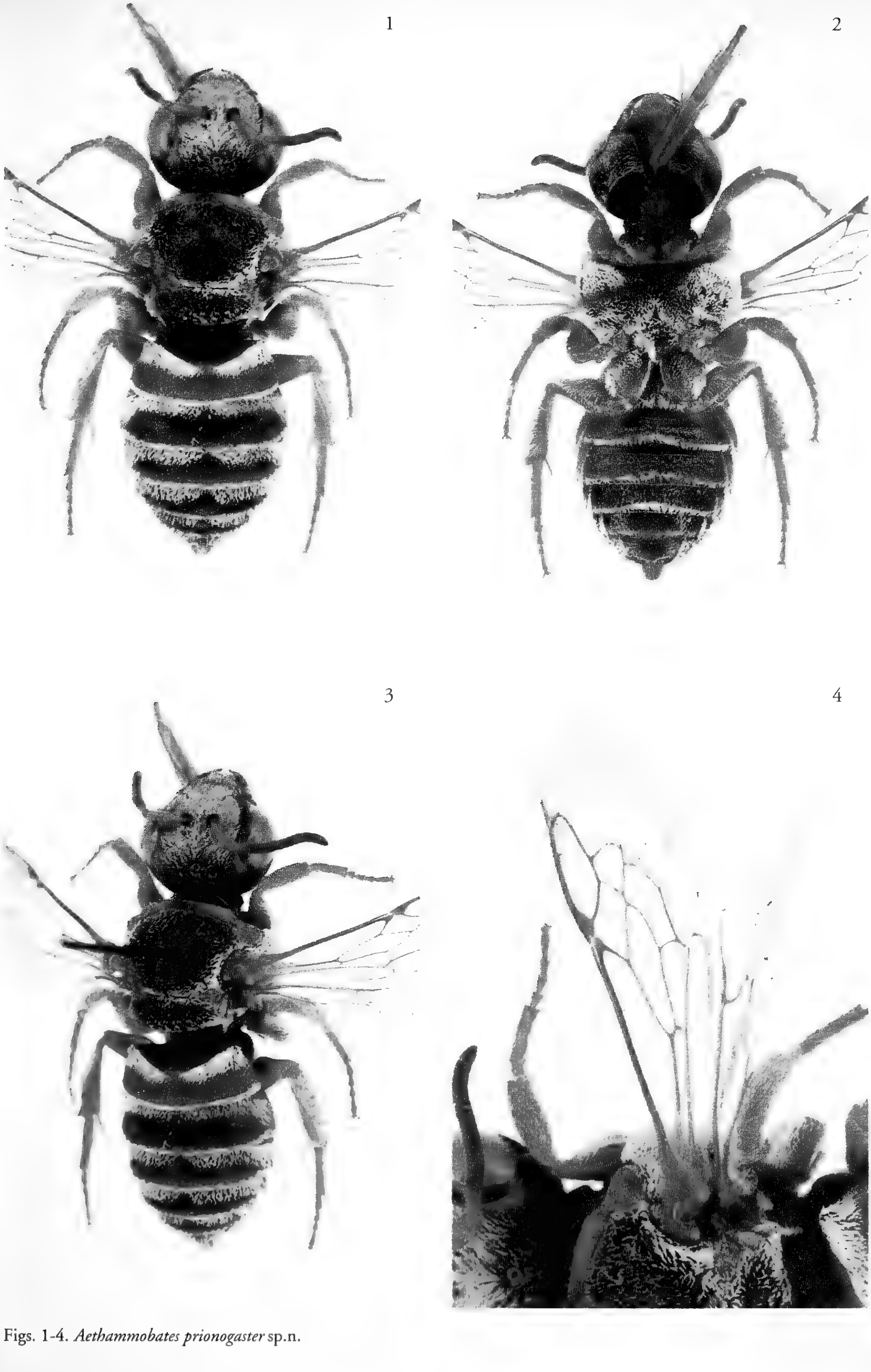
Vestiture. The face, dorsal surface of pronotum, peripheries of mesoscutum and scutellum, mesepisterna, and outer ventral surfaces of posterior coxae, all more or less densely clothed with white squamiform or subsquamiform pubescence, that on the pronotum apparently particularly dense (matted in type); elsewhere on head and mesosoma sparser, the individual hairs becoming longer and less squamiform. Terga with broader, white, medially emarginate, laterally expanded, basal fasciae and narrow, entire, apical fasciae, filling the depressed marginal areas, of squamiform pubescence; tergum 5 nearly completely covered. Disc of pygidial plate with similar pubescence. Sterna 2-4 with weak submarginal fasciae, sterna 5 and 6 medially with fine, dense, erect pubescence (as noted in generic description - possibly homologous with pre-genital brush in *Nomada*).

Integument of head and mesosoma black with extensive pale areas. Clypeus, anterior extremities of paraocular areas, malar areas, labrum, small maculae adjacent to summits of eyes, larger maculae on genal areas adjacent to mandibles, extending narrowly upwards almost to summits of eyes, labrum and all head appendages (except the mandibles apically) castaneous, the flagellum darker. Lateral lobes of pronotum, axillae, tegulae, sclerites of wing bases, wing veins (the costa darker), and legs (the coxae basally darker) castaneous. Metasoma castaneous, terga 2-5 discally progressively, irregularly (possibly the result of post-mortem decomposition) darker; sterna 2 and 3 discally largely, 4 and 5 almost wholly, dark. Labrum smooth, moderately strongly, irrergularly punctate; anterior face of pronotum smooth, impunctate; mesoscutum and scutellum smooth, moderately densely, simply punctate; terga smooth, medially densely, laterally reticulately, punctate, the punctation coarsest on tergum 2, on tergum 1 about equal to that of mesoscutum, on terga 3-5 progressively finer. Margins of pygidial plate reflexed.

Derivatio nominis. – Gr. πριον – ώδης / ωτός, serrated, + gaster.

Discussion

Both Alexander (1990) and Roig-Alsina (1991) have recently published cladistic analyses of nomadine bees. Roig-Alsina's analysis was based primarily (15 out of 22 characters) on characters exclusive to the female, and is consequently of limited use in the present context. Alexander's analyses were based on (1) larval characters only, (2) on adult characters of those genera where larvae were known, (3) on both larval and adult characters of these genera, and (4) on the adult characters of all genera known to him. It is this last analysis, (4), that is relevant to the placement



Figs. 1-4. *Aethammobates prionogaster* sp.n.

Table 1 Data matrix for characters as listed by Alexander, Appendix 6; codings in accordance with Alexander, Appendices 3 and 5.

Characters

	1	**2**	**4**	**5**	**a**	**6**	**7**	**8**	**9**	**10**	**11**
Holcopasites	1	0	0	0	1	0	0	1	0	0	0
Schmiedeknechtia	1	0	0	0	-[1]	0	0	0	0	0	0
Aethammobates	0	0	1	0	0	0	-[2]	0	1	0	2

	12	**13**	**14**	**15**	**16**	**17**	**b**	**c**	**18**	**d**	**19**
Holocopasites	0	0	0	0	0	1	1	0	1[4]	1	0
Schmiedeknechtia	0	0	0	0	0	1	1	0	1[4]	1	0
Aethammobates	1	1	0	0	0	0[3]	0	1	1	1	1

	20	**21**	**e**	**f**	**g**[5]	**22**	**h**	**23**	**24**	**29**	**32**
Holocopasites	1	0	1	0	0	0	2	1	0	1	0
Schmiedeknechtia	1	0	1	0	0	0	2	1	0	1	0
Aethammobates	1	0	1	?	0	0	2	1[6]	0	0	0[7]

Notes on matrix

(1) character a: Antennal sockets below mid-level of eyes, but not far below; no code. – (2) character 7: 'Length/width of first flagellomere' = 3: no code. – (3) character 17: No 'patches of appressed squamiform setae': Alexander presumably refers to discrete metasomal maculations of *Holocopasites* and *Schmiedeknechtia*. – (4) character 18: Incorrectly coded '0' by Alexander: vein 1st r-m of forewing is absent (two submarginal cells). – (5) character g: 'arising from' in Alexander's Appendix 5 presumably means 'rising from' (i.e., in lateral aspects bends upward from ventral plane of mesosoma immediately before intermediate coxae). – (6) character 23: a weak, short, dorso-basal carina present on posterior coxa. – (7) character 32: Coded '0' since apex narrowly rounded, subacuminate, but galea is more than weakly sclerotized.

of *Aethammobates*. Alexander's data matrix (his Appendix 6) employed 46 characters, of which six applied solely to the female, leaving 40 in which *Aethammobates* could potentially be compared. In practice, since the holotype and only known specimen of Aethammobates has not been dissected (cf. Roig-Alsina's comment, 1991: 25, on the pre-episternal sulcus in *Rhopalolemma*), comparison has been limited to 33 characters. These have been covered in the description given above, and are now given in coded form, following Alexander's Appendices 3 and 5, as an extension of his data matrix, in Table 1. This table reproduces Alexander's codings, but substitutes observed values for six characters marked with a *quaere* in his matrix.

It should be noted that Alexander's codings, here and elsewhere, cannot always be accepted because he did not see certain described and undescribed taxa that would have necessitated different coding or the adoption of additional codes; however, a complete revision of his data matrix, which might well result in significant changes in his cladogram, is beyond the scope of the present paper. Important characters that should be taken into account in future work on the phylogeny and classification of the Nomadinae include the presence of facial foveae in some *Nomada* (a group of, chiefly, *Panurgus* parasites); the development of an anal truncation, with associated modifications of the apical sterna, among the pasitines (Bischoff 1923: 585, Analstutz); and modifications of the antenna in such genera as *Morgania* and *Pasitomachthes*, where the scape and pedicel may be coalescent, forming a single functional unit (Baker 1971: 7, footnote).

Inspection of the extended matrix confirms *a priori* impressions that *Aethammobates* shares a preponderance of characters with *Holcopasites* and *Schmiedeknechtia* and must be placed in the Holcopasitini.

While obviously most nearly related to *Holcopasites* [Nearctic, revised by Linsley (1943, as *Neopasites*) and by Hurd and Linsley (1972)] and *Schmiedeknechtia* [western palaearctic, revised by Popov (1933)], and sharing such derived characters as the lateral processes of the metanotum and certain venational details, *Aethammobates* is not close to either. It differs from both in, among other characters:

1. The dorso-ventrally compressed form of mesosoma and metasoma.
2. The mid-dorsally exposed pronotum with sharply differentiated dorsal, densely pubescent and anterior, glabrous surfaces. (In lateral aspect, the pronotum resembles that of *Pae* (Sphecoidea) as illustrated by Bohart & Menke (1976: 15, fig. 3A),] In *Holcopasites* and *Schmiedeknechtia* the pronotum is, as in most other bees, recessed beneath the mesoscutum with only its lateral lobes and, when the head is deflexed, the collum conspicuous in dorsal aspect.
3. The V-shaped interantennal carina.
4. The strongly expanded intermediate femora.

5. The pronounced basal truncation of the mesosoma.
6. The form of the first metasomal tergum, which is broadly, deeply emarginate, with prominent antero-lateral angles (see fig. 3) and the anterior and dorsal surfaces sharply, rectangularly separated.
7. The presence of basal and marginal tergal fasciae and the absence of of discrete spot- or bar-like markings.

Of these, characters 1-6 appear as autapomorphies. *Aethammobates* differs further, from male *Holcopasites*, in the 13-segmented antennae, and from *Schmiedeknechtia* in the form of the pygidial plate, which is not narrowed basad; in not having the inner orbits convergent below; in not having the anterior mandibular articulations in contact with the eyes; and in the venation: in *Schmiedeknechtia* either both 1 m-cu and 2 m-cu are received by second Rs, or (*Cyrtopasites*, a single species with convex mesoscutum and fine and sparse punctation) 1 m-cu is interstitial with or slightly precedes 1 r-m.

Biology

It is interesting to speculate on the possible host of *Aethammobates*. Known hosts of *Holcopasites* and *Schmiedeknechtia* are panurgines. *Camptopoeum* and *Meliturgula* are possible candidates, but the former. which is normally abundant where it does occur, and which appears not to have been recorded from the Cairo area (it is not represented in recent, extensive Egyptian collections), has species of *Parammobatodes* as its regular parasites. The somewhat flattened shape of *Aethammobates* suggests some correlation with habits or host. Both sexes of *Meliturgula* have a conspicuously broad or flattened metasoma: regional species are few in number and rare in collections; nothing is known of their biology.

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FOUR SPECIES ADDED TO THE *BAETURIA NASUTA* GROUP, WITH NOTES ON TAXONOMY AND BIOGEOGRAPHY (HOMOPTERA, TIBICINIDAE)

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A new concept is proposed for the *nasuta* group of the cicada genus *Baeturia* Stål, 1866. Four species are added to this group, bringing the total number of its species to twelve. One of these species (*B. guttulipennis* Blöte, 1960) is redescribed and three (*B. gibberosa*, *B. splendida*, and *B. retracta*) are described as new. Implications for the biogeographic pattern of the group are, that the *nasuta* group can no longer be seen as a typical central New Guinea group; most of the species can apparently be found in northern New Guinea.

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Key words. – *Baeturia*, *nasuta* group, taxonomy, biogeography, New Guinea.

The *nasuta* group was recognized as a monophyletic group consisting of eight New Guinean species of the genus *Baeturia* Stål (de Boer 1982). The monophyly of that group is based on two presumed apomorphies: a narrow and angularly swollen postclypeus and four sclerotized ridges on the tymbals. *B. guttulipennis* Blöte was not included in the *nasuta* group, since it does not share these apomorphies. However, now that most of the remaining species of *Baeturia* have been revised and placed in monophyletic species groups, it appears that *B. guttulipennis* is more closely related to the *nasuta* group than to any other species group. It is proposed here to change the concept of the *nasuta* group and to include *B. guttulipennis* in that group. Furthermore, three new species can be added to the *nasuta* group, these species do share the original apomorphies of that group.

Species of the *nasuta* group, as previously defined, were mainly distributed in the central mountain ranges of New Guinea. Its distribution pattern has been compared to that of the cicada genus *Cosmopsaltria* Stål, which also centres in the montane parts of central New Guinea (de Boer 1982; Duffels 1986; Duffels & de Boer 1990) and it was suggested that the similarities between these patterns might find a common cause in the paleogeology of New Guinea. The present additions to the *nasuta* group greatly alter its general distribution pattern and necessitate a reconsideration of its paleogeographic history.

MATERIAL AND METHODS

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

AMNH: American Museum of Natural History, New York; AMS: Australian Museum, Sydney; BMNH: Natural History Museum (formerly: British Museum (Natural History)), London; BPBM: Bernice P. Bishop Museum, Honolulu; Moul: Personal collection Mr M.S. Moulds, Sydney; RMNH: Nationaal Natuur historisch Museum (formerly: Rijksmuseum van Natuurlijke Historie), Leiden; SMN: Staatliches Museum für Naturkunde, Stuttgart; ZMA: Institute for Systematics and Population Biology (Zoölogisch Museum), Amsterdam.

The following geographical sources have been used: Atlas van tropisch Nederland (1938), The Times Atlas of the World (1968) and the 'List of New Guinea localities' published by the Bishop Museum (1966).

After overnight softening, male genitalia were examined by pulling out the pygofer with a sharp needle inserted between pygofer and 8th abdominal segment. The aedeagus was pulled out at the same time, by inserting the needle between the claspers. Measurements are based on all available specimens.

PHYLOGENY

Baeturia belongs to a larger group of genera, the

'*Baeturia* and related genera complex', as defined earlier (de Boer 1990). A phylogenetic analysis of this genus complex, with the oriental Prasiini as defined by De Jong (1985) as outgroup, is in preparation. The ensuing phylogenetic discussions are based on the preliminary results of that analysis.

The monophyly of the *nasuta* group

The monophyly of the *nasuta* group is based on three presumed apomorphies. Males of the *nasuta* group are easily identified by the almost transparent lateral sides of the abdomen, usually restricted to segments 3-7. Only *B. marmorata* does not show this character. A similar transparency of the male abdomen was found in a monophyletic group of three species of the genus *Gymnotympana* (unpublished), but not in other related taxa. A laterally transparent abdomen is regarded as apomorphous for the *nasuta* group (1 in fig. 1b) and the similar transparency in three *Gymnotympana* species must be explained by parallelism.

A strongly curved aedeagus, with lateral lobes at its basal curve, is regarded apomorphous for the genus *Baeturia*. The aedeagus of the species of the *nasuta* group differs from that of other species by a longer and more slender apical part, distally of the lateral lobes (fig. 11), which is regarded apomorphous (2 in fig. 1b). A very similarly elongate, but stouter, aedeagus was found in *B. loriae* and *B. pigrami* of the *loriae* group (de Boer 1994a). The elongation of the aedeagus in these two groups cannot be regarded as homologous in the most parsimonious solution.

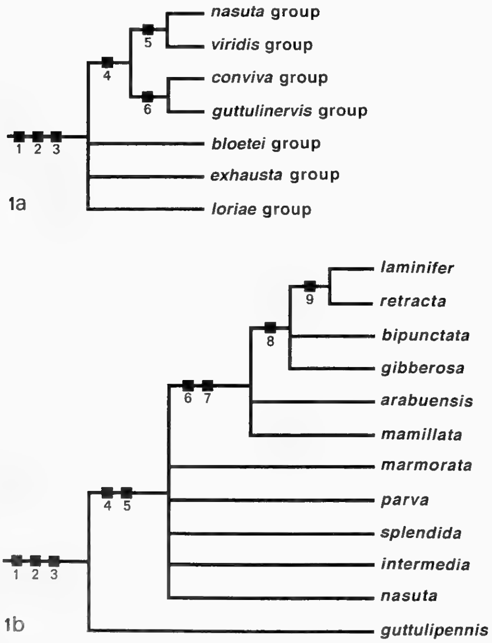


Fig. 1. Cladograms. – a. Cladogram of *Baeturia*, numbers refer to characters discussed in the section on the phylogenetic position of the *nasuta* group; b. Cladogram of the *Baeturia nasuta* group, numbers refer to characters discussed in the sections on the monophyly and ingroup phylogeny of the *nasuta* group.

The male pygofer is characterized by a strongly bent and dorsally flattened caudodorsal beak. This shape of the caudodorsal beak is shared by all species and regarded apomorphous for the *nasuta* group (3 in fig. 1b). In other species, which have a similarly strongly bent beak, the beak is convexly curved dorsally (comp. the *viridis* group, de Boer 1992).

The phylogenetic position of the *nasuta* group

Baeturia is a monophyletic genus, for which a frontally rounded and protruding postclypeus, a triangle-shaped medial thorn on the fore femur, and lobate lateral crests on the aedeagus are the presumed apomorphies (1, 2, 3 in fig. 1a). *Baeturia* can be subdivided into seven monophyletic species groups: the *bloetei* group (de Boer 1989), the *conviva* group (de Boer 1986), the *exhausta* group (de Boer 1994b) the *guttulinervis* group (de Boer 1994c), the *loriae* group (de Boer 1994a), the *viridis* group (de Boer 1992), and the *nasuta* group (de Boer 1982).

The *nasuta* group is presumed to form a monophyletic group with the *conviva*, *guttulinervis*, and *viridis* groups. The large, often conically-shaped, distinctly posteriorly projecting protuberance on the lateral lobe of pygofer is regarded synapomorphous for these four species groups together (4 in fig. 1a). Furthermore, these four groups share a very stout and strongly bent caudodorsal beak. The occurrence of a similarly bent caudodorsal beak in several Melanesian species of the *bloetei* group must be explained by parallel development.

The *nasuta* and *viridis* groups are sister groups, sharing an angularly bent caudodorsal beak as supposed synapomorphy (5 in fig. 1a). In the species of these two groups the dorsal margin of the pygofer is not continuously rounded with the dorsal margin of the caudodorsal beak. Furthermore, these species share a generally truncate, but sometimes bluntly rounded or bicuspidate, caudodorsal beak. Species of other groups of *Baeturia* generally have a more narrowly rounded or pointed beak, while a truncate beak only sporadically occurs. The *conviva* and *guttulinervis* groups are sister groups based on a shared apical swelling of the clasper (this swelling is almost globular in the *guttulinervis* group) and a dorsally strongly rounded pygofer (6 in fig. 1a), but the relative position of the remaining species groups of *Baeturia* is not clear.

Ingroup phylogeny

The species of the *nasuta* group are very similar in general appearance. The species differ mainly in the shape of the claspers and some clasper characters indicate phylogenetic relationships. Most other differences observed are either species specific characters, or characters that also occur outside the *nasuta* group. It is not possible to construct a fully resolved and unambiguous cladogram for the group, based on the limited number of characters now available. Nevertheless, some remarks on ingroup phylogeny can be made (see fig. 1b).

B. guttulipennis presumably forms the sister taxon of all other species of the *nasuta* group; these other species share four tymbal ridges (three in *B. parva*) and a more angularly swollen postclypeus, which are the original apomorphies for the *nasuta* group (4, 5 in fig. 1b). *B. guttulipennis* and B. *nasuta* however, share similar brown markings on the tegmina and an apically rounded male caudodorsal beak, and could be sister species. *B. nasuta* and *B. intermedia* share an almost identical clasper and are presumably either sister species or part of a paraphyletic subgroup.

B. arabuensis, B. bipunctata, B. laminifer, B. mamillata, B. retracta and *B. gibberosa* share a distinct dorsal protrusion on the clasper as presumed synapomorphy (6 in fig. 1b). That *B. nasuta* and *B. intermedia* should also be included in this group, as was suggested before (de Boer 1982) seems unlikely, since the weakly developed dorsal crest of the claspers of *B. nasuta* and *B. intermedia* is very similar to that found in many other *Baeturia* species. The remaining species of the *nasuta* group share a dorsally smoothly rounded clasper.

B. arabuensis and *B. mamillata* share a posteriorly directed and almost finger-shaped protrusion, and are possibly sister species. *B. bipunctata, B. gibberosa, B. laminifer* and *B. retracta* have a much broader dorsal protrusion on the clasper, which is regarded as synapomorphous (8 in fig. 1b). *B. laminifer* and *B. retracta* share a laminiform and square-shaped dorsal protrusion on the clasper as presumed synapomorphy (9 in fig. 1b). *B. bipunctata* and *B. gibberosa* have a more triangular, hump-shaped, protrusion; these are either sister species or part of a paraphyletic subgroup.

Females of most of the species that have a dorsal protrusion on the clasper, as far as they could be identified, generally have a truncate caudodorsal beak, which character is unique for these species and presumably apomorphous at that level (7 in fig. 1b). Only the females that presumably belong to *B. arabuensis* and the females of *B. gibberosa* have a pointed beak as those in *B. guttulipennis, B. nasuta,* and *B. parva.* The female of *B. splendida* has a bluntly rounded, almost truncate, caudodorsal beak.

BIOGEOGRAPHY

The *nasuta* group is distributed in New Guinea and some adjacent islands, some species reach to the Bismarck Archipelago or the Admiralty Islands.

Study of the New Guinean cicadas indicates that the various genera or monophyletic species groups show different patterns of distribution. The genera seem concentrated with most, and often endemic, species in different parts of the island. These parts of New Guinea, thus recognized as areas of endemism (Duffels & de Boer 1990), largely coincide with frag-

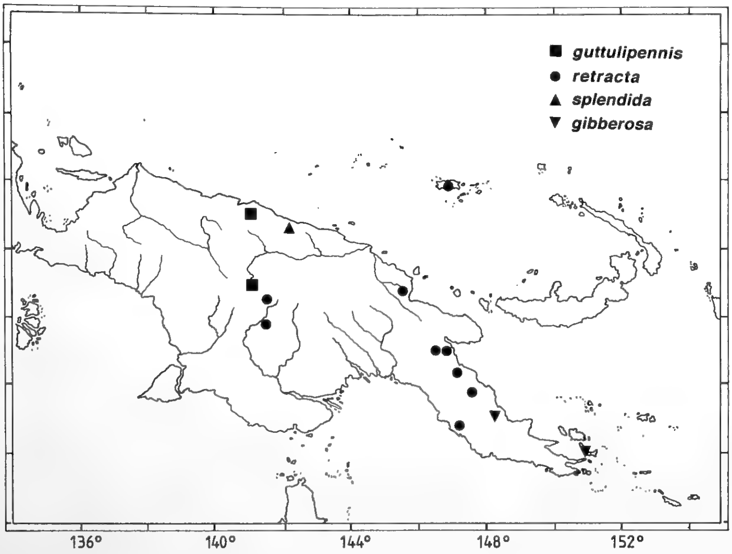


Fig. 2. Distribution of *Baeturia gibberosa, B. guttulipennis, B. retracta,* and *B. splendida.*

ments of a historic island arc, that collided at different times and in various places with the northern craton of the Australian continent, to form present day New Guinea (for geological reviews see Daly et al. 1991; Rangin et al. 1990a, 1990b; Pigram & Davies 1987). It is supposed that the various genera of New Guinean cicadas evolved on isolated island arc fragments previous to their collision with the Australian continent (de Boer 1994c).

The *nasuta* group was regarded as a typical central New Guinea group (de Boer 1982) and, as such, has been compared to the genus *Cosmopsaltria* Stål (Duffels 1986; Duffels & de Boer 1990). *Cosmopsaltria* and the *B. nasuta* group both appeared to be concentrated in the central mountain ranges of New Guinea. The distributions of *B. arabuensis*, *B. mamillata* and *B. nasuta*, from the Wissel Lakes to well into the Papuan Peninsula, are indeed very similar to that of many species of *Cosmopsaltria* (Duffels 1983). A similar historical explanation for the distribution patterns found in these two groups seemed required. Such an explanation can be found in supposing that both *Cosmopsaltria* and the *nasuta* group evolved on the Sepic Arc terrane as defined by Pigram & Davies (1987), which is the first of the island arc fragments that collided with the Australian continent, and which developed into the central mountain ranges of New Guinea. However, the phylogenetic level of the groups (*Cosmopsaltria* as sister group of *Diceropyga*, *Rhadinopyga*, *Aceropyga*, and *Moana* (Duffels 1986, 1993), and the *nasuta* group as a subgroup of *Baeturia*) possibly indicates a considerable age difference, which contradicts to a contemporal evolution on the Sepic Arc fragment.

With the four species here added to the *nasuta* group, this group as a whole no longer has a typical central New Guinea distribution. In fact, the number of species that occurs in northern New Guinea about equals that of central New Guinea. Only four species (*B. arabuensis*, *B. intermedia*, *B. mamillata*, and *B. nasuta*) can be said to have a central mountain range distribution, though two (*B. mamillata*, and *B. nasuta*) also occur in the Papuan Peninsula. The distributions of *B. laminifer* and *B. retracta* are very similar; they are recorded from southern New Guinea (unpublished data for *laminifer*), the most eastern part of northern New Guinea, and the Papuan Peninsula. *B. laminifer* is recently recorded from New Britain (unpublished) and *B. retracta* is recorded from the Admiralty Islands. These two species are absent from the western parts of the central mountain ranges. *B. gibberosa* is possibly restricted to the Papuan Peninsula and Normanby Island. *B. splendida* and, possibly, *B. guttulipennis* are endemic to northern New Guinea (it is not certain that the female allotted to the latter species really belongs to *B. guttulipennis*). Also *B. parva* is distributed in northern New Guinea, but its distribution extends to the Vogelkop Peninsula, Misool, Biak, the Bismarck Archipelago, and Admiralty Islands. The two remaining species (*B. bipunctata* and *B. marmorata*), both from Araucaria camp and Rattan camp on the northern slopes of the central mountains of western New Guinea, should presumably be regarded more as northern, than as central New Guinean: several other species groups with a predominantly northern New Guinea distribution (e.g. the *viridis* group and the *guttulinervis* group) also have species in that area.

The distribution pattern of the *nasuta* group in its present concept is more in agreement with that of other groups of *Baeturia*, most of which seem to concentrate in northern New Guinea, while similarities with *Cosmopsaltria* have become less obvious and a paleobiogeographical comparison with that genus seems no longer relevant.

TAXONOMY

Description of the *nasuta* group

Species of the *nasuta* group are all very small sized. The specimens are shorter than 2.5 cm and generally do not exceed 2.0 cm. Males are easily recognized by their laterally transparent abdomen (this character is absent in *B. marmorata*). Body generally yellowish brown or reddish brown coloured and covered with many irregularly shaped brown speckles. Females generally darker coloured and more densely speckled (*B. splendida* unspeckled with greenish head and thorax).

Head (fig. 3a): Narrow, 2.3-2.8 x as wide as long. Vertex narrower than in most other *Baeturia* species, ocelli close together. Distance between lateral ocelli less than 2 x as wide as, and sometimes narrower than, frontal ocellus, and generally about as long (0.7-1.2 x) as distance between lateral ocellus and eye. Vertex 1.6-2.5 x as wide as postclypeus. Postclypeus in dorsal view narrow (1.1-2.2 x as wide as long) and triangularly protruding beyond vertex lobes, though with rounded anterior margin. Postclypeus distinctly swollen ventrally, its anterior margin (lateral view) often angularly bent (fig. 3b).

Legs: Fore femur (Fig. 6) with row of three erect and sharply pointed spines, diminishing in length towards tibia. The most distal spine often bicuspidate, forming a very small 4th spine. Most proximal spine slightly shorter than distance to middle spine. Middle spine triangular, very broad at its base.

Tegmina and wings: Hyaline, though tegmina sometimes with darkly suffused spots along veins. Tegmina with 8, wings with 6 apical areas. Hyaline border along hind margin of tegmen distinct, though narrow. This border slightly broader in wing. Veins ochraceous, sometimes tinged with red, and set with many long setae.

Tymbals: With 3-5, generally 4, parallel sclerotized ridges from dorsal to ventral tymbal margin. Often traces of red between dorsal parts of tymbal ridges.

Opercula: Male operculum fairly small, its distal part not covering tymbal cavity in ventral view and nearly always shorter than meracanthus, generally not reaching to anterior margin of 2nd abdominal segment. Operculum in ventral view reaching to under, or medially of, meracanthus. Female operculum smaller than that of male, sickle-shaped and erect.

Abdomen: Male abdomen conspicuous by almost transparent sides, its dorsal and distal parts darkened and brown speckled, ventral parts unspeckled. Lateroventral row of dark spots generally very distinct. Hind margins of abdominal segments often reddish. First and second sternites adjacent. First tergite very short and often partly hidden under metanotum (in *B. arabuensis* distinctly longer than in other species). Second tergite medially with almost straight anterior margin. Auditory capules well developed, globularly swollen. Female abdomen more robust than that of male, darker coloured, and more densely speckled. Ovipositor sheaths sometimes reaching beyond apex of caudodorsal beak. Female caudodorsal beak often truncate at apex.

Male genitalia: Caudodorsal beak strongly bent, making an almost right angle with dorsal margin of pygofer. Dorsal margin of pygofer not continuously rounded into dorsal margin of beak, and weakly concave near apex of beak. Caudodorsal beak very broad and straight, dorsally flattened, and with bluntly rounded or truncate, often weakly concave, apex. Lateral lobe of pygofer with strongly swollen, often conically shaped, protuberance, projecting posteriorly beyond margin of pygofer. Claspers fairly long, parallel, and generally directed posteriad. Apical part of clasper hardly bent down, with large and sharply edged ventral hollow. Aedeagus S-curved with lateral lobes at basal curve. Apical part of aedeagus extremely long and slender (compared to other species of *Baeturia*). Aedeagal pore narrow and oval.

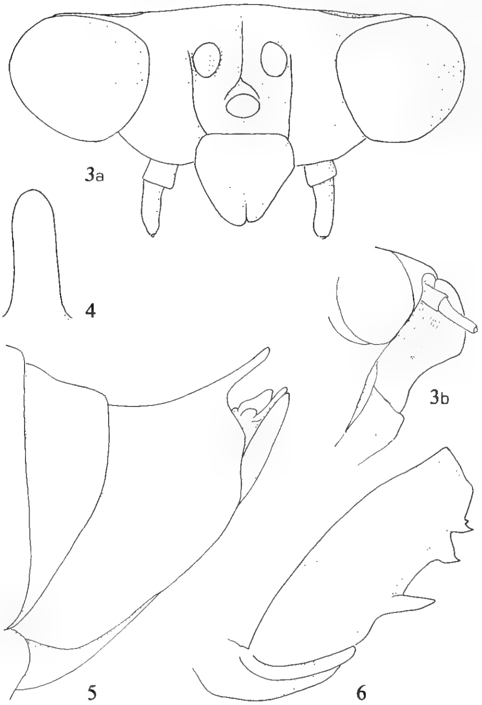
Baeturia guttulipennis Blöte

(figs. 2-13)

Baeturia guttulipennis Blöte, 1960: 69, fig. 15; de Boer, 1994c.

Material examined: Bewani R. territ., 1200 m, 1939, W. Stüber, ♂ holotype, RMNH; Bivak 39A, Star Range, 1150 m, 6.vii.1959, 1 ♀ *Baeturia guttulipennis* ? det. H.C. Blöte, RMNH.

B. guttulipennis is easily separated from other species of the *nasuta* group by the dark spots along the veins of tegmina and by its five tymbal ridges. Similar dark spots in tegmina were found in several other species of *Baeturia*, e.g. *B. guttulinervis* Blöte (de Boer 1994c), *B. pigrami* De Boer and *B. silveri* De Boer (de Boer 1994a), and, though less distinct, in *B. nasuta* Blöte (de Boer 1982).



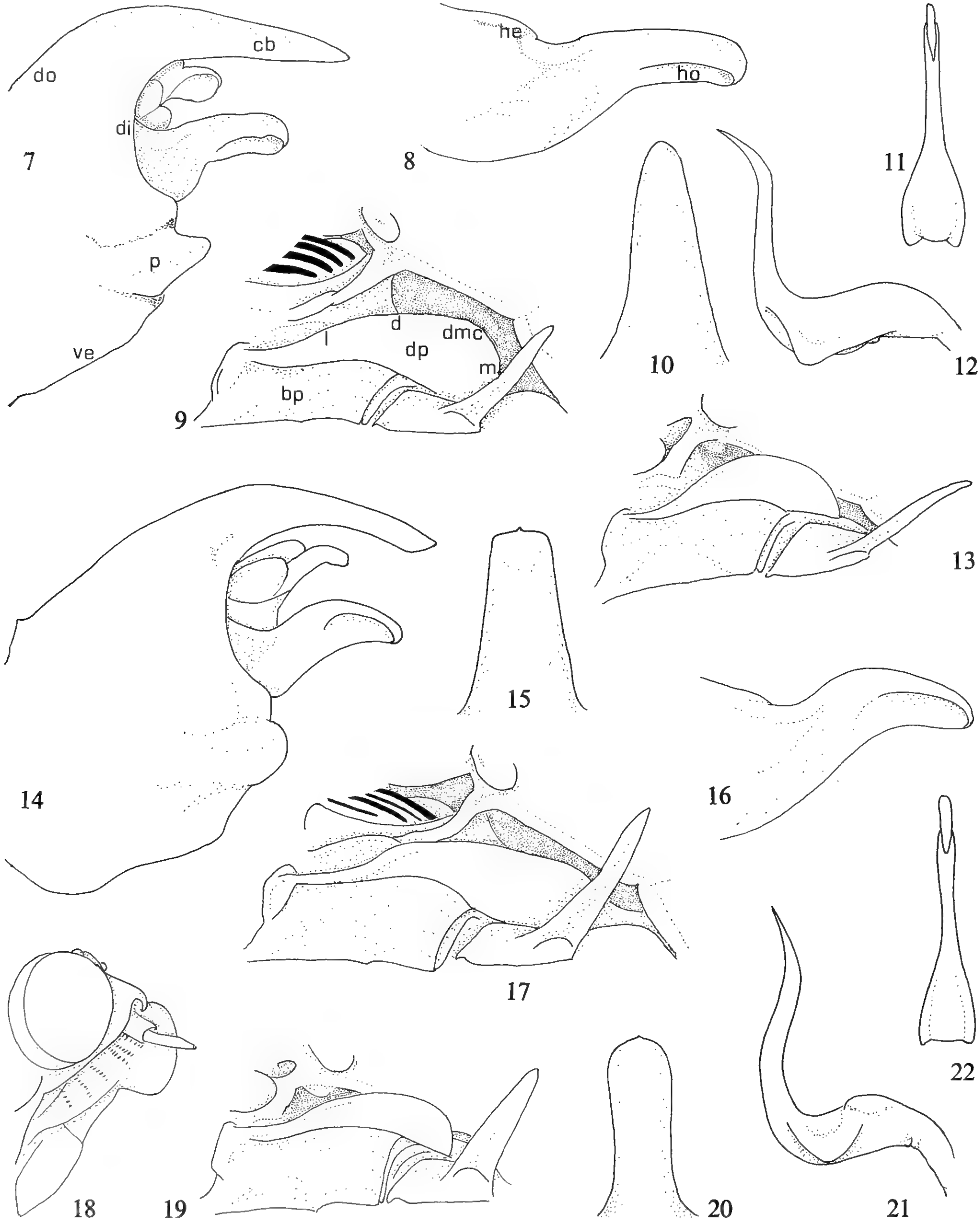
Figs. 3-6. *Baeturia guttulipennis* Blöte, 1960. – 3a, head in dorsal view, holotype; 3b, head in lateral view, holotype; 4, female caudodorsal beak in dorsal view; 5, female genital segment in lateral view; 6, fore femur, holotype.

Description

Body of male light ochraceous brown and weakly speckled with brown. Female darker, red-brown and more densely speckled. Female head and thorax larger than in male. Tegmina of males 1.2 x as long as body length, of females 1.5 x. Male abdomen 1.3 x as long as head and thorax, of females 1.1 x.

Head (fig. 3a): Ochraceous, brown-stained mainly on vertex lobes. Postclypeus bluntly rounded anteriorly, weakly protruding in male, more strongly in female. Postclypeus 1.4-2.0 x as wide as long. Postclypeus in lateral view (fig. 3b) distinctly swollen, anterior margin forming an almost right angle at 1/2 its length, and concave to anteclypeus.

Thorax: Pronotum ochraceous with dark speckling predominantly in medial band and on medial parts of



Figs. 7-13. *Baeturia guttulipennis* Blöte, 1960: 7, pygofer in lateral view, holotype; 8, clasper, holotype; 9, male operculum, holotype; 10, male caudodorsal beak in dorsal view, holotype; 11, aedeagus from behind, holotype; 12, aedeagus in lateral view, holotype; 13, female operculum. 14-22. *Baeturia splendida* sp. n.: 14, pygofer in lateral view; 15, male caudodorsal beak in dorsal view; 16, clasper; 17, male operculum; 18, head in lateral view; 19, female operculum; 20, female caudodorsal beak in dorsal view; 21, aedeagus in lateral view; 22, aedeagus from behind. Lettering: bp = basal part of operculum; cb = caudodorsal beak; d = distal margin of operculum; di = = distal margin of pygofer; dmc = distomedial corner of operculum; do = dorsal margin of pygofer; dp = distal part of operculum; he = clasper heel; ho = clasper hollow; l = lateral margin of operculum; m = medial margin of operculum; p = protuberance on lateral lobe of pygofer; ve = ventral margin of pygofer.

pronotal lobes, unspeckled in and along its fissures. Mesonotum greenish brown, weakly brown speckled in male, but densely speckled in female. Male with two brown spots in front of cruciform elevation.

Legs: Ochraceous, often reddish towards tarsi, and brown speckled. Fore femur (Fig. 6) with row of three or four sharply pointed and erect spines.

Tegmina and wings: Tegmina with dark brown markings concentrated along veins. Wings hyaline. Veins ochraceous brown, densely set with setae.

Tymbal organ: Five darkly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin. Four intercalary ridges form a lateral band across tymbal.

Opercula: Male operculum (fig. 9) very small and not covering tymbal cavity. Distal part of operculum erect and reaching to about 2/3 the length of meracanthus, but not reaching to abdomen. Lateral margin of distal part short, concavely bent into crest around distolateral corner of basal part, and convexly bent into long and almost straight distal margin. Distomedial corner rounded, medial margin straight. Female operculum (fig. 13) almost as large as that of male, broadly sickle-shaped and curved to abdomen, with almost continuously rounded distal margin.

Abdomen: Male abdomen weakly inflated, yellow brown and brown speckled, though ventrally unspeckled. Tergites 3-6 almost transparent laterally. A distinct lateroventral row of brown spots on tergites 3-7. First tergite very short and medially partly hidden under metanotum. Female abdomen more robust than that of male, dark reddish brown, and densely speckled. Lateroventral spots on tergites 3-7 almost lost in speckling. Ovipositor sheaths not reaching to apex of caudodorsal beak (fig. 5). Female caudodorsal beak in dorsal view (fig. 4) sharply pointed at apex.

Male genitalia: Pygofer in lateral view as in fig. 7. Dorsal margin weakly convex, strongly bent into almost straight caudodorsal beak. Distal margin concave, gradually bent into straight margin of beak. Protuberance on lateral lobe of pygofer rounded and conically projecting posteriad. Pygofer lobe forming an angular corner just above this protuberance. Ventral margin almost straight, but angularly bent just under lateral protuberance. Ventral margins converge to sharp angle at base of pygofer opening. Caudodorsal beak in dorsal view (fig. 7) rounded at apex. Clasper (fig. 8) almost straight and directed posteriad, with long and slender, dorsally smoothly rounded, apical part. Basal part of clasper with weakly developed clasper heel. Clasper hollow fairly long. Aedeagus (fig. 12) with very long and slender apical part and well developed lateral lobes. Aedeagus from behind (fig. 11) very slender, aedeagal pore narrow, oval shaped and truncate at apex.

Measurements: Body length ♂: 18.6 mm, ♀: 18.2 mm; tegmen length ♂: 22.9 mm, ♀: 28.0 mm; head length ♂: 1.4 mm, ♀: 1.8 mm; pronotum length ♂: 2.4 mm, ♀: 2.8 mm; mesonotum length ♂: 3.8 mm, ♀: 4.8 mm; head width ♂: 3.7 mm, ♀: 4.3 mm; width of pronotal collar ♂: 5.3 mm, ♀: 6.5 mm.

Distribution (fig. 2). – The male holotype of *B. guttulipennis* comes from Bewani in northeastern Irian Jaya; a female that possibly belongs to the species comes from the Star Range in central eastern Irian Jaya.

Baeturia splendida sp. n.

(figs. 2, 14-22)

Holotype male: 'NEW GUINEA NE / Torricelli Mts. / Mokai Vill. 750 m / xii-16-31-1958' (print); 'W.W. Brandt / Collector / Bishop' [print], BPBM. – Paratypes: same data as holotype 5♀, BPBM; same data but 8-15.xii.1958, 3♀; 1-23.i.1959, 1♀, all BPBM.

Only one male and several females are known of this species. *B. splendida* is easily recognized by its greenish colour, with a pattern of brown markings. Due to this colour pattern the females too are easily identified. The colour pattern is unique within the *nasuta* group.

Description

Head and thorax olive green, abdomen yellowish brown. Tegmina of male 1.2 x as long as body length, of females 1.3-1.4 x. Male abdomen 1.2 x as long as head and thorax, of females 0.9-1.1 x.

Head: Olive-green. Vertex lobe with dark brown spot between eye and lateral ocellus. Postclypeus distinctly protruding, bluntly rounded anteriorly, and 1.1-1.8 x as wide as long. Postclypeus in lateral view (fig. 18) distinctly and angularly swollen, anteriorly almost globularly inflated.

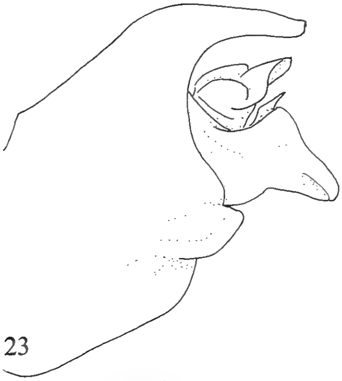
Thorax: Pronotum greenish and unmarked. Mesonotum green with two large semi-oval paramedian brown spots at pronotal margin, reaching to about half-length of mesonotum. No dark spots in front of cruciform elevation.

Legs: Greenish, yellow-brown towards tarsi. Fore femur with row of four sharply pointed and erect spines.

Tegmina and wings: Hyaline. Veins greenish, and set with setae.

Tymbal organ: Four weakly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin. Three intercalary ridges form a lateral band across tymbal.

Opercula: Male operculum (fig. 17) very small and not covering tymbal cavity. Distal part of operculum erect and reaching to about half-length of meracan-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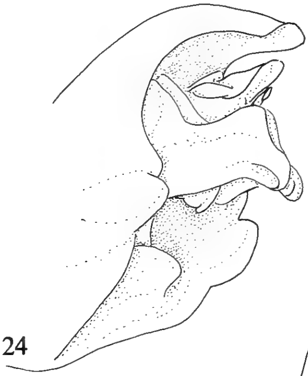
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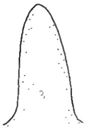
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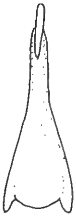
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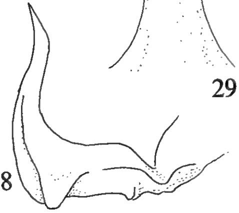
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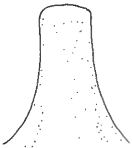
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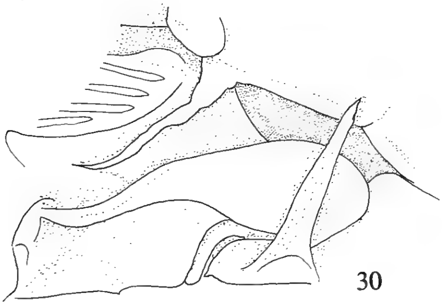
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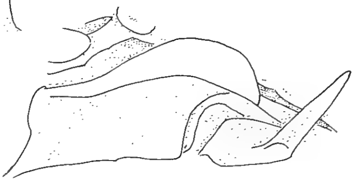
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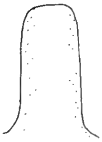
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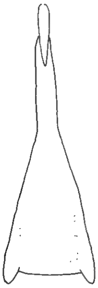
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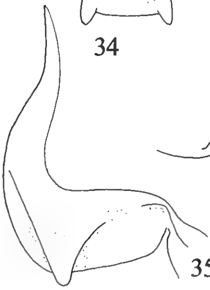
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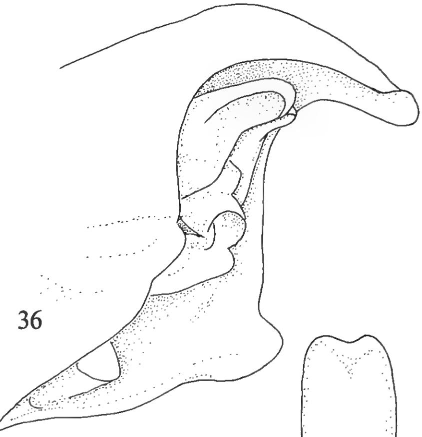
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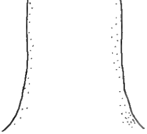
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thus, not reaching to abdomen. Lateral margin of distal part short, concavely bent into crest around distolateral corner of basal part, and convexly bent into long and almost straight distal margin. Distomedial corner rounded, medial margin straight. Female operculum (fig. 19) almost as large as that of male, broadly sickle-shaped and erect, with almost continuously rounded distal margin.

Abdomen: Male abdomen hardly inflated, yellow brown, darker brown in distal part. Third and 4th tergites almost transparent laterally. A distinct lateroventral brown spot on 3rd tergite and a slightly smaller lateral spot on 8th tergite. First tergite very short and medially partly hidden under metanotum. Female abdomen more robust than that of male, light brown, with a dark brown lateroventral spot on 3rd tergite. Ovipositor sheaths not reaching to apex of caudodorsal beak. Female caudodorsal beak in dorsal view (fig. 20) weakly convex, almost truncate, at apex.

Male genitalia: Pygofer in lateral view as in fig. 14. Dorsal margin weakly convex, angularly bent into almost straight caudodorsal beak. Distal margin concave, almost continuously bent with margin of beak. Protuberance on lateral lobe of pygofer bluntly rounded and weakly projecting posteriad. Pygofer lobe forming an angular corner just above this protuberance. Ventral margin angularly bent at about 1/3 its length and weakly concave towards base. Ventral margins converge to sharp angle at base of pygofer opening. Caudodorsal beak in dorsal view (fig. 15) almost truncate at apex, but ending in very small and sharply pointed medial thorn. Clasper (fig. 17) curving upwards with long and slender, dorsally smoothly rounded and recurving, apical part. Basal part of clasper without clasper heel. Clasper hollow fairly long. Aedeagus (fig. 21) with very long and slender apical part. Basal part of aedeagus with small and angular dorsolateral protuberances. Lateral lobes small, hardly projecting in lateral view. Aedeagus from behind (fig. 22) very slender. Aedeagal pore narrow, oval-shaped and truncate at apex.

Measurements: Body length ♂: 16.5 mm, ♀: 16.0-19.1 mm (x̄ 18.0 mm ± 0.9); tegmen length ♂: 20.6 mm, ♀: 22.0-25.5 mm (x̄ 24.6 mm ± 1.0); head length ♂: 1.5 mm, ♀: 1.6-1.9 mm (x̄ 1.8 mm); pronotum length ♂: 2.3 mm, ♀: 2.8-3.2 mm (x̄ 2.9 mm); mesonotum length ♂: 4.0 mm, ♀: 4.0-5.2 mm (x̄ 4.8 mm); head width ♂: 3.3 mm, ♀: 4.0-4.8 mm (x̄ 4.6 mm); width of pronotal collar ♂: 5.1 mm, ♀: 5.7-7.0 mm (x̄ 6.6 mm).

Distribution (fig. 2). – *B. splendida* is only known from the Torricelli mountains in northern Papua New Guinea.

Etymology. – *Splendidus* (Latin) refers to the beautiful colour pattern of this species.

Baeturia gibberosa sp. n.
(figs. 2, 23-31)

Holotype: 'New Guinea SE / Popondetta / 25 m vi.66' (-print); 'Shanahan- Lippert / Light Trap / Bishop Museum' (print), ♂, BPBM. – Paratypes: NEW GUINEA: Popondetta, 60 m, 1-4.ix.1963, J. Sedlacek, 2♂, BPBM; Popondetta, Inbora Plant'n, 23.ix.1963, P. Shanahan, 2♂, BPBM; NORMANBY: Wakaiuna, Sewa Bay, 5-9.xi.1956, W.W. Brandt, 1♀, BPBM; same data but 1-10.xii.1956, 1♀; 11-20.xii.1956, 1♀, both BPBM; Wamula, 400-500 m, 31.xii.1988, R. de Keyzer, 3♂, Moul.

B. gibberosa is easily recognized by the rectangular dorsal corner of its clasper.

Description

Body ochraceous brown, sometimes tinged with red, and densely speckled with brown. Tegmina of males 1.1-1.2 x as long as body length, of females 1.3 x. Male abdomen 1.3-1.5 x as long as head and thorax, of females 1.0 x.

Head: Ochraceous, brown speckled. Postclypeus weakly protruding and bluntly rounded anteriorly, 1.7-2.2 x as wide as long. Postclypeus in lateral view distinctly swollen with straight anterior margin, concave towards anteclypeus.

Thorax: Pronotum ochraceous, brown speckled. Mesonotum greenish brown, slightly brown speckled. Two dark spots in front of cruciform elevation.

Legs: Ochraceous and weakly speckled. Fore femur with row of four sharply pointed and erect spines.

Tegmina and wings: Hyaline. Veins ochraceous, moderately set with setae.

Tymbal organ: Four weakly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin. Three intercalary ridges form a lateral band across tymbal.

Opercula: Male operculum (fig. 30) small and only partly covering tymbal cavity. Distal part of operculum oval shaped, slightly erect and reaching to about 2/3 of length of meracanthus, in some specimens reaching to anterior margin of 2nd abdominal

Figs. 23-31. *Baeturia gibberosa* sp. n. – 23, pygofer in lateral view; 24, pygofer from aslant; 25, clasper; 26, female caudodorsal beak in dorsal view; 27, aedeagus from behind; 28, aedeagus in lateral view; 29, male caudodorsal beak in dorsal view; 30, male operculum; 31, female operculum

Figs. 32-39. *Baeturia retracta* sp. n. – 32, female caudodorsal beak in dorsal view; 33, pygofer in lateral view; 34, aedeagus from behind; 35, aedeagus in lateral view; 36, pygofer from aslant; 37, male caudodorsal beak in dorsal view; 38, female operculum; 39, male operculum.

segment. Lateral margin of distal part fairly long and directed mesiad, concavely bent into crest around distolateral corner of basal part, and forming an obtuse angle with straight distal margin. Medial part of operculum angularly rounded, extending medially of meracanthus. Female operculum (fig. 31) short, sickle-shaped and erect.

Abdomen: Male abdomen not inflated, ochraceous brown and brown speckled, though ventrally unspeckled. Segmental hind margins reddish. Tergites 3-6 almost transparent laterally. A distinct lateroventral row of brown spots on tergites 3-8. First tergite very short and medially partly hidden under metanotum. Female abdomen red-brown and densely speckled. Female caudodorsal beak (fig. 26) sharply pointed at apex.

Male genitalia: Pygofer in lateral view as in fig. 23. Dorsal margin weakly concave, but convexly bent into almost straight caudodorsal beak and concave near apex of beak. Distal margin concave, and continuously bent into margin of beak. Protuberance on lateral lobe of pygofer bluntly rounded and weakly projecting posteriad. Pygofer lobe forming a small angular corner just above this protuberance. Ventral margin almost straight, but convexly bent just under lateral protuberance. Ventral margins converge to sharp angle at base of pygofer opening (fig. 24). Caudodorsal beak in dorsal view (fig. 29) truncate at apex. Clasper (fig. 25) almost straight and directed posteriad. Apical part of clasper forming a distinct and angularly protruding dorsal crest, giving the clasper a humped appearance. Clasper hollow fairly short. Basal part of clasper gradually widening, not forming an angular clasper heel. Aedeagus (fig. 27) with fairly long and slender apical part, but much shorter than in most other species of this group, and well developed lateral lobes. Aedeagus from behind (fig. 28) very slender, aedeagal pore narrow, oval-shaped and truncate at apex.

Measurements: Body length ♂: 14.7-17.8 mm ($\bar{x}$ 15.9 mm ± 1.0), ♀: 16.5-17.7 mm ($\bar{x}$ 17.2 mm ± 0.5); tegmen length ♂: 17.1-19.1 mm ($\bar{x}$ 18.1 mm ± 0.8), ♀: 21.9-22.3 mm ($\bar{x}$ 22.1 mm ± 0.9); head length ♂: 1.2-1.5 mm ($\bar{x}$ 1.3 mm), ♀: 1.5-1.9 mm ($\bar{x}$ 1.7 mm); pronotum length ♂: 1.9-2.3 mm ($\bar{x}$ 2.1 mm), ♀: 2.6-2.9 mm ($\bar{x}$ 2.8 mm); mesonotum length ♂: 2.9-3.5 mm ($\bar{x}$ 3.2 mm), ♀: 4.1-4.6 mm ($\bar{x}$ 4.4 mm); head width ♂: 2.5-3.7 mm ($\bar{x}$ 3.3 mm), ♀: 4.0-4.3 mm ($\bar{x}$ 4.2 mm); width of pronotal collar ♂: 4.3-5.2 mm ($\bar{x}$ 4.6 mm), ♀: 5.9-6.4 mm ($\bar{x}$ 6.2 mm).

Distribution (fig. 2). – *B. gibberosa* is recorded from Popondetta on the Papuan Peninsula and from Normanby Island.

Etymology. – *Gibberosus* (Latin) humpbacked refers to the hump-shaped dorsal protrusion of the clasper.

Baeturia retracta sp. n.
(figs. 2, 32-39)

Holotype: 'PAPUA NEW GUINEA / Tabubil, Western Province / 5°15' S 140° 13' E / 13 oct. 1992 / R.B. Lachlan' (print, day and month written); 'On loan from / M.S. Moulds / Sydney' [print, violet label], ♂, AMS). – Paratypes: same data as holotype but 17.x.1992, 1♂, Moul; same data but 29.xi.1992, 1♂, Moul; Garaina, 11-14.vii.1969, J.L. Gressitt, 1♂, BPBM; Gurakor, Wampit R. Valley, 45 mi from Lae, 670 m, 8.v.1959, L.J. Brass, Sixth Archbold Exped. to Papua New Guinea, 1♀, AMNH; Gurakor, 7.vii.1965, H. Pyka, 1♂, SMN; Iongai, 1700-1900 m, 9.xi.1965, J. & M. Sedlacek, 1♀, BPBM; Iongai, 10 km E of Mt. Albert Edward, 1450-1800 m, 8-10.xi.1965, J. Sedlacek, 1♂, BPBM; Kiunga, 18.vii.1970, O.K. McCaw, 1♂, AMS; Kiunga, 5° 15' S 141° 05' E, 2280 m, 25.v.1970, O.K. McCaw, 1♀, Moul; Kiunga, Fly River, 35 m, viii.1969, J. Sedlacek, 1♀, BPBM; Koitaki, 1500 ft, x-xi.1928, Pemberton, 1♂, BPBM; Wau, Morobe Distr., 1050-1100 m, 15.xii.1961, J., J.H. & M. Sedlacek, 1♂, BPBM; Yagaum, Madang, 3-5.vi.1965, H. Pyka, 1♂, SMN; MANUS: Manus isl., 24.i.1966, 1♂, SMN.

B. retracta can be recognized by its erect and retracted claspers, which lie for the greater part concealed within the pygofer. The species is closely related to *B. laminifer* Blöte, sharing a very similar clasper with a similarly square, laminiform, dorsal protrusion. This protrusion, however, is completely concealed within the pygofer, and therefore hardly visible in *B. retracta*. *B. retracta* is regarded as a separate species, since the retraction of the clasper appears to be a constant character. Furthermore, *B. retracta* tends to have a more strongly swollen postclypeus, while males have a slightly shorter operculum and a shorter, more rounded, protuberance on the lateral lobe of the pygofer.

Description
Body of males light yellow-brown or greyish brown and distinctly speckled with brown. Females more red-brown and more densely speckled. Female head and thorax larger than in male. Tegmina of males 1.1-1.3 x as long as body length, of females 1.2-1.4 x. Male abdomen 1.2-1.5 x as long as head and thorax, of females 1.0-1.3 x.

Head: Ochraceous, densely brown speckled. Postclypeus weakly protruding, almost oblong-shaped and bluntly rounded anteriorly. Postclypeus 1.4-2.0 x as wide as long. Postclypeus in lateral view distinctly swollen with strongly convex anterior margin.

Thorax: Pronotum ochraceous or greyish brown, with brown speckling concentrated in, often somewhat reddish, medial band and on medial parts of pronotal lobes. Mesonotum greenish brown, densely brown speckled. Two brown spots in front of cruciform elevation.

Legs: Ochraceous, often reddish towards tarsi, and weakly speckled. Fore femur with row of three or four sharply pointed and erect spines.

Tegmina and wings: Hyaline. Veins ochraceous, and densely set with setae.

Tymbal organ: Four weakly sclerotized parallel ridges spanning the tymbal from dorsal to ventral margin. Three intercalary ridges form a lateral band across tymbal.

Opercula: Male operculum (fig. 39) very small and not covering tymbal cavity. Distal part of operculum erect and reaching to about half-length of meracanthus, but not reaching to abdomen. Lateral margin of distal part short, concavely bent into crest around distolateral corner of basal part, and angularly bent into long and concave distal margin. Distomedial corner rounded, medial margin straight. Male from Iongai with larger, more oval-shaped, operculum. Female operculum (fig. 38) almost as large as that of male, broadly sickle-shaped and erect, with almost continuously rounded distal margin.

Abdomen: Male abdomen not inflated, ochraceous brown and brown speckled, though ventrally unspeckled. Segmental hind margins sometimes reddish. Tergites 3-6 almost transparent laterally. A distinct lateroventral row of brown spots on tergites 3-8. First tergite very short and medially almost completely hidden under metanotum. Female abdomen more robust than that of male, dark reddish brown, and densely speckled. Lateroventral spots on tergites 3-8 very distinct. Ovipositor sheaths not reaching to apex of caudodorsal beak. Female caudodorsal beak in dorsal view (fig. 32) truncate at apex (pointed in Iongai specimen).

Male genitalia: Pygofer in lateral view as in fig. 33. Dorsal margin concave, but convexly bent into almost straight caudodorsal beak and concave near apex of beak. Distal margin almost straight, but concavely bent into straight margin of beak. Protuberance on lateral lobe of pygofer bluntly rounded and weakly projecting posteriad. Pygofer lobe sometimes forming a small rounded corner just above this protuberance. Ventral margin almost straight, but convexly bent just under lateral protuberance and weakly concave near base. Ventral margins converge to sharp angle at base of pygofer opening (fig. 36). Caudodorsal beak in dorsal view (fig. 37) weakly bicuspidate at apex. Clasper strongly upcurved, reaching into basal part of caudodorsal beak. Dorsal part of clasper with laminiform and square-shaped protrusion. Clasper hollow fairly short. Aedeagus (fig. 35) with long apical part, but shorter and broader than in most other species of this group, and with well developed lateral lobes. Basal part of aedeagus very stout. Aedeagus from behind (fig. 34) long and slender, though fairly broad between its lateral lobes. Aedeagal pore narrow, oval-shaped and truncate at apex.

Measurements: Body length ♂: 14.9-19.6 mm (x̄ 17.2 mm ± 1.4), ♀: 16.3-18.1 mm (x̄ 17.5 mm ± 0.7); tegmen length ♂: 18.2-21.9 mm (x̄ 20.6 mm ± 1.1), ♀: 21.4-25.9 mm (x̄ 23.0 mm ± 1.7); head length ♂: 1.3-1.5 mm (x̄ 1.4 mm), ♀: 1.6-1.8 mm (x̄ 1.7 mm); pronotum length ♂: 2.1-2.5 mm (x̄ 2.2 mm), ♀: 2.4-2.7 mm (x̄ 2.6 mm); mesonotum length ♂: 3.2-4.1 mm (x̄ 3.7 mm), ♀: 3.9-4.8 mm (x̄ 4.2 mm); head width ♂: 3.4-3.8 mm (x̄ 3.7 mm), ♀: 3.9-4.2 mm (x̄ 4.1 mm); width of pronotal collar ♂: 4.7-5.6 mm (x̄ 5.1 mm), ♀: 5.7-6.3 mm (x̄ 5.9 mm).

Distribution (fig. 2). – *B. retracta* is widely distributed in Papua New Guinea, and also recorded from Manus Island of the Admiralty Islands.

Etymology. – *Retracta* refers to the retracted claspers of this species.

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A REVISION OF THE NEW WORLD GENUS *ERPETOGOMPHUS* HAGEN IN SELYS (ODONATA: GOMPHIDAE)

Garrison, R. W., 1994. A revision of the New World genus *Erpetogomphus* Hagen in Selys (Odonata: Gomphidae). – Tijdschrift voor Entomologie 137: 173-269, figs. 1-230, tabs. 1-4 [ISSN 0040-7496]. Published 15 December 1994.

This revision of adult *Erpetogomphus* includes a phylogenetic assessment of all 21 species using outgroup comparison and parsimony algorithm, descriptive biogeography, keys to both sexes, synonymies, descriptions, type designations, and illustrations, including distribution maps of all species. Six new species are described: *E. agkistrodon, E. leptophis, E. elaphe, E. liopeltis, E. bothrops, E. heterodon. Erpetogomphus coluber* is considered a junior synonym of *E. compositus, E. natrix* is considered a subspecies of *E. lampropeltis*, and a neotype is designated for *E. cophias.* Phylogenetic assessment of 41 mostly somatic characters shows *Erpetogomphus* to be partitioned into three monophyletic groups: 1) six dark green species (*E. constrictor, E. sabaleticus, E. tristani, E. agkistrodon, E. schausi, E. ophibolus*) with mostly allopatric or parapatric distributions along the eastern coast of Mexico south into northern Colombia and Venezuela, 2) two species (*E. leptophis, E. eutainia*) with distributions from southern Texas south through Mexico and up the west coast to Michoacan states, and 3) 13 remaining species (*E. elaphe, E. elaps, E. liopeltis, E. bothrops, E. viperinus, E. designatus, E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*) with distributions in the central United States south through Mexico to Costa Rica. Derived characters states were gleaned mostly from primary and secondary genitalic characters (head structure, penis, hamules, caudal appendages, vulvar lamina); but satisfactory resolution of terminal clades, especially of the third group, is difficult due to apparent character reversals.

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Key words. – Odonata; Gomphidae; *Erpetogomphus*; systematics; keys; cladistics; phylogeny; biogeography.

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INTRODUCTORY PART

Introduction

No other group of Middle American Gomphidae has been in need of revision as much as the genus *Erpetogomphus* Hagen *in* Selys. The last species were described by Williamson and Williamson (1930), and although several odonatists have since received species which are possibly undescribed, there has been a hesitancy to describe them because so many species are rare or poorly known. Several years ago, I collected a few specimens of one species I thought new, but I realized that an examination of most of the types would be necessary before I could resolve the problem.

This paper is the result of those investigations. My purpose here is to: 1) describe and figure all species currently going under the generic name *Erpetogomphus*, 2) select lectotypes and establish type localities, if possible, and 3) construct a cladogram of all the known species so that phylogenetic relationships and distribution patterns can be adduced for the genus. I have examined types for all taxa except for two species, *E. cophias* (type lost), and *E. ophibolus*. The last species is distinct, and no confusion exists about its identity or type deposition. A neotype is selected for *E. cophias*. I also provide keys for all species.

Twenty-three names (table 1) have been included in *Erpetogomphus*, but three, *E. severus* Selys, *Herpetogomphus rupinsulensis* Walsh, and *H. pictus* Needham (= *Ophiogomphus rupinsulensis* (Walsh)) have been transferred to *Ophiogomphus*. Another, *E. menetriesii* (Selys) I consider to be a *nomen dubium*, for reasons detailed below; and six new species are described. One species thought lost, *E. boa* Selys, has been rediscovered, and *E. viperinus* auctorum is really an undescribed species. I suspect that several new species will be found in Mexico and Central America, and I hope this paper will make it easier for others to describe those new species.

The difficulties I have encountered during this study have mostly been due to the paucity of specimens of various species which have been considered rare. I have successfully associated both sexes of all current species except the male of *E. agkistrodon*, which is unknown. My task of recording aspects of intraspecific variation has been made considerably easier by various museum authorities and individuals listed under acknowledgements.

History

The genus *Erpetogomphus* was described (as a subgenus) by Selys (1858) to receive two previously described species, *Gomphus menetriesii* Selys, 1850, and *Ophiogomphus crotalinus* Hagen *in* Selys (the latter originally described from a pair in 1854), as well as two new species, *Erpetogomphus elaps* Selys, and *E. cophias* Selys. In the 'Appendice' of the same paper, Hagen described *E. compositus* and *E. designatus*. Selys described *E. boa* in 1859 and *E. viperinus* in 1868. Some of these species were briefly redescribed or discussed by Selys and Hagen in 1859, 1869, 1873, and 1878. In 1879, Selys redefined the subgenus *Herpetogomphus* (an unjustified emendation of *Erpetogomphus*, see Cowley, 1934), under which were included eight species: *E. compositus*, *E. designatus*, *E. viperinus*, *E. menetriesii*, *E. elaps*, *E. boa*, *E. cophias*, and *E. crotalinus*. Calvert (1899) redescribed *E. viperinus* (now *E. bothrops* sp. n.) based on material collected in Tepic, and included a diagnosis of the females of *E. viperinus* and *E. elaps*. Kirby (1890), in a synonymic catalogue of the world Odonata, designated *Herpetogomphus crotalinus* as the type species of the genus. Calvert (1905) included a synopsis for all *Erpetogomphus* from Middle America and described *E. eutainia*, *E. ophibolus*, *E. sipedon*, and *E. diadophis*. Calvert (1912a) added *E. tristani*. Ris (1917) described *E. constrictor* and redescribed what he thought to be the second known male of *E. boa*. In 1918 Williamson described *E. sabaleticus* from a pair from Colombia, and Kennedy (1918) described *E. lampropeltis* from California. Calvert (1919) described *E. schausi* from a male from Guatemala. Finally, Williamson and Williamson (1930) described two new species from Baja California, *E. coluber* and *E. natrix*. In the same paper, they presented a synopsis of what was known for all species. Their summary makes clear that only a few common species were represented in collections, and that many others were poorly known and/or described from insufficient material.

The status of the name *Erpetogomphus menetriesii* (Selys)

This name was first applied by Selys to an incomplete male supposedly from Brazil. Selys (1850) briefly compared it to *Paragomphus genei*, as follows: 'Its colouration yellow, almost without spots, prevents confusion of this species with any other in Europe, but it resembles in this respect *G. pallidus* (Ramb.) of Southern America whose stature is stronger, and *Gomphus menetriesii* (new) from Brazil, but the feet of the last are mostly black, the ♂ abdomen is bordered by black on the two sides, etc...'. The same specimen was redescribed it in 1854 as follows: 'Head yellow, except for space between ocelli, that between the eyes and ciliated margin of the occiput black. Front of thorax yellow, with 2 median, contiguous stripes, almost obliterated, pale red, antehumeral and humeral stripe equidistant.

♂ Appendages lacking. From: Brazil?' The type is said to be in the 'Musée de St- Pétersburg'.

Table 1. Species-group names used in the genus *Erpetogomphus*

Name	Original Genus	Original Reference	Type locality	Location of type	Type status	Reference for first placement in *Erpetogomphus*	Present placement
agkistrodon	*Erpetogomphus*	This paper	Jalapa, Mexico	UNAM (♂)	Holotype	This paper	*E. agkistrodon*
boa	*Erpetogomphus*	Selys 1859	Vera Cruz, Mexico	IRSN (♂)	Lectotype	Selys 1859	*E. boa*
bothrops	*Erpetogomphus*	This paper	Rio Otapa, Veracruz State, Mexico	USNM (♂)	Holotype	This paper	*E. bothrops*
coluber	*Erpetogomphus*	Williamson & Williamson 1930	San José de Comandu, Baja Calif., Mexico	UMMZ (♂)	Holotype	Williamson & Williamson 1930	*E. compositus*
compositus	*Erpetogomphus*	Hagen *in* Selys 1858	Pecos River, Texas; corrected to vicinity of Roswell, NM[1]	MCZC (♀)	Holotype	Hagen *in* Selys 1858	*E. compositus*
constrictor	*Erpetogomphus*	Ris 1917	Misantla, Veracruz, Mexico	SMF (♂)	Lectotype	Ris 1917	*E. constrictor*
cophias	*Erpetogomphus*	Selys 1858	Mexico	MNHP (♂)	Neotype	Selys 1858	*E. cophias*
crotalinus	*Ophiogomphus*	Hagen *in* Selys 1858	Mexico	MCZC (♂)	Lectotype	Hagen *in* Selys 1858	*E. crotalinus*
designatus	*Erpetogomphus*	Hagen *in* Selys 1854	Pecos River, Texas; corrected to vicinity of Roswell, NM[1]	MCZC (♂)	Lectotype	Hagen *in* Selys 1858	*E. designatus*
diadophis	*Erpetogomphus*	Calvert 1905	Texas	BMNH (♂)	Holotype	Calvert 1905	*E. eutainia*
elaphe	*Erpetogomphus*	This paper	Costa Rica	FSCA (♂)	Holotype	This paper	*E. elaphe*
elaps	*Erpetogomphus*	Selys 1858	Mexico	MNHP (♂)	Holotype	Selys 1858	*E. elaps*
eutainia	*Erpetogomphus*	Calvert 1905	Guerrero, Mexico	BMNH (♂)	Holotype	Calvert 1905	*E. eutainia*
heterodon	*Erpetogomphus*	This paper	Aragon, New Mexico	USNM (♂)	Holotype	This paper	*E. heterodon*
lampropeltis	*Erpetogomphus*	Kennedy 1918	Fillmore, California	USNM (♂)	Holotype	Kennedy 1918	*E. l. lampropeltis*
leptophis	*Erpetogomphus*	This paper	Blue Creek, Belize	FSCA (♂)	Holotype	This paper	*E. leptophis*
liopeltis	*Erpetogomphus*	This paper	La Estanzuela, Nuevo Leon, Mexico	FSCA (♂)	Holotype	This paper	*E. liopeltis*
menetriesii	*Ophiogomphus*	Selys 1854	Brazil?	Lost		Selys 1858	*Nomen dubium*
montanus	*Herpetogomphus*	Selys 1878	Yellow Town, Montana	IRSN♂ (♂)	Holotype	Selys 1879	*Ophiogomphus severus montanus*
natrix	*Erpetogomphus*	Williamson & Williamson 1930	San Jose de Comandu, Baja Calif., Mexico	UMMZ (♂)	Holotype	Williamson & Williamson 1930	*E. lampropeltis natrix*
ophibolus	*Erpetogomphus*	Calvert 1905	Atoyac, Veracruz, Mexico	BMNH (♂)	Holotype	Calvert 1905	*E. ophibolus*
pictus	*Herpetogomphus*	Needham 1897	Ithaca, New York	CUIC (♂)	Holotype	Needham 1897	*Ophiogomphus rupinsulensis*[2]
rupinsulensis	*Herpetogomphus*	Walsh 1862	Rock Island, Illinois	Lost		Walsh 1862	*Ophiogomphus rupinsulensis*[3]
sabaleticus	*Erpetogomphus*	Williamson 1918	Cristalina, Colombia	UMMZ (♂)	Holotype	Williamson 1918	*E. sabaleticus*
schausi	*Erpetogomphus*	Calvert 1919	Purulta, Guatemala	ANSP (♂)	Holotype	Calvert 1919	*E. schausi*
severus	*Ophiogomphus*	Hagen 1874	Colorado	Lost♂ (♂, ♀)		Selys 1878[4]	*Ophiogomphus severus*[5]
sipedon	*Erpetogomphus*	Calvert 1905	Guadalajara, Mexico	BMNH (♀)	Holotype	Calvert 1905	*E. sipedon*
tristani	*Erpetogomphus*	Calvert 1912	Oricuajo, Costa Rica	ANSP (♂)	Holotype	Calvert 1912	*E. tristani*
viperinus	*Erpetogomphus*	Selys 1868	Orizaba, Veracruz, Mexico	IRSN (♂)	Lectotype	Selys 1868	*E. viperinus*

[1] See remarks under *E. designatus.*; [2] Transferred to *Ophiogomphus* by Needham (1899); [3] Transferred to *Ophiogomphus* by Hagen (1874)
[4] As *Herpetogomphus;* [5] Transferred to *Ophiogomphus* by Selys (1879)

In 1858, Selys discussed *E. menetriesii* under *E. crotalinus* (in translation):

'N.B. In the Synopsis des Gomphines, I described under the name of *Ophiogomphus? Menetriesii* an incomplete male individual, which was communicated to me a long time ago by the knowledgeable M. Menetries. Now, I am inclined to believe that this is not a species distinct from *crotalinus.*

One reason that made me suppose the species different, was its occurrence in *Brazil,* but it was still necessary that this fact be duly confirmed and that the missing anal appendages be known.

This ♂ is a little smaller than our specimens [the presently described males and female of *E. crotalinus*], the space around the ocelli is distinctly black, the appearance of the reddish antehumeral stripes more closely approaches the median [stripes], the humeral is more distinct and more elongated, the base of the abdomen is less swollen, the dorsal yellow stripe of 3rd, 4th, and 5th segments seems modified: it consists of spots of three lobes [each], whose posterior isn't visibly narrowed into a little round head. (This note is based on diagnosis and a description made a long time ago, so that I have not been able to compare the specimen since I have had *crotalinus* at hand.)

A female, same indication of origin [Brazil] from the Mus. St. Petersburg, communicated to M. Hagen by M. Menetries differs very slightly from *crotalinus* by the following: 6 cells under the pterostigma.; costa yellower, tarsi black, the first article [tarsomere] of the posterior [leg] yellow, black tibiae bilineated with yellow outside; femora yellow with a double black external line shorter and finer at the ends. Abdomen thicker, marked with black; 9th segment black above with a dorsal round spot, touching the posterior margin. [Abdominal segment] 10 and appendages light red, the end of these last [structures] pale *not marked with black* [italics are Selys']. Vertex more black. Dimensions a little more robust.

Not being certain of its identity, I fear to cause confusion later by putting the name *E. menetriesii* in true *crotalinus* from Mexico, even though I have already published this name [*menetriesii*] in speaking of another species (page 102 Revue des Odonates, 1850; and Synopsis des Gomphines, 1854).

If its identity is confirmed, it would be necessary to replace the name of *E. crotalinus* with that of *E. Menetriesii.*'.

Finally, Selys (1878) described *Herpetogomphus menetriesii* based on 'un mâle in complet [in MNHP]' and female [in IRSN] from Guatemala. He states: 'I believe it identical with the ♂ example described in Synopsis No. 20 [1854] and reported with doubt as *crotalinus* in the Monographie [1858].' Calvert (1905) pointed out the inconsistencies of the three descriptions and left open the question of what *E. menetriesii* really is.

According to the original description (Selys, 1854), *E. crotalinus* cannot be *E. menetriesii.* A supplementary male of *E. crotalinus* described in 1858 (in ZMHB, examined) is unusual in having faint antehumeral stripes, but no *E. crotalinus* I have examined fits the description of *E. menetriesii* of 1854 (with middorsal, antehumeral and humeral stripes).

The 1854 description is too brief to indicate what *E. menetriesii* is, and I cannot associate it with any known species. According to Hagen (1861), it was destroyed. I have been unable to trace the 1858 female described by Selys, but I was able to examine the 'pair' described in 1878. The two specimens, which have determination labels by Selys, are really two females of *E. eutainia* Calvert. However, I cannot be certain that these females are conspecific with Selys' original description of *E. menetriesii.* Selys and others apparently had difficulty in associating specimens of *E. eutainia,* because a male from Texas in the IRSN is given the manuscript name of *Erpetogomphus berus,* another female is identified as *Cyanogomphus ?mexicanus* (by R. Martin), and, of course, the two females, one in the IRSN, the other in the MNHP, are labelled as *E. menetriesii.*

Thus, the original description of *E. menetriesii* may refer to *E. eutainia,* but because no one can ever be sure of this, I propose that *E. menetriesii* should be considered a *nomen dubium.*

Biology

Little is known of the biology of the genus, though their habits as recorded in the literature mirror the behaviour of other Gomphidae. Adults are most commonly found near shores of streams and rivers, but they may also be found in agricultural stubble or on tree branches near streams. Many species are seldom encountered and only a few species appear to be common in collections.

Available notes taken from the literature, personal correspondence, and personal observations cited under various species accounts indicate that female *Erpetogomphus* oviposit by swiftly tapping the water's surface or by hovering motionless over moderately swift water systems. Details of copulation and copulation time are largely unknown, although the bizarre male and especially female morphological adaptations for achieving the tandem position in *E. tristani* have been detailed by Calvert (1912a).

Larvae of *E. designatus, E. compositus,* and *E. lampropeltis* were keyed by Needham and Westfall (1955), and illustrations and full descriptions of *E. crotalinus* and *E. lampropeltis natrix* were given by Novelo and González (1991). The larva of *E. sabaleticus* was recently described and illustrated by Belle (1992).

Table 2. Characters used in cladistic analysis of *Erpetogomphus* adults. ♂ (male) or ♀ (female) in parentheses indicates sex to which character pertains. An asterisk (*) indicates an ordered multistate character. Numbers in parentheses following character states refer to figure numbers.

Number/character	Primitive state	Derived state(s)
1. Postocciput width (♀)	tumid, convex	linear
2. Postocciput (♀)	not visible from above	visible from above
3. Occiput (♀)	semicircular	transverse
4. Vertex (♀)	with long median trough	with no trough
5. Postocellar ridge (♀)	incomplete	complete
6. Vertex:	sexually dimorphic	not sexually dimorphic
7. Frontoclypeal suture	with black	with no black
8. Hind margin of metepimeron	with black	with no black
9. Hind wing 3-celled anal loop	present	absent
10. Anterior hamule* (♂)	states 1-5 (fig. 208)	state 0 (fig. 208)
11. Posterior hamule* (♂)	states 1-4 (fig. 209)	state 0 (fig. 209)
12. Tip of posterior hamule* (♂)	states 1-5 (fig. 210)	state 0 (fig. 210)
13. Posterior lobes of penis segm. 1 (♂)	small	well developed, divided lobes
14. Penis: segment 3 dorsally (♂)	with pair of tubercles	lacking tubercles
15. Penis: segment 4 (♂)	about twice as long as wide (fig. 211)	about as long as wide (fig. 211)
16. Prepuce of penis* (♂)	states 1-3 (fig. 212)	state 0 (fig. 212)
17. Lateral lobe of penis-shape* (♂)	states 1-5 (fig. 213)	state 0 (fig. 213)
18. Membranous hood of penis (♂)	not overlapping distally	overlapping
19. Shape of cornua of penis* (♂)	states 1-6 (Fig. 214)	state 0 (fig. 214)
20. Development of cornua of penis* (♂)	reduced (1), absent (2)	present (fig. 214)
21. Length of vulvar lamellar plates (♀)	about 0.25 length of sternite	≥ 0.50 length of sternite
22. Medial margins of vulvar lamina (♀)	folded under	not folded under
23. Postlamellar ridge (♀)	Y-shaped	semicircular
24. Postlamellar ridge with juncture (♀)	posterior to plates (e.g. figs. 184, 195)	at or before margin of plates (fig. 192)
25. Ventral base of cercus (♂)	with large blunt tooth	with no tooth (fig. 94).
26. Ventral base of cercus (♂)	with no carina	with a carina
27. Distal part of cercus ventrally (♂)	with no carina	with a carina
28. Dorsal surface of cercus (♂)	with a tubercle	without a tubercle
29. Ventral surface of cercus (♂)	linear or concave	convex
30. Curvature of epiproct with tips (♂)	about parallel to base	at about 90° to base
31. Tips of epiproct (♂)	spatulate or bidentate	pointed
32. Penis segment 3 (♂)	short and stocky	longer than wide
33. Penis guard (♂)	quadrate in cross-section	circular in cross-section
34. Epiprocts (♂)	approximate and curved at distal 0.50	not approximatebarely curved
35. Spermatheca (♀)	states 1-2 (fig. 215)	state 0 (fig. 215)
36. Dorsal surface of epiproct (♂)	with dorsal spine (fig. 95)	unarmed
37. Ventral base of cercus (♂)	with pebble-like carina	otherwise (fig. 97)
38. Membranous hood of penis (♂)	partially (1) or wholly (2) exposing subcuticular membrane	completely covering subcuticular membrane
39. Ventral base of cercus (♂)	with carina ending in tooth (fig. 116)	with carina (if present) not ending in tooth
40. Postocciput (♀)	with lateral depressions (fig. 165)	with no lateral depressions
41. Occiput (♀)	with a posteriorly directed medial spine fig. 151	without a spine

PHYLOGENICS AND BIOGEOGRAPHY

Phylogenetic analysis

I have attempted to construct a cladogram based on an algorithm which infers phylogenies based on the presence of shared derived characters. Using the outgroup comparison method of Watrous and Wheeler (1981), I consider *Ophiogomphus* to be the outgroup to *Erpetogomphus*, following Carle (pers. comm.) in his assessment of gomphid dragonfly classification. In this analysis, I have used the most austral species, *O. severus* Hagen.

The genus *Erpetogomphus* has never been easily defined (Calvert 1905, Needham and Westfall 1955), these authors using a series of characters to characterize the genus. A synapomorphy apparently unique to *Erpetogomphus* is the condition of the epiprocts of the males: all have gently (at least 110°) to strongly dorsally curved, non-divergent epiprocts.

Carle (1986), in his treatment of the higher classification of the Gomphidae, included *Erpetogomphus* in the tribe Onychogomphini of the subfamily Onychogomphinae. In his key to the eight subfamilies of Gomphidae, he characterized the Onychogomphinae as follows: 1) hind femur shorter than head, 2) anal triangle typically 4-celled with small rectangular cell along inner margin, 3) anterior hamuli with shoulder and end hook forming lateral u-shaped notch, and, 4) female sternum 9 with large U- or V-shaped basal membranous area. Within this subfamily, the tribe Onychogomphini (including *Erpetogomphus*) is distinguished from the tribe Crenigomphini by the following characters (antagonistic characters for Crenigomphini in parentheses): postgenal suture present (absent), male tibial laminae present (absent), penile segment one (= peduncle) without cuplike thin-walled hood (with bilobed cuplike thin-walled hood), female sternum 9 with dome-shaped membranous area not extending to distal half of sternum (this structure extending to distal half of sternum). None of these characters is stated by Carle (1986) to be uniquely derived for any of the above categories. Carle (pers. comm.) and I agree that *Ophiogomphus* is the most likely outgroup to *Erpetogomphus*, and we agree that both should be placed in the Onychogomphini. Three characters seem unique to the New World Onychogomphini, which include only *Ophiogomphus* and *Erpetogomphus*: 1) rami of male epiprocts contiguous along all or most of their length, 2) female sternum 8 with a well-defined costate postlamellar ridge separating the soft membranous area from the posteriorly sclerotized area (this ridge reduced in *Ophiogomphus*), 3) presence of a lateral lobe on the ventrolateral margin of the fourth penile segment (fig. 213) (reduced in *Ophiogomphus*, and not specialized in the *E. ophibolus* group). This last character seems to be a unique synapomorphy for *Ophiogomphus* and *Erpetogomphus*.

Carle (1992) further separated *Erpetogomphus* into three subgenera, two of which were new: *Calogomphus* (type species *E. eutainia*) and *Erpetocyclops* (type species *E. ophibolus*). Both Carle (pers. comm.) and I consider *Erpetogomphus* to be composed of three monophyletic groups as discussed below. While several earlier versions of my cladogram using series of characters and different states generally support a conservative grouping of the genera into three monophyletic groups, I do not think it necessary to provide subgeneric rank to those groups.

A suite of 41 characters, 7 of which are multistate (table 2), was analyzed using the HENNIG86 computer program (Farris, 1988), with the following options: The character set was first run using the ie* (guaranteed to find the most parsimonious trees) option where all characters were ordered and each was equally weighted (default options). All autapomorphies were included from this analysis. The final set of 41 characters was finally chosen from larger sets, each with different coding sequences, because this set seemed to be the most heuristic. The resultant analysis yielded six equally parsimonious trees. A Nelsen (consensus) tree (length 106, consistency index 0.62) was then generated from the six trees. The resultant characters, tree, and matrix are shown in figs. 208-216, and tables 2-3. As this manuscript was in review, Jan van Tol kindly ran the same data set on PAUP 3.1.1 for the Macintosh (Swofford 1993) using unordered as well as ordered sequence of multistate characters. His results, which he kindly communicated to me, resulted in 61 semistrict consensus trees each with a length of 94 for unordered multicharacter states. His resulting cladogram is similar to that in fig. 216 except that the entire *E. crotalinus* group (except for three sister groups: *E. elaphe* and *E. elaps*; *E. sipedon* and *E. lampropeltis*; and *E. boa* and *E. cophias*) collapses to a polytomious assemblage. (I recorded a similar cladogram when multistate characters were listed as unordered for HENNIG86.) When all multistate characters were run as ordered on PAUP 3.1.1, the resulting cladogram was the same as shown for fig. 216.

I have not been totally successful in resolving several of the terminal clades, due to high degree of apparent homoplasies. The best characters are those of the secondary genitalia of the male (hamules, penis); but, despite a thorough examination of these structures, I am still uncertain of the correct interpretation of character polarity for several of these complex, multistate character sets (figs. 208-210, 213-214). Little difficulty was encountered in assigning states to members of the *E. ophibolus* and *E. eutainia* groups, and their generalized tracks also independently supplement in understanding their phylogeny; but the same characters in males of the *E. crotalinus* group show, if my cladogram is correct, a bewildering complex of character reversals for some characters. The generalized tracks within the *E. crotalinus* group (fig. 226) also provide few clues to possible speciation events, except for that between the *E. elaps* and *E. crotalinus (*s.s.*)* groups.

Individual clades are numbered as shown in fig. 216, each of which is discussed below.

Clade 1.1. – ***E. ophibolus*** group (six species: ***E. constrictor, E. sabaleticus, E. tristani, E. ophibolus, E. agkistrodon, E. schausi***) = subgenus *Erpetocyclops* Carle

Character 3. – female occiput semicircular (parallel development in Clade 1.22112, *E. liopeltis*)

Character 5. – female postocellar ridge incomplete (parallel development in Clade 1.211, *E. leptophis*)

Character 6. – vertex sexually dimorphic (state not known for male *E. agkistrodon*, but probably follows for other members of this clade)

Character 11, state 1. – male with posterior hamule triangular (fig. 209)

Character 12, state 1. – male with tip of posterior hamule acuminate (fig. 210)

Character 16, state 1. – male with prepuce well-developed (fig. 212)

Character 17, state 1. – male with lateral lobe vestigial, broadly angulate with no serrations (fig. 213)

Clades 1.11 (*E. constrictor, E. sabaleticus, E. tristani, E. ophibolus*), 1.12 (*E. agkistrodon*), 1.13 (*E. schausi*). Clade 1.11 is defined by the following synapomorphies:

Character 20, state 2 - male with loss of cornuae of penis (fig. 214). Most Gomphidae (including the outgroup, *Ophiogomphus severus*), have a pair of long, strap-like cornuae. I have hypothesized the character transformation for this structure throughout the genus (fig. 214).

Character 25. – ventral base of cercus of male with large blunt tooth (fig. 94)

Character 28. – dorsal surface of cercus of male with a tubercle (fig. 94)

I have found no synapomorphy for uniting 1.12 (*E. agkistrodon*) and 1.13 (*E. schausi*). The former is known only from the holotype female, the latter by two males and a teneral female.

Clades 1.111 (*E. constrictor*), 1.112 (*E. sabaleticus*), 1.113 (*E. tristani*)

Character 29. – curvature of epiproct of male with tips completely recurved so as to lie parallel to base

Clade 1.21. – *E. eutainia* group (two species: ***E. eutainia, E. leptophis***) = subgenus *Calogomphus* Carle

Character 10, state 1. – anterior hamule with equally divided arms (fig. 52-53, 208) at distal 0.25

Character 11, state 2. – posterior hamule digit-shaped (fig. 209)

Character 14. – dorsal surface of third segment of penis of male with two tubercles

Character 16, state 2. – prepuce of male reduced, largely hidden by frill-like lateral lobe (fig. 212)

Character 17, state 2. – lateral lobe of penis of male frill-like (fig. 213)

Character 35, state 1. – spermatheca of female a single tube (fig. 215). I was only able to study this structure in *E. eutainia*, as only the allotype of *E. leptophis* is known. Due to other synapomorphies listed above, I hypothesize that *E. leptophis* will possess single, rather than paired, spermatheca.

Clade 1.22. – *E. crotalinus* group (13 species: ***E. elaphe, E. elaps, E. liopeltis, E. bothrops, E. viperinus, E. designatus, E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias***) = subgenus *Erpetogomphus* Hagen *in* Selys

Character 16, state 3. – prepuce of penis of male lacking

Character 35, state 2. – spermatheca of female paired, each forming a long, narrow sac (fig. 215)

Clade 1.221. – *E. elaps* subgroup (five species: ***E. elaphe, E. elaps, E. liopeltis, E. bothrops, E. viperinus***)

Character 17, state 3. – unique shape of lateral lobe (fig. 213)

Clade 1.2211 (*E. elaphe, E. elaps, E. liopeltis, E. bothrops*)

No satisfactory synapomorphy has been found for this clade. One character, the spatulate tip of the epiproct (fig. 129) separates *E. viperinus* from its sister species.

Clade 1.22111 (*E. elaphe, E. elaps, E. liopeltis*)

No synapomorphy has been found, but the transverse condition of the female postocciput in *E. bothrops* and in *E. viperinus* (fig. 166) split *E. bothrops* from the other three sister species.

Clade 1.221111 (*E. elaphe, E. elaps*)

Character 22. – vulvar lamina of female with margin folded under ventrally (figs. 180- 181)

Clade 1.222 (*E. designatus, E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*)

No satisfactory synapomorphy has been found to unite the *E. crotalinus* group (*sensu stricto* [s.s.]). The one aberrant species in the group is *E. designatus.* It alone has the following characters which separate it from the other 7 species: 1) tip of posterior hamule lacking a tooth (recurrence of this state from the *E. eutainia* group) and 2) unique shape and position of the lateral lobe (fig. 82). The shape of the anterior hamule of *E. designatus* (fig. 60) is, however, like that of *E. sipedon, E. lampropeltis, E. crotalinus,* and *E. compositus,* which thus unites these species into a clade.

The widely distributed *E. designatus* has been difficult to place cladistically in this study. It combines characters of the *E. elaps* group (for example, linear condition of lateral lobe and acuminate condition of the cornua) and even apomorphic characters common to the *E. crotalinus (*s.s.*)* group as noted above.

Clade 1.2222 (*E. sipedon, E. lampropeltis, E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*)

Character 12, state 5. – tip of posterior hamule of male with anteapical tooth

Character 17, state 5. – unique shape of lateral lobe of fourth segment of penis of male (fig. 213). The small, semicircular condition of the lateral lobe present in Clade 1.2222 is similarly developed in Clade 1.12 (*E. schausi*).

Clades 1.22221 (*E. sipedon*), 1.22222 (*E. lampropeltis*), and 1.22223 (*E. crotalinus, E. heterodon, E. compositus, E. boa, E. cophias*)

No satisfactory apomorphy has been found to dichotomize these clades. The distinctive shape of the cornuae of *E. sipedon* and *E. lampropeltis* (figs. 83-85) has separated these two species from clade 1.22223.

Table 3. Character matrix used in producing Nelsen (consensus) tree shown in Fig. 216.

Character No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Ancestor	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Oph. severus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
constrictor	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	1
sabaleticus	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	1
tristani	1	1	1	1	1	1	1	1	0	0	1	1	1	0	0	1	1	1	1
ophibolus	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	1	1	1
agkistrodon[1]	0	0	1	0	1	1?	1	1	0	0?	1?	1?	1	0	0	1?	?	1?	?
schausi	1	1	1	0	1	1	1	1	0	0	1	1	1	0	0	1	5	1	1
eutainia	0	1	1	0	0	0	1	1[2]	0	1	2	2	1	1	0	2	2	1	1
leptophis	1	1	0	0	1	0	1	1	0	1	2	2	1	1	0	2	2	0	1
elaphe	1	0	0	0	0	0	0	0	0	3	3	2	1	0	1	3	3	1	2
elaps	1	0	0	0	0	0	0	0	0	2	3	5	1	0	1	3	3	1	2
liopeltis	1	1	1	0	0	0	0	0	0	2	3	4	1	0	1	3	3	1	2
bothrops	0	1	0	0	0	0	0	0	0	2	3	5	1	0	1	3	3	1	2
viperinus	0	1	0	0	0	0	0	0	0	2	3	3	1	0	1	3	3	1	2
designatus	0	1	0	0	0	0	0	0	0	4	3	2	0	0	1	3	4	0	2
sipedon	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1	3
lampropeltis	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1	3
crotalinus	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1	4
heterodon	0	1	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1	5
compositus	0	0	0	0	0	0	0	0	0	4	3	5	1	0	1	3	5	1	5
boa	1	1	0	0	0	0	0	0	0	5	4	5	1	0	1	3	5	1	6
cophias	1	0	0	0	0	0	0	0	0	5	4	5	1	0	1	3	5	1	6

[1] Only the holotype ♀ is known for this species. Male characters were scored as ? (unknown), on 0? or 1?, based on affinity with rest of the *E. ophibolus* group. [2] Character prevalent in this species. [3] Basal carina weak in *E. boa.*
[4] This structure not examined for this species. Plesiomorphy/apomorphy hypothesized by examination of spermatheca in closely related species, and placement of these taxa in cladogram due to other synapomorphies.

Clades 1.222231 (*E. crotalinus*) and 1.222232 (*E. heterodon, E. compositus, E. boa, E. cophias*)

No satisfactory apomorphy has been found for clade 1.222232. *Erpetogomphus crotalinus* was separated because of the unique shape of its cornuae (fig. 86).

Clades 1.2222321 (*E. heterodon*), 1.2222322 (*E. compositus*), 1.2222323 (*E. boa, E. cophias*)

The unique shape of the cornua (figs. 87-89) has segregated *E. heterodon* and *E. compositus* from clade 1.2222323. Apomorphies for the last clade, representing the two closely related species, *E. boa* and *E. cophias,* are:

Character 10, state 5. – unique shape of the anterior hamule of male (fig. 208)

Character 11, state 4. – unique shape of the posterior hamule of male (fig. 209)

Character 19, state 6. – unique shape of the cornua of male (fig. 214)

The clades mentioned above have problems primarily within the *E. crotalinus* group (*sensu lato,* [*s.l.*]), and most dichotomies are based on one or two highly complex character states of the penis. I realize that my interpretation of the morphoclines of this character is open to reevaluation, which could result in a somewhat different shuffling of some species within the larger group. Only two species in this group, *E. boa* and *E. cophias,* are easily characterized as a monophyletic group.

A further analysis to resolve some of the difficulties described above will have to await further specimens and a proper analysis of their larvae. As stated earlier, I have not assigned formal names to subordinate clades, because further investigation may involve transfer of some monophyletic or paraphyletic groups to other clades, nor can I see any purpose in a proliferation of infrageneric names.

Cladospecies

Of the 21 species described here, seven (33%) can be defined by autapomorphies and can be termed cladospecies (Ackery and Vane-Wright, 1984). These cladospecies with their uniquely derived character states are shown below.

Clade 1.112. *E. ophibolus.* Character 36, dorsal surface of epiproct of male with a dorsal spine (fig. 95)

Clade 1.211. *E. leptophis.* Character 41, female occiput with a posteriorly directed medial spine (fig. 151)

Clade 1.212. *E. eutainia.* Character 37, ventral base of cercus of male with a pebble-like carina.

Clade 1.2211112. *E. elaphe.* Character 10, state 3,

22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
0	1	1	1	0	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0
0	1	1	1	0	1	1	0	1	1	1	1	1	0	0	0	0	0	0	0
0	1	1	1	0	1	1	1	1	1	1	1	1	0^4	0	0	0	0	0	0
0	1	1	1	0	1	1	1	0	0	1	1	1	0^4	1	0	0	0	0	0
0	1	0	0?	0	1?	0?	1	0	1	1	1	1	0	0	0	0	0	0	0
0	1	1	1	0	1	0	1	0	1?	1	1	1	0?	0	0	0	0	0	0
0	0	1	0	0	0	0	1	0	1	1	1	1	0^4	0	1	0	0	0	0
0	0	1	0	1	0	0	1	0	1	1	1	1	1	0	0	0	0	0	1
1	1	0	0	1	1	0	1	0	1^2	1	1	1	1^4	0	0	0	0	0	0
1	1	0	0	1	1	0	1	0	1	1	1	1	2^4	0	0	0	0	0	0
0	1	0	0	1	1	0	1	0	1	1	1	1	2	0	0	0	0	0	0
0	1	0	0	1	1	0	1	0	1	1	1	1	2^4	0	0	0	0	0	0
0	1	1	0	1	1	0	1	0	0	1	1	1	2	0	0	0	0	0	0
0	1	0	0	0	0	0	1	0	1	1	1	1	2	0	0	0	0	0	0
0	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	2	0	0	0
0	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0
0	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0
0	1	0	0	0	0	0	1	0	0	1	1	1	2	0	0	0	0	0	0
0	1	0	0	0	0	0	1	0	1	1	1	1	2	0	0	1	0	0	0
0	1	1	0	1^3	1	0	1	0	0	1	1	1	2	0	0	0	0	0	0
0	1	1	0	0	0	0	1	0	1	1	1	1	2^4	0	0	0	1	1	0

unique shape of anterior hamule of male (fig. 208)

Clade 1.22221. *E. sipedon.* Character 38, state 2, membranous hood of penis of male wholly exposing subcuticular membrane.

Clade 1.2222322. *E. compositus.* Character 38, state 1, membranous hood of penis of male partially exposing subcuticular membrane.

Clade 1.22223232. *E. cophias.* Character 39, ventral base of cercus in male with carina ending in tooth (fig. 116), and Character 40, postocciput of female with lateral depression (fig. 165). These two characters are probably correlated: I hypothesize that the postoccipital depressions of the female receive the inferior carinal tooth of the cerci of the male during copulation.

I have been unsuccessful in finding autapomorphies for the 14 other species, and they can be termed paraspecies (Ackery and Vane-Wright, 1984). A further, more detailed analysis of these species may yield autapomorphies. The cladist may question the status of species recognized by single or combinations of plesiomorphic characters, but I agree with Ackery and Vane-Wright (1984: 10), who cogently argue: 'the traditional groupings often (but by no means always) turn out to be good. The cladist must, therefore, always retain respect for the 'Gestalt' approach (especially when practised by field workers), unless armed with concrete evidence for some contrary arrangement.'.

Distribution patterns

Table 4 details the distributional patterns of all New World Gomphidae according to five political regions: Canada/Alaska, U. S. A., Mexico, Central America, and South America. All speciose (*i.e.*, N ≥ 3 species) gomphid genera in the New World have proportionally more species in the United States and in South America than *Erpetogomphus. Erpetogomphus* has the most species in Mexico (76%). Central America follows with 48%, the United States with 24%. No other genus is proportionally as speciose in Mexico. The *Gomphus* complex of genera (*Arigomphus, Gomphus* and subgenera, *Stylurus*), and *Ophiogomphus* are dominantly North American, and several genera (*Agriogomphus, Aphylla, Archaeogomphus, Cyanogomphus, Gomphoides, Neogomphus, Phyllocycla, Phyllogomphoides, Progomphus,* and *Zonophora*) are South American. *Epigomphus* is most speciose in Central America, where 46% of all described species occur, closely followed by South America.

Figure 217 shows the density and approximate overall distribution of species of *Erpetogomphus* as shown by 150 km squares. Of the five species found in the United States, most are found in the southwestern states. The most northerly distribution for the genus is Grant County, Washington (46°50'N), for *E. compositus* (Paulson and Garrison, 1977). The greatest concentration in species is in south-central Mexico between approximately 18°-20°N with eight species (31%) of all the total number of species in the genus found in southern Veracruz alone.

Descriptive biogeography

In this section I describe the current distribution range (= tracks) of various monophyletic groups based on my cladogram. Unfortunately, the numerous problems associated with the cladistic analysis concomitant with the poorly known or spotty distributions (most of which may be due to inadequate collecting in parts of Mexico) preclude a discussion of vicariance biogeography. However, I do discuss possible speciation sequences within the *E. ophibolus* and *E. eutainia* groups.

The cladogram (fig. 216) for *Erpetogomphus* divides the 21 known species into three monophyletic groups. The generalized track for the genus is shown in fig. 218. The first two groups, the *E. ophibolus* and *E. eutainia* groups, have generalized tracks encompassing south Texas, eastern Mexico south into northern Colombia and Venezuela (figs. 219-220). The *E. ophibolus* group comprises six closely related species united by seven derived character states. Figure 221 shows that the distribution of all six species except *E. schausi* are largely allo- or parapatric. Little can be said of *E. agkistrodon* or *E. schausi* due to paucity of records. *Erpetogomphus ophibolus* occupies an area between two disjunct populations of *E. constrictor*. Further collecting may show *E. constrictor* to be sympatric or parapatric with *E. ophibolus*. Aside from *E. agkistrodon* and *E. schausi*, the track of *E. ophibolus* was probably the first to separate from the *E. ophibolus* group, a hypothesis consistent with the results of my cladogram (fig. 216). The three remaining species, *E. constrictor*, *E. tristani*, and *E. sabaleticus*, are closely related sister taxa whose tracks are largely parapatric. Presumably their differentiation (by allopatric speciation?) took place from a common ancestor which occupied part of the present range of all three species.

The tracks of the second monophyletic group comprises just two species, the relatively widespread *E. eutainia* and the peripheral *E. leptophis* (fig. 222). The latter, known only from the holotype and allotype from Belize, is sympatric with *E. ophibolus*, but its genealogical affinities are unquestionably with *E. eutainia* (fig. 216). *Erpetogomphus leptophis* probably arose as a peripheral isolate from *E. eutainia*, or from a common ancestor, since it is a more apomorphic species than *E. eutainia*.

The remaining 13 species comprise two monophyletic subgroups, one predominantly austral, the other more boreal. Their generalized tracks are shown in figs. 223-226. The *E. elaps* subgroup contains five species, whose somewhat limited distributions occupy the western and eastern lowlands of Mexico south along the mountainous areas into Costa Rica. *Erpetogomphus elaps* and *E. elaphe* are closely related sister species which are parapatric in Guatemala. A slight but consistent southern variant of *E. elaps* occupies the area between more northerly typical populations of *E. elaps* and *E. elaphe* (see discussion under *E. elaps*): it may be an incipient species. These two (or three?) species, like those for *E. constrictor, E. tristani*, and *E. sabaleticus*, probably arose from an *E. elaps*-like ancestor or from one another. Interpretations of the tracks of the remaining three species is problematical due to the uncertain position of *E. liopeltis* in my cladogram. It possesses characters common to *E. bothrops* and *E. viperinus*. No convincing apomorphy unites *E. liopeltis* with the sister taxa *E. elaps* and *E. elaphe*, so its genealogical relationship must remain in doubt. The two species with the greatest ranges (*E. elaps* and *E. bothrops*) are broadly sympatric; *E. liopeltis* and *E. viperinus* are allopatric.

The *E. crotalinus* (s.s.) subgroup comprises the boreal group of eight species, with at least one representative occurring throughout most of the southern half of the United States. Their complex, mostly overlapping distributions (fig. 226) and questionable phylogenetic sequence in the cladogram preclude any meaningful discussion on their biogeography. *Erpetogomphus boa* and *E. cophias* stand out because of three synapomorphies. Their limited distribution and close proximity indicate speciation, possibly by allopatric means. *Erpetogomphus sipedon* and *E. heterodon* make up the only other allopatric species pair in this complex subgroup. Although distribution of *E. heterodon* and *E. compositus* overlap, I have seen no evidence of these two species collected together.

It is obvious that a more thorough knowledge of the phylogeny of the genus will be necessary before interpretation of biogeographical events is possible. Of particular interest will be a methodological interpretation of the biogeography of the genus, for then we may be able to determine which species tracks are the result of dispersal and gene flow or vicariant events.

Characters

The best diagnostic characters for males are found in the caudal appendages, accessory genitalia, and overall body maculation. Most species are easily identified by the caudal appendages. The cerci (superior appendages) assume a wide variety of shapes (figs. 92-

Table 4. Distribution of species of New World Gomphidae. Number under each region = area of region in square miles; % directly under area = % of total land area; N = total number of species; number under each region = total number of species; number in parentheses () = percent of total number of species in genus. Phylogenetic classification is after Carle (1986). Genera are arranged alphabetically under each tribe.

Genus	N	Canada/Alaska 4,438,221 mi^2 29.5%	U.S.A.[1] 3,022,261 mi^2 20.2%	Mexico 761,530 mi^2 5.2%	Cent. Amer.[2] 208,800 mi^2 1.1%	South Amer. 6,597,386 mi^2 43.9%
Hageniinae						
Hagenini						
Hagenius	1	1 (100)	1 (100)			
Octogomphinae						
Hemigomphini						
Neogomphus	3					3(100)
Octogomphini						
Lanthus	2	1 (50)	2 (100)			
Octogomphus	1	1 (100)	1 (100)	1 (100)		
Stylogomphus	1	1 (100)	1 (100)			
Gomphinae						
Gomphini						
Arigomphus	7	3 (43)	7 (100)			
Dromogomphus	3	1 (33)	3 (100)			
Gomphus[3]	38	13 (34)	38 (100)	1 (3)		
Stylurus	13		12 (92)	4 (31)		
Epigomphinae						
Epigomphini						
Epigomphus	26	6 (23)	12 (46)	10 (38)		
Austrogomphinae						
Archaeogomphini						
Archaeogomphus	5			1 (20)	1 (20)	5 (100)
Cyanogomphini						
Agriogomphus	4			1 (25)	1(25)	3 (75)
Cyanogomphus	6					6(100)
Tibiagomphus	2					2(100)
Onychogomphinae						
Onychogomphini						
Erpetogomphus	21		5 (24)	16 (76)	10 (48)	1 (5)
Ophiogomphus	18	8 (44)	18 (100)			
Lindeniinae						
Gomphoidini						
Aphylla	19[4]		3 (16)	2 (11)	3 (16)	18 (95)
Gomphoides	3					3 (100)
Idiogomphoides	2					2 (100)
Peruviogomphus	2					2 (100)
Phyllocycla	31			3 (10)	4 (13)	27 (87)
Phyllogomphoides	43		2 (5)	12 (28)	7 (17)	27 (63)
Lindeniini						
Cacoides	1					1 (100)
Melanocacus	2					2 (100)
Mitragomphus	1					1 (100)
Progomphini						
Progomphus	59[5]		4 (7)	9 (15)	7 (12)	52 (77)
Zonophorini						
Desmogomphus	2				1 (50)	2 (100)
Diaphlebia	2					2 (100)
Perigomphus	1				1 (100)	1 (100)
Zonophora	10					10 (100)
TOTAL	329	35 (10.6)	97 (29.4)	50 (15.2)	47 (14.3)	180 (54.7)

[1] Excluding Hawaii; [2] Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica, Panama; [3] Includes subgenera *Gomphurus, Gomphus, Phanogomphus, Stenogomphurus;* [4] One species, *A. caraiba,* is endemic to Hispaniola and Cuba, not included in N; [5] Three species, *P. integer, P. serenus, P. zephyrus,* are endemic to the Greater Antilles, not included in N.

116), but they are never longer than segments 9 and 10 combined. All males of the *E. ophibolus* group, except for *E. schausi* (and possibly the unknown male of *E. agkistrodon*) have a dorsal appendage on the distal third of the cercus. The dorsal surface of the cercus may be straight as in *E. elaps*, strongly curved as in *E. schausi* and *E. viperinus*, angulate as in most species in the *E. crotalinus* group, or concave as in the *E. boa* and *E. cophias* group. The inferior third of the cercus forms a strong carina in *E. cophias* (weakly so in *E. boa*), in the *E. crotalinus* group, and in *E. eutainia*. In the lighter coloured species of the *E. crotalinus* group, the carina does not contrast with the rest of the appendage. A unique series of pebble-like structures characterizes the basal carina in *E. eutainia*. The inferior carina was used by Calvert (1905), although he wrongly placed *E. eutainia* among individuals lacking such a carina. Instead of a basal carina, the *E. ophibolus* group, *E. bothrops* and *E. viperinus* have an inferior carina on the distal third of the appendage. This structure is weak in *E. elaps*.

The epiprocts (inferior appendages) are not as varied as the cerci. In most of the *E. ophibolus* group, they are strongly curved so that their distal third is nearly parallel to the basal 0.30. The epiproct of *E. ophibolus* is unique in having an anteriorly directed projection on its dorsal surface near the middle. The epiprocts are remarkably similar throughout the remaining groups: they form a gentle curve with the tips at approximately 90° to the basal third of the appendage.

The penes of most species possess a semi-hyaline pair of flagella or cornuae best seen in dorsal view. The cornuae are considerably reduced in the *E. ophibolus* group (except for *E. schausi*). Their shape provides a useful character to differentiate among *E. designatus*, *E. compositus*, and *E. lampropeltis*. The tip of each cornua is bluntly rounded in the *E. crotalinus* group (except for *E. crotalinus*). In all others, the tip forms a sharp point.

The spiny lateral lobes of the penis are well developed and frill-like in *E. eutainia* and *E. leptophis*, primarily knife-like or pointed in *E. viperinus*, *E. liopeltis*, *E. bothrops*, *E. elaps*, and *E. elaphe*, and a protruding semicircle in most members of the *E. crotalinus* and *E. cophias* groups. When the penis is viewed laterally, the lateral lobe is on edge, because this structure rotates posteriorly with its flat portion placed mediodistally. The lateral lobes are poorly developed in *E. constrictor*, *E. tristani*, and *E. sabaleticus* (possibly also in *E. agkistrodon*), but those species and *E. schausi* have a unique ventral, arcuate prepuce.

The anterior hamules are always divided, but the posterior arm in the *E. tristani* group forms more of a shoulder than a branch. The bifurcation occupies the distal 0.25 of the hamule in the *E. ophibolus*, *E. elaps*, and *E. eutainia* groups, the distal 0.50 in the *E. crotalinus* group, and the entire length of the appendage in *E. boa* and *E. cophias*.

The posterior hamules are always more prominent than the anterior pair. They are broadly triangular in the *E. ophibolus* group, but they possess an anterior shoulder in the *E. crotalinus* group. In *E. eutainia* and *E. leptophis*, the posterior hamule forms a small finger-like appendage. All known species except *E. designatus*, *E. elaphe*, *E. leptophis*, and *E. eutainia* possess a black apical tooth. This distal tooth is rotated laterally in *E. viperinus* and in some *E. bothrops*.

The best structural characters for separating the females are those associated with the vertex, occiput, postocciput (note: my use of the term, 'postocciput' is *not* equivalent to the structure immediately surrounding the occipital foramen, but, instead refers to the medioposterior side of the head behind and below the occipital crest), and vulvar lamina. Calvert (1905) relied on the curvature of the posterior border of the occiput, but it is variable within species. I do not use it here. Better characters are the shapes of structures on the vertex. In *E. constrictor*, *E. tristani*, and *E. sabaleticus*, the median ocellus is placed within a deep longitudinal trough which accommodates the strongly curved epiproct of the male. In all other species may be found a transverse trough (figs. 145-146) or a pair of anterolateral pits (fig. 137) anterior to the median ocellus. These pits correlate with the shape of the tip of the male epiproct, and these depressions are also present on the vertex of males. Their shape is useful in distinguishing between the closely related pairs, *E. viperinus* and *E. bothrops*, and between *E. compositus* and *E. lampropeltis*. A complete postocellar ridge is present only in all members of the *E. tristani* group and *E. leptophis*. In all others, the middle part of the ridge is lacking, leaving only postocellar tubercles. Females of a few species have autapomorphic characters, such as the raised median area of the occiput of *E. designatus* (figs. 156-157), the posteriorly directed pointed protuberance on the occiput of *E. leptophis* (fig. 151) or the postoccipital depressions of *E. cophias* (fig. 165).

The vulvar laminae vary in the shape of the plates. The simple horizontal plates are bisected by a small V-shaped cleft in the *E. ophibolus* group. The plates are corrugated and more membranous in *E. boa* and *E. cophias*, often succumbing to much post mortem distortion. In the *E. crotalinus* group, each plate is a large, rectangular, planar structure which meets the other only at the anterior angle. The resulting median cleft is only a third or less the width of each plate; but the cleft is wider and U-shaped in *E. designatus*. A further widening of the cleft is evident in the *E. elaps* group. The plates form two small, widely separated, digit-like structures in *E. eutainia* and *E. leptophis*.

A Y-shaped postlamellar ridge is found posterior to the vulvar lamina. The posterior stem of the Y is absent in *E. eutainia* and *E. leptophis*, so that the ridge forms a semicircle (figs. 178-179).

I have found no structural differences between the females of *E. heterodon* and *E. sipedon*. Body pattern must be used to differentiate females of those species. *Erpetogomphus tristani* and *E. sabaleticus*, and *E. elaphe* and *E. elaps* are also closely related pairs, and their females are distinguishable only by locality.

In well-preserved specimens, body maculation provides useful characters. Dark thoracic maculation predominates in the *E. tristani* group, in *E. leptophis*, and in southernmost specimens of *E. eutainia*. All of those have a well-defined dark stripe bordering the posterior margin of the metepimeron. *Erpetogomphus cophias*, *E. crotalinus*, and most *E. elaps* have nearly immaculate body patterns. Thoracic maculation is usually stable, but there is variability in *E. lampropeltis*, *E. compositus*, *E. designatus*, *E. elaps*, and *E. eutainia*. Two formerly named species, *E. natrix* and *E. coluber*, I consider subspecies of *E. lampropeltis* and *E. compositus*, respectively: I have found no morphological characters which separate those forms. Thoracic patterns in *E. elaps* are often nearly absent (fig. 13), and more extensive dark markings characterize populations of *E. eutainia* in the north, less extensive in the south (figs. 7-9).

Abdominal patterns are characterized by a combination of light and dark banding patterns separated dorsally by pale longitudinal stripes. The least amount of black occurs in *E. cophias* and *E. crotalinus*, the most in *E. agkistrodon*.

A sharp, prominent, middorsal posterior spine on abdominal segments 8 and 9 is found in many males of *E. ophibolus*, *E. bothrops*, *E. liopeltis*, and *E. viperinus*. The spine is variable and cannot be used reliably to distinguish among species. For example, many *E. bothrops* have no indication of a middorsal spine, but it is well developed in others. The spines are also found on abdominal segment 9 in some females of the *E. ophibolus* group.

Erpetogomphus species groups

I divide the 21 species into five groups. I believe the unknown male of one species (*E. agkistrodon*) will follow those characters listed for that sex discussed below.

1. *E. ophibolus* group (= subgenus *Erpetocyclops* Carle, 1992). Males (probably so for *E. agkistrodon*, when discovered): With a distinct curved prepuce, posterior hamule forming a triangle culminating in a sharp black tooth. Females: Vulvar lamina simple, small, relatively undifferentiated postocellar ridge complete, though curved in *E. tristani*, *E. sabaleticus*, and *E. constrictor*. Six species: *E. tristani*, *E. sabaleticus*, *E. constrictor*, *E. ophibolus*, *E. agkistrodon*, *E. schausi*.
2. *E. eutainia* group (= subgenus *Calogomphus* Carle, 1992). Males: Prepuce small, obscured by lateral lobes of penis; lateral lobes of penis strongly developed, forming a spiny frill; posterior hamule finger-like, lacking an apical tooth. Reduced prepuce present. Females: Vulvar lamina small, finger-like, widely separated; post-laminar ridge semicircular, not Y- shaped. Two species: *E. leptophis*, *E. eutainia*.
3. *E. elaps* group. Males: Lateral lobe of penis knife-like. Females: Vulvar lamina connected anteriorly, but separated by a cleft 1.0 or more the width of each plate. Five species: *E. bothrops*, *E. liopeltis*, *E. viperinus*, *E. elaphe*, *E. elaps*.
4. *E. crotalinus* group. Males: Superior surface of cercus angulate (except for *E. compositus*); anterior hamule divided at distal half. Females: Vulvar lamina large, planar, rectangular, meeting at anterior margins only, resultant cleft one third the width of each plate (except for *E. designatus*). Six species: *E. crotalinus*, *E. lampropeltis*, *E. compositus*, *E. heterodon*, *E. sipedon*, *E. designatus*.
5. *E. cophias* group. Males: Anterior hamule talon-like, divided along its full length; posterior hamule broadly spatulate, surmounted by a small, black, curved anteapical tooth. Females: Vulvar lamina diagonally corrugated; distal and lateral margins with a strongly raised semicircular ridge. Two species: *E. boa*, *E. cophias*.

SYSTEMATIC PART

Introduction

Under each species, I have endeavoured to include a complete synonymy (some minor references may be lacking for *E. designatus*, a common species in the eastern United States), a full description, type data, diagnosis, remarks, biology, distribution, and material examined. For new species, I have designated allotypes when the opposite sex was available, but I have not established allotypes for syntypic material. Under comments, I have quoted older authors (Ris, Selys, Hagen), when this information contributes to the history of the species. For *E. agkistrodon*, I include a discussion of what the male should be like, based on my cladogram. Unless otherwise stated, measurements are taken from 20 males and 20 females, when available, and from as many localities as possible. Abdominal measurements include caudal appendages. Full locality data are given for all species, except for the following species where abundant material was available: *E. eutainia, E. elaps, E. viperinus, E. designatus, E. l. lampropeltis, E. l. natrix, E. crotalinus,* and *E. compositus*. For these species, I have listed states, counties, brief data, and repository. Full locality data for these specimens are available from me. Maps represent distribution records from collections. For some common and well known species (such as *E. bothrops*, *E. compositus*, *E. crotalinus*, *E. designatus*), I include records from published sources I consider reliable.

Abbreviations for figure legends and synonymies are: abd. = illustration(s) of abdomen; app. = illustrations(s) of caudal appendages; cat. = listed in catalogue, descr. = description of male, female, larva, or all, may include keys; distr. = documents or mentions distribution of taxon; ept. = illustration(s) of epiproct; sep. = [page number of] separate (see Cowley (1937) for pagination of reprint of Selysian monographs and synopses of Odonata); thx. = illustration(s) of thorax; vl. = illustration(s) of vulvar laminae.

Abbreviations in descriptions are as follows: anx = antenodal crossveins, pnx = postnodal crossveins, cs = crossveins.

New names proposed in this paper follow the ophidian example set by Selys, Hagen, Calvert, and Williamson. All should be considered as nouns in apposition.

Most illustrations are from type material, which I believe will aid further researchers when describing new species. All illustrations were executed with the aid of a camera lucida with a Wild M-8 stereoscopic microscope.

Erpetogomphus Hagen in Selys, 1858

Erpetogomphus Selys, 1858 (Type species *Ophiogomphus crotalinus* [Hagen *in* Selys], 1854; designated by Kirby 1890: 61). – Selys 1858: 329 (69 sep.) (characters of genus); Selys 1859: 535 (9 sep.) (addition of generic characters); Hagen 1861: 98 (brief descr. of genus); Walsh 1863: 253 (comparison with other American gomphid genera); Brauer 1868: 372 (in key to genera of Gomphidae); Karsch 1890: 371 (mentioned in Gomphidae classification); Calvert 1905: 147 (key to Middle American Gomphidae); Calvert 1909: 468 (distr.); Calvert 1912a: 289 (distr. of genus); Kennedy 1917a: 544 (comments on larvae); Tillyard 1917: 296 (distr.); Ris 1921: 343 (comparison with *Mesogomphus* [= *Paragomphus*]); Garman 1927: 125 (note on genus); Needham and Heywood 1929: 78 (descr.); Byers 1930: 52 (descr.); Cowley 1934: 241 (nomenclature of *Erpetogomphus*); Tinkham 1934: 218 (comments on distr. in Tex.); Fraser 1940: 544 (possible affinities with *Onychogomphus* based on penis morphology); Needham 1941: 240 (comments on larva); Needham 1944: 172 (verification table, larva); Wright and Peterson 1944: 152 (in key to larvae of nearctic Gomphidae); Needham & Westfall 1955: 139 (treatment of genus); Pritchard & Smith 1956: 114 (key to larvae of nearctic Gomphidae, key to genera of Gomphidae); Ferguson-Beatty 1956: 369 (proventriculus of larva); Musser 1962: 13 (diagnosis of larvae); Gloyd 1963: 147 (molar structure of adult); Westfall 1984: 158 (in key to larvae of nearctic Gomphidae); Chao 1984: 79 (uncertainty of *Erpetogomphus* in subfamily Onychogomphinae); Carle 1986: 313 (characters of genus within Onychogomphini); Belle 1988: 99 (in key to neotropical genera of Gomphidae); Bridges 1991: II.17 (cat.); Novelo-G. & Peña-O. 1991: 129 (origin of *Erpetogomphus* in Mexico); Gonzalez-S. & Novelo-G. 1991: 97 (adults in Mexico); Novelo-G. & Gonzalez-S. 1991: 150 (larvae in Mexico); Belle & Quintero 1992: 93 (in key to adults and larvae of Panamanian Gomphidae); Carle 1992: 148 (key, *Erpetocyclops* subg. n. [type = *E. ophibolus* Calvert], *Calogomphus* subg. n. [type = *E. eutainia* Calvert]).

Herpetogomphus Walsh, 1862: 388 (unjustified emendation of *Erpetogomphus*). – Hagen 1875a: 42 (cat.); Selys 1879: 63 (2 sep.) (modification of generic characters); Kirby 1890: 60 (cat.); Carpenter 1897: 452 (distr.); Needham 1897: 166 (in key to nearctic Gomphidae); Needham 1899: 234 (venation); Calvert 1899: 386 (comments on Selys' classification); Needham & Hart 1901: 53 (in key to larvae of North American Gomphidae); Förster 1914: 73 (comparison with *Ammogomphus*); Seemann 1927: 19 (key to larvae, adults of western U. S. Gomphidae); Needham 1940: 389 (key, verification table).

Medium sized to small neotropical Gomphidae of slender build.

Head. – Eyes widely separated, characters of the mouth parts, clypeus, frons typical of the Gomphidae. Vertex variable, often interspecifically and, in the *E. ophibolus* group, sexually dimorphic. Anterior margin of vertex with a transverse trough, or a pair of transverse pits anterior or anterolateral to median ocellus, median ocellus anterior to lateral ocelli, or in some members of the *E. ophibolus* group, this structure at posteriormost part of deep, longitudinal trough, thus causing median ocellus to be posterior to lateral ocelli (figs. 145-146); median surface of vertex at vicinity of lateral ocelli and postoccipital tubercle mostly planar, but members of *E. ophibolus* group with a complete postocellar ridge, which may be bilobed (*E. agkistrodon*, fig. 148) or, in remainder of group, vestigial; occiput highly variable according to species and sex, *E. ophibolus* group with occiput small, semicircular, in other groups roughly trapezoidal, with posterior part broader than anterior part, its dorsal surface roughly planar to nearly vertically inclined, some species with slight to strongly tumid area medially, one species (female of *E. leptophis*) with a posteriorly projected medial spine; rest of occiput variable, semicircular, linear, weakly to strongly notched medially, or sinuate; condition of crest often variable within a few species; postocciput variable, most in the *E. ophibolus* group convexly arcuate, in others slightly convex to linear, postocciput mostly not visible from above, but conspicuously so in others (*e.g.*, female of *E. compositus*); lateral margins of one species (females of *E. cophias*) with transverse depressions.

Thorax. – Prothorax and synthorax typical of the

Gomphidae, but with great differences in maculation and colouration due to species and age differences. Pale colour pale green, apple green to vivid blue green, usually lighter ventrally and often with a slight dusting of white pruinosity ventrally and around coxae. Synthorax immaculate to heavily patterned with full complement of thoracic stripes. Legs moderately short, with femora slightly swollen and usually pale basally, with dark brown to black distally; tibiae in almost all species black, prothoracic tibiae of males with small keel occupying distal 0.15 of mesal ventral margin.

Wings (figs. 227-230) variable inter- and intraspecifically. Fore wing moderately narrow, with 11-21 antenodal crossveins, 5-16 postnodal crossveins, no subcostal crossvein; pterostigma prominent, about 4 times as long as wide, widest medially with its posterior margin slightly convex, surmounting 4-8 crossveins, the proximal a brace vein; anterior margin of costa in many species pale, becoming dark at pterostigma; arculus at vicinity of second antenodal, the sectors not stalked, separated at base by distance greater than width of each sector; supratriangular, triangular, and subtriangular crossveins absent; paranal cells variable in number, often numbering 5-7, smaller species usually with zero or few supplementary marginal cells behind paranal cells, other species with irregular row of up to 6-7 supplementary cells; no apical or medial planates, discoidal field of two rows. Hind wing with 7-14 antenodal crossveins, 7-14 postnodal crossveins; anal triangle of 2-4 cells, often with one of them in the latter condition small; anal loop absent (some specimens with a vestigial anal loop of 3 cells, but this condition rare); one paranal cell at Y interspace, two paranal cells at X interspace. Wing colouration entirely hyaline or flavescent at bases in some species. Hind wing length 21-36 mm.

Abdomen cylindrical, narrowest medially in males, transverse carinae on segments 3-7; auricles well developed in male, inner margin denticulate; auricle vestigial in female; male posterior margin of tergites 8 and especially 9 in a few species prolonged into a medial point, but this condition variable intraspecifically; segments 8-9 moderately clubbed, with moderate foliate extensions; female with apical abdominal segments hardly widened, foliar expansions small. Colour pattern and maculation variable between species and within sexes; all species with a pale green to pale orange middorsal stripe, sometimes extending full length of segment, but progressively less so on more posterior segments; dark brown to black dorsolateral stripe present on first 7 segments, usually constricted or separated medially, giving most of abdomen a serial dark and pale appearance; posterior part of segment 7, all of segments 8-10 tan to dark red brown, especially middorsally and ventrolaterally. Length of abdomen including appendages: ♂: 29-40 mm, ♀: 29-41 mm.

Abdominal appendages of male with cerci of great diversity according to species, but these structures always as long as segment 10, cercus usually gently decumbent at apical 0.30; rarely with a dorsal appendage. Ventral carina present basally, or distally, or absent, depending on species, epiprocts divided at base but contiguous along most of their length, gently to strongly curved at distal 0.50 to 0.30, depending on species; this structure lacking any accessory spines, or protuberances (except for *E. ophibolus*, fig. 95); tips of epiprocts assuming a wide variety of shapes and forms, and often variable intraspecifically (*e.g., E. bothrops*, figs. 127-128).

Vulvar lamina of female variable interspecifically, but never more than 0.50 length of segment 9, vulvar plates small, digit-like to forming large, contiguous, triangular or quadrangular plates, a moderate to large V- or U-shaped notch medially; postlamellar ridge always present, semicircular in only two species (*E. eutainia, E. leptophis*), in all others forming an inverted Y; stem of Y originating before or often at level of vulvar plates, some species with a well defined semicircular depression on each side of posterior stem.

Male genitalia variable among species: anterior lamina not prominent; anterior hamule smaller than posterior hamule, usually with the distal end hidden from view by posterior lamina; anterior lamina dark, divided at various heights according to species, but with posterior branch usually less conspicuous, smaller, and anterior branch more prominent; posterior lamina usually pale, linear in two species (*E. eutainia, E. leptophis*); in all others with a moderately wider base, its tip usually adorned with an apical or anteapical hook directed cephalad or cephalolaterad. Penis with basal (first) segment prominent, with a semicircular rim, especially so laterally, posteriorly with a pair of prominent lobes, or these lobes vestigial; second segment moderately long, third short, with a pair of small, nipple-like sclerotizations dorsally in two species (*E. eutainia, E. leptophis*); fourth segment highly variable specifically, with or without a prepuce, most species with a well defined lateral lobe; in most of the *E. ophibolus* group, lateral lobe small and pointed; membranous hood short to long and overlapping; a pair of flattened membranous cornuae of various lengths and shapes present on apical part of segment; in most of the *E. ophibolus* group, cornuae absent or vestigial; penis guard short, quadrate in cross-section.

A more complete discussion of the male and female genitalia is given under discussions of the species group accounts and in the cladistics section.

Keys

The keys should work for most specimens, but the worker may have difficulty when trying to determine poorly preserved material. I have used morphological characters for both sexes wherever possible, but some species pairs (*e.g.*, females of *E. heterodon* and *E. sipedon*, or *E. tristani* and *E. sabaleticus*) show little or no morphological differentiation. For them, I have had to rely on colour pattern. Abdomens of some females, particularly those laterally compressed, may need to be relaxed so that the vulvar lamina can be seen.

Key to *Erpetogomphus* males

1. Cercus with a prominent superior tooth at about 0.75 of appendage length (figs. 92-94) 2

– Cercus with dorsal surface convexly angulate (fig. 112), smoothly curved (fig. 103), straight (fig. 100), or with a concavity (fig. 115) 5

2 (1). Epiproct smoothly curved, with tip pointing dorsally or posterodorsally, a small, sharp, anteriorly directed superior tooth at middle of epiproct (fig. 95). Southern Mexico, Belize .... *ophibolus*

– Epiproct strongly curved so that distal 0.30 is parallel to basal 0.30, tip of epiproct pointing anteriorly, superior surface of epiproct with no tooth 3

3 (2). Ventral margin of cercus smoothly concave (fig. 92). Northeastern Mexico to Costa Rica .... *constrictor*

– Ventral margin with a large ventral tubercle at 0.50-0.75 length of cercus (figs. 93-94). Costa Rica south to Colombia and Venezuela 4

4 (3). In lateral view, superior tooth of cercus as long as rest of appendage, so that appendage appears to end in two equal branches (fig. 93). Panama, Colombia, Venezuela .... *sabaleticus*

– In lateral view, superior tooth of cercus less than 0.50 as long as remainder of appendage (fig. 94). Costa Rica, northern Panama .... *tristani*

5 (1). Metathoracic tibiae either entirely yellow externally (fig. 169), or yellow with median longitudinal black line. Western Mexico, southeastern Arizona .... *crotalinus*

– Metathoracic tibiae entirely brown or black externally; never with any yellow (*e.g*, figs. 168, 170) 6

6 (5). Basal 0.25 to 0.30 of lower margin of cercus with a distinct longitudinal carina which may end in a small ventral tooth (*e.g., E. cophias*, fig. 116) 7

– Basal part of cercus with no ventral carina, though a small tubercle may be present at basal 0.15-0.20 of appendage (*e.g.*, figs. 99, 102) 14

7 (6). With a dark stripe bordering posterior margin of metepimeron (figs. 8-9). Southern Mexico, Belize through Costa Rica .... *eutainia* (in part)

– Without a dark stripe on posterior margin of metepimeron 8

8 (7). In lateral view, ventral margin of cercus with carina terminating in a distinct ventral tooth at basal 0.30 of appendage (fig. 116); thorax almost immaculate, at most barely an indication of a dark antehumeral stripe (fig. 27). Michoacan and Morelos states of western Mexico .... *cophias*

– Ventral margin of cercus with longitudinal carina not terminating in a ventral tooth; thorax with well-defined dark antehumeral stripe, though it may be an elongated, isolated spot (*e.g.*, fig. 23) 9

9 (8). Dorsal surface of cercus distinctly angulate in lateral view (figs. 110, 112) 10

– Dorsal surface of cercus smoothly curved (fig. 112) 13

10 (9). Sides of thorax almost entirely green, with only a small, ill-defined dark humeral stripe; second lateral stripe incomplete, dark only below metathoracic spiracle, or absent; and third lateral stripe present only on upper 0.30 of suture (fig. 23), or absent (fig. 19) 11

– Sides of thorax green with usual complement of dark thoracic stripes; second lateral stripe may be incomplete, but humeral and third lateral stripes always present (figs. 17, 20-21) 12

11 (10). Dark antehumeral stripe incomplete, not touching humeral stripe (fig. 23); tip of cercus acute, but not gradually narrowing posteriorly (figs. 110-111); cornuae of penis without mesal lobes (fig. 87). New Mexico, western Texas, northern Mexico .... *heterodon*

– Dark antehumeral stripe complete, usually connected to humeral stripe (fig. 19); tip of cercus drawn out into a narrow cylindrical point (figs. 105-106); cornuae with mesal lobes (fig. 83). Durango, Jalisco, Morelos, and Puebla states of central Mexico .... *sipedon*

12 (10). Tip of cercus strongly acuminate (fig. 104), dark antehumeral stripe not connected to

collar (fig. 17) (except in some Mexican individuals), base of wings flavescent (except in some Mexican individuals, fig. 18), median area of occiput with a strongly raised tubercle (fig. 156). Eastern U.S. to Arizona, northern Mexico .... *designatus*

– Tip of cercus blunt, not acuminate (figs. 107-108); dark antehumeral stripe always connected to collar (ssp. *natrix*, fig. 21), or largely connected to humeral stripe (ssp. *lampropeltis*, fig. 20); base of wings hyaline, median area of occiput only slightly raised (fig. 160). Southern California, Arizona, New Mexico, western Texas, Baja California, Durango state, Mexico .... *lampropeltis*

13 (9). Ventral carina at base of cercus black, contrasting with remainder of appendage; this carina usually denticulate; thorax blue-green in life; sides of posterior hamules parallel, linear (fig. 52). Southern Texas to southern Mexico .... *eutainia* (in part)

– Ventral carina at base of cercus pale, the same colour as rest of appendage, this carina smooth; thorax pale green in life; sides of posterior hamules converging toward tip, not linear (fig. 66). Southwestern United States, Baja California .... *compositus*

14 (6). Distal 0.5 of cercus concave dorsally, this area covered with thick, long bristles (fig. 115). Southern Veracruz state, Mexico .... *boa*

– Distal 0.5 of cercus straight or convex (*e.g.*, figs. 99, 103) 15

15 (14). Ventral margin of cercus straight (figs. 99, 100) or forming a gentle concave curve (fig. 98) so that appendage appears linear 16

– Apical 0.30 of ventral margin of cercus curved downward 18

16 (15). Thorax entirely yellow-green (fig. 13), or with only an antehumeral and faint indication of a dark middorsal and antehumeral stripe (figs. 11-12); face entirely pale. Mexico south to Costa Rica. 17

– Thorax blue-green with full complement of dark thoracic stripes (fig. 10); face blue-green with extensive dark brown frontoclypeal stripe. Belize ....*leptophis*

17 (16). Distal branch of anterior hamule thick, as high as gap separating the two branches (fig. 54); posterior hamules with no distal tooth (fig. 54). Guatemala south to Costa Rica .... *elaphe*

– Distal branch of anterior hamule narrow, not as high as gap separating the two branches (figs. 55-56); posterior hamules with a distal tooth (fig. 55). Mexico to Guatemala .... *elaps*

18(15). Thorax blue-green, with full complement of dark stripes, including second lateral stripe and stripe on posterior margin of metepimeron (fig. 6); face (fig. 142) predominantly dark, with a well defined blue green spot on frons. Guatemala, Costa Rica .... *schausi*

– Thorax blue-green or yellow-green; sides lacking complete dark second lateral stripe (except in some *viperinus*; incomplete in some *bothrops*) and without dark stripe on posterior margin of metepimeron; face predominantly pale, with dark areas limited to sutures 19

19(18). Tip of epiproct in posterior view terminating in a blunt point (fig. 129); southern Veracruz state, Mexico..................*viperinus*

– Tip of epiproct in posterior view spatulate (fig. 126), broadly truncate (fig. 127), or bidentate (fig. 128) 20

20 (19). Larger species (hind wing 30-31 mm); epiprocts in lateral view curved, extending 0.50 or less the length of cerci (fig. 101), epiprocts in posterior view truncate or slightly bidentate; dark antehumeral and humeral stripes combined or nearly so (fig. 14); posterior hamular tooth prominent, directed laterocephalad or cephalad. Nuevo Leon, Michoacán, San Luis Potosí states, Mexico. (fig. 199) .... *liopeltis*

– Smaller species (hind wing 21-28 mm); epiprocts in lateral view curved, extending 0.75- 0.90 the length of cerci (fig. 102), epiprocts in posterior view bidentate or truncate (fig. 128); dark antehumeral and humeral stripes separate (fig. 15); posterior hamular tooth not as prominent, more strongly directed cephalad. Tamaulipas, Mexico, south to El Salvador (fig. 199) ....*bothrops*

Key to *Erpetogomphus* females

1. Medial area of occiput with a posteriorly pointed protuberance (fig. 151) ... *leptophis*

– Medial area of occiput variously shaped, but never with a posteriorly directed protuberance 2

2 (1). Occiput with a shallow oval depression on each side posterior to elevated rim (fig. 165). Michoacán and Morelos, Mexico .... *cophias*

– Occipital area posterior to elevated rim entire, with no shallow depressions 3

3 (2). Outer surfaces of metathoracic tibiae entirely yellow, or yellow with a median longitudinal black line (fig. 169). Western Mexico,

southeastern Arizona .... *crotalinus*

– Outer surfaces of metathoracic tibiae entirely black (*e.g.*, figs. 168, 170) 4

4 (3). Median ocellus posterior to lateral ocelli, the former lying within a deep longitudinal trough (figs. 145-146) 5

– Median ocellus at level of or anterior to lateral ocelli, no longitudinal trough 6

5 (4). Dorsal surface of vertex with sides of trough roughly parallel, or only slightly converging anteriorly (fig. 145). Northeastern Mexico, south to Costa Rica .... *constrictor*

– Dorsal surface of vertex with sides of trough strongly converging anteriorly ......(fig. 146)
Costa Rica, western Panama .... *tristani*
Central Panama, Colombia, Venezuela .... *sabaleticus*

6 (4). Vertex with transverse ocellar ridge bilobed behind median ocellus (figs. 148-149) 7

– Vertex with transverse ocellar ridge entire (fig. 147), low and almost vestigial (fig. 150), or absent, its lateral ends forming oval tubercles posterior to lateral ocelli (*e.g.*, fig. 150) 8

7 (6). Occiput transversally narrow, forming a shallow semicircle (fig. 148). Jalapa, Mexico .... *agkistrodon*

– Occiput wide, forming a full semicircle (fig. 149). Guatemala, Costa Rica .... *schausi*

8 (6). Vertex with transverse ocellar ridge entire, prominent, and concave posteriorly (fig. 147). Southern Veracruz, Mexico, Belize ....*ophibolus*

– Vertex with median area bare, or at most only slightly raised (*e.g.*, fig. 150) 9

9 (8). Vulvar lamina followed on segment 9 by distinct and prominent semicircular ridge, never with a posteriorly directed arm (fig. 178). Southern Texas, eastern Mexico, Belize to Guatemala and Costa Rica .... *eutainia*

– Vulvar lamina followed on segment 9 by a Y-shaped ridge (e.g., fig. 195) 10

10 (9). Vulvar lamina with each plate strongly corrugated diagonally, distal and lateral margins of each plate forming a strongly raised semicircular ridge (figs. 195-196); a median tumid swelling on postocciput immediately behind occipital ridge (fig. 167) [includes *liopeltis*, but properly goes to 10']. Southern Veracruz, Mexico .... *boa*

– Vulvar lamina with each plate entire (fig. 185) or bisected diagonally by only one groove (fig. 186); distal and lateral margins of each plate planar, not forming a strongly raised semicircular ridge; postocciput not differentiated, evenly curved (fig. 166) [tumid in *liopeltis*] 11

11 (10). Median surface of occiput with a strongly raised tubercle (fig. 156). Eastern United States west to Arizona, northern Mexico .... *designatus*

– Median surface of occiput planar or at most slightly raised (fig. 152) 12

12 (11). Lobes of vulvar lamina separated by an almost U-shaped interval 3 to 4 times as wide as either lobe (figs. 180-181)
Mexico south to Guatemala .... *elaps*
Guatemala to Costa Rica .... *elaphe*

– Lobes of vulvar lamina separated by a triangular or semicircular interval 0.5 to 1.0 the width of each lobe (*e.g.*, figs. 182, 187) ...13

13 (12). With a second complete dark lateral stripe on thorax (*e.g.*, figs. 20-21, 24) 14

– Second dark lateral stripe completely lacking or vestigial, at most extending from base to just above metathoracic spiracle (*e.g.*, fig. 36) 15

14 (13). Occiput in dorsal view narrow, its width less than width between median ocellus and occiput; postoccipital area easily visible (fig. 163); base of wings with flavescent infusion between Sc and R at least up to first anx and cubitoanal area; top of abdomen with light areas ivory or with a tinge of orange, usually not different from white on sides. Southwestern United States, Baja California .... *compositus*

– Occiput in dorsal view wide, its width almost equal to width between median ocellus and occiput; postoccipital area not visible (fig. 160); base of wings hyaline; top of abdomen with light areas much darker than white on sides. Southwestern United States, Baja California, Durango state, Mexico .... *lampropeltis*

15 (13). Occiput narrow, vestigial, with only a small medially arched area (fig. 153); post-occiput with a median tumid area (as in fig. 167). Nuevo Leon, Michoacan, San Luis Potosí states, Mexico .... *liopeltis*

– Occiput not especially narrow, extending full width (*e.g.*, figs. 154-155, 159, 162); post-occiput planar or, at most, only slightly convex medially (as in fig. 166) 16

16 (15). Stem of postlamellar ridge with a well defined circular or oval depression on either side; junction of Y of postlamellar ridge usually posterior to hind margin of vulvar laminar plates (fig. 183) 17

– Stem of postlamellar ridge with only a slight depression or, more often, without any circular or oval depression on either side; junction of Y of postlamellar ridge at or anterior to hind margin of vulvar laminar plates (figs. 187-188, 193) 18

17 (16). A deep pit at anterior margin of frons anterolateral to median ocellus (fig. 155); cleft between vulvar laminar plates wide, forming an obtuse arc greater than 100°; dark humeral and antehumeral stripes combined or nearly so (fig. 16); larger species (hind wing 31-34 mm). Southern Veracruz, Mexico .... *viperinus*

– Anterior margin immediately anterior to median ocellus forming a narrow V-shaped trough with base of postfrons (fig. 154); cleft between vulvar laminar plates narrow, forming a V- shaped notch of not more than 90° (fig. 183); dark humeral and antehumeral stripes separate (fig. 15); smaller species (hind wing 17-31 mm). Tamaulipas, Mexico, south through El Salvador .... *bothrops*

18 (16). Dark antehumeral stripe complete, usually connected at its upper end to narrow humeral stripe (fig. 19). Jalisco, Morelos, and Puebla, Mexico .... *sipedon*

– Dark antehumeral stripe vestigial, forming an isolated elongate spot, not connected to vestigial humeral stripe (fig. 23). Southwestern United States, northern Mexico .... *heterodon*

Key to *Erpetogomphus* males based primarily on characters of abdominal segments 2 and 3

I include this key for male specimens lacking the posterior abdominal segments. The key should allow a high probability of identification, though some species (*E. ophibolus, E. sabaleticus, E. tristani, E. constrictor,* for example) appear inseparable by penis structure and are distinguished only by the caudal appendages. For those species, I have added other somatic characters and/or geographic data with which to separate them. The key does not include *E. agkistrodon,* the male of which is unknown.

1. Ental surface of penis with a prepuce (*e.g.*, fig. 76), this structure reduced and partially hidden by frill-like lateral lobe in *leptophis* (fig. 76) and *eutainia* (fig. 75); thoracic pale colouration in life deep blue green, dark thoracic stripes always present on sides (*e.g.*, fig. 10) 2

– Ental surface of penis lacking a prepuce (*e.g.*, fig. 90); thoracic pale colour in life yellow green (except for *viperinus* and probably *liopeltis*); dark lateral thoracic stripes often (but not always – figs. 16, 18) reduced or absent 8

2 (1). Posterior hamule digit-shaped (figs. 52-53), its tip broadly rounded; anterior hamule divided at upper 0.30 to 0.25, its posterior branch well defined, its tip almost meeting larger anterior branch (figs. 52-53); lateral lobe of penis composed of large spinulose frill (figs. 52-53); cornuae well developed, their apices pointed 3

– Posterior hamule triangular, its tip armed with a spine (fig. 47); anterior hamule with only a posterior shoulder (*e.g.*, fig. 47); lateral lobe of penis reduced to a small, semicircular, spinulose frill (fig. 74) or vestigial (fig. 70); cornuae vestigial (fig. 74) or present (fig. 70) 4

3 (2). Membranous hood of penis about 3 times as long as wide, apices overlapping (fig. 76) [Note: this character is based on the only known specimen, the holotype; other specimens may show variability similar to *eutainia.*]; dark second and third lateral stripes connected at upper ends, forming an isolated pale spot below subalar carina; dark lateral stripe along posterior margin of metepimeron well defined (fig. 10); caudal appendages as in fig. 98; Belize ..... *leptophis*

– Membranous hood of penis reduced, less than 2 times as long as wide, though apices may overlap (fig. 75); dark second and third lateral thoracic stripes not connecting (fig. 7-9); dark lateral stripe along posterior margin of metepimeron absent (fig. 7) or present primarily in populations of central Mexico (fig. 8) south through Costa Rica (fig. 9); caudal appendages as in fig. 97 .... *eutainia*

4 (2). Cornuae of penis present; their tips divergent (fig. 74); lateral lobe a small, circular, spinulose frill (fig. 74); Guatemala and Costa Rica .... *schausi*

– Cornuae vestigial (fig. 71); lateral lobe vestigial, forming a small, acute point (fig. 71) 5

5 (4). Appendages as in fig. 93; Central Panama south to Colombia and Venezuela .... *sabaleticus*

– Mexico south through Costa Rica and northern Panama 6

6 (5). Epiproct smoothly curved, with tip pointing dorsally or posterodorsally, a small, sharp, anteriorly directed superior tooth at middle of epiproct (fig. 95). Southern Mexico, Belize .... *ophibolus*

– Epiproct strongly curved so that distal 0.30 is parallel to basal 0.30, tip of epiproct pointing anteriorly, superior surface of epiproct with no tooth 7

7 (6). Appendages as in fig. 92; Mexico south through Costa Rica .... *constrictor*

– Appendages as in fig. 94; northern Costa Rica through northern Panama ...... *tristani*

8 (1). Anterior hamule divided at base; its branches resembling a claw; posterior hamule broadly spatulate (figs. 68-69) 9

– Anterior hamule divided at lower 0.30 to upper 0.25 posterior arm short and truncate or acute; posterior hamule broadly triangular 10

9 (8). Dark antehumeral and humeral stripes united, forming a broad, dark stripe over first lateral suture (fig. 26); southern Veracruz, Mexico .... *boa*

– Thorax almost entirely pale, with only a vestigial antehumeral stripe (fig. 27); Michoacán and Morelos states of Mexico ... . *cophias*

10 (8). Lateral lobe of penis linear, at least 3 times longer than wide; its posterior margin spinulose (figs. 77-78, 82, etc.) 11

– Lateral lobe of penis round, about as long as wide, its margin spinulose (fig. 86) 16

11 (10). Lateral lobe of penis almost recumbent against ental margin of fourth segment (fig. 82); anterior hamule divided at distal 0.5 of segment; posterior hamule lacking a distal tooth (fig. 60); posterior margin of first segment (peduncle) of penis strongly cleft, each lobe on either side of cleft protruding well beyond posterior margin of segment; southern United States west to Arizona, northern Mexico .... *designatus*

– Lateral lobe of penis prominent, directed almost perpendicularly to ental margin of fourth segment; anterior hamule divided at distal 0.30 of segment, posterior hamule with a distal tooth (except for *elaphe* from Guatemala south through Costa Rica); posterior margin of first segment of penis weakly bilobed, lobes on either side of emargination only slightly extending beyond posterior margin of segment; northern Mexico south through Costa Rica 12

12 (11). Distal branch of anterior hamule thick, as tall (high) as gap separating the two branches (fig. 54); posterior hamule with no distal tooth (fig. 54); Guatemala south to Costa Rica .... *elaphe*

– Distal branch of anterior hamule narrow, not as tall (high) as gap separating the two branches (figs. 55-56); posterior hamule with a distal tooth 13

13 (12). Distal tooth of posterior hamule bent anteriorly so that it lies in same direction as the planar surface of hamule (figs. 55-56); Mexico south to Guatemala .... *elaps*

– Distal tooth of posterior hamule bent laterally or anterolaterally so that it points distally and perpendicularly from planar surface of hamule (fig. 59) [Note: This condition appears universally only in *E. viperinus*, but variation in this condition occurs in *E. bothrops* and *E. liopeltis*; some specimens of these last two species may not be separable from *E. elaps* by this character]; Mexico south through Guatemala 14

14 (13). Base of postfrons medially with a pair of deep pits, each anterolateral to median ocellus (fig. 137). Southern Veracruz, Mexico .. .. *viperinus*

– Base of postfrons medially with a transverse arcuate trough immediately anterior to median ocellus (fig. 136) 15

15 (14). Smaller species (hind wing 21-28 mm); dark antehumeral and humeral stripes separate (fig. 15); posterior hamule with apical tooth shorter, less prominent, more strongly curved laterally over tip of hamule. Tamaulipas, Mexico, south through El Salvador (fig. 199) .... *bothrops*

– Larger species (hind wing 30-31 mm); dark antehumeral and humeral stripes connected (fig. 14); posterior hamule with apical tooth longer, more linear, not as strongly curved laterally over tip of hamule. Nuevo Leon, Michoacan, San Luis Potosí, Mexico .... *liopeltis*

16 (10). Cornuae of penis with tips long, narrow, and attenuate; medial lobe present (fig. 86); extensor surfaces of tibiae yellow, or yellow with a median longitudinal black line; south-eastern Arizona south through central Mexico .... *crotalinus*

– Cornuae of penis with tips bluntly rounded (figs. 87-88); medial lobe present (figs. 83-84) or absent (figs. 87-88); extensor surfaces of tibiae black, never with yellow 17

17 (16). Tips of cornuae bluntly rounded; medial lobe absent (figs. 87-88) 18

– Tips of cornuae with a well defined medial lobe (figs. 83-84) 19

18 (17). Median part of base of postfrons with a transverse arcuate trough immediately anterior to median ocellus (as in fig. 138); western United States .... *compositus*

– Base of postfrons medially with a pair of deep pits, each anterolateral to median ocellus (as in fig. 138); western Texas, western

New Mexico, Chihuahua, Mexico .... *heterodon*

19 (17). Penis in dorsal view with membranous hood short, exposing a subcutaneous membranous hood which forms the posterior margin of segment [be sure to examine closely: rotation of penis to dorsolateral view will reveal a raised hood anterior to subcutaneous membrane], (fig. 83); Jalisco, Morelos, and Puebla, Mexico .... *sipedon*

– Penis in dorsal view with membranous hood long, completely covering subcutaneous membrane, thus forming posterior margin of segment (figs. 84-85); western Texas, southern and central New Mexico and Arizona, southwestern California, Baja California, Durango state, Mexico .... *lampropeltis*

Erpetogomphus constrictor Ris

(figs. 1-thx, 28-abd, 97-hamules, 70-penis, 92-app, 145-♀ vertex, 171-vl, 198-distr)

Erpetogomphus constrictor Ris, 1917: 154 ('Nach 3♂, 1♀ von Misantla, Vera Cruz, Mexiko, VI 1911, die ich dem schweizerischen Sammler W. Gugelmann verdanke.'). – Williamson and Williamson 1930: 12 (summary of status); Montgomery 1973: 239 (derivation of name); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Dunkle 1988: 46 (Honduras); Maes et al. 1988: 36 (Nicaragua); Bridges 1991: VII.51 (cat.); Tsuda 1991: 95 (cat.).

Description

Male. – Labium grey, becoming dark grey medially, labrum entirely brown to grey green with dark brown margin and large inverted medial triangular spot; base of mandibles grey green, anteclypeus grey green; postclypeus brown except for small triangular green spots above lateral lobes; ventral margin of frons brown joining brown of postclypeus, thus forming a large brown frontoclypeal stripe; remainder of frons green; extreme base of frons, vertex, and occiput dark brown; area immediately anterior to median ocellus with a shallow longitudinal trough, postocellar tumid areas prominent, a lower incomplete transverse ridge posterior to median ocellus but not continuous with each postocellar tumid area laterally; occiput planar, its crest costate, linear, fringed with dark brown hairs; postocciput brown, linear to gently concave medially; rear of head brown.

Prothorax brown, paler dorsally, anterior and posterior lobes green, some specimens with two small green midlateral spots (almost touching) on median lobes; synthorax (fig. 1) with prominent, well defined dark stripes on green background as follows: middorsal stripe narrowing anteriorly at collar, costal margins of antealar sinus and area along this structure connecting with humeral stripe; antehumeral stripe connecting with humeral basally and dorsally, but its upper end often not touching brown below antealar crest, or, if so, then isolating small area of green; second and third lateral stripes connecting at upper 0.25, isolating small green spot, second lateral stripe swollen in vicinity of metaspiracle and, in some specimens, enlarged and touching third lateral stripe; posterior margin of metepimeron, metasternum, and venter of thorax grey green to tawny. Venter of profemora grey green, remainder of femora dark brown, becoming black distally; tibiae, tarsi, armature black.

Wings hyaline, venation and pterostigma black.

Venational statistics. Fifth (rarely fourth or sixth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0-1; anx: fore wing 13-17/14-17, hind wing 10-12/10-13; pnx: fore wing 10-14/9-14, hind wing 9-12/9-13; cs under pterostigma.: fore wing 5-7/4-7, hind wing 4-7/5-7; anal triangular cells: 3- 5/3-4. Hind wing 25-30 mm.

Abdomen with segment 1 brown, green laterally and with a green middorsal stripe; segment 2 brown except for green auricles, ventral margin, and narrow middorsal stripe, annulus black; segment 3 primarily black with green middorsal stripe extending from black annulus of segment 2 and ending at distal annulus, a pale grey green anterolateral spot becoming narrower along ventral margin and disappearing at 0.25 to 0.75 of segment length; segments 4-6 similar to segment 3 but with pale middorsal stripe ending at posterior 0.10 to 0.25 of segment, segment 6 in some specimens with anterolateral white connecting dorsally with pale green middorsal stripe; segment 7 grey green on anterior 0.50 to 0.60, except for dark transverse carina, posterior part of segment brown to black; segments 8-10 red brown, becoming darker dorsally and ventrally, especially along foliate margins, posterior medial margin of segment 9 bluntly pointed or slightly so. Abdomen 31-35 mm.

Cercus (fig. 92) grey green, becoming dark brown posteriorly, arcuate with a prominent laterally compressed dorsal tubercle on distal 0.75 of cercus, extreme base with a black ventral tooth (mostly hidden by posterior margin of abdominal tergite 10), a ventral carina on distal 0.25 of cercus, tip of cercus with a black tooth; epiprocts dark brown, strongly curved at distal 0.50 so that distal 0.5 of appendage is parallel, distal 0.30 sulcate medially on exterior surface. Accessory genitalia. Hamules (fig. 47) small; anterior hamule brown, divided at distal 0.30, posterior branch a well developed shoulder; posterior hamule roughly triangular, its tip with a spine; penis (fig. 70) with cornuae slightly bilobate or transverse at base, a well developed prepuce, lateral lobe a small tooth.

Female. – Head markings similar to male but with dark median spot on labrum larger, often connecting with ventral brown, thus separating green into two lateral spots; some specimens with an entirely brown labrum; brown on frontoclypeal suture more extensive laterally, so that entire postclypeus may be brown; brown at base of antefrons with a median extension which, in some specimens, connects with brown frontoclypeal suture, thus dividing frontal green into two spots. Morphology of vertex and occiput differs from male as follows: a large longitudinal trough on vertex with median ocellus recessed posterior to lateral ocelli (fig. 145); bottom of median furrow with longitudinal convex area; lateral margins of trough formed by median ocellar protuberances connecting posteriorly forming a semicircular ridge; occiput small, forming a narrow semicircle, crest covered with long brown hairs; postocciput brown, convex.

Pro- and synthorax as in male, but with dark areas more extensive.

Venational statistics (n = 15). Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-5/0-3; anx: fore wing 14-17/14-17, hind wing 11-12/11-12; pnx: fore wing 11-14/11-14, hind wing 10-14/11-13; cs under pterostigma.: fore wing 5-7/5-7, hind wing 5-7/5-7. Hind wing 28-31 mm.

Abdomen (fig. 28) with segment 1 brown, a green spot posterolaterally and with a complete green middorsal stripe; segment 2 brown except for following green areas: wide middorsal stripe narrowing posteriorly, longitudinal lateral stripe connecting just anterior to auricle and narrowing slightly to posterior margin of segment, a thin pale margin at venter of segment; segment 3 similar to segment 2 but lateral pale stripe ending posteriorly at transverse carina, middorsal green narrowly acuminate posteriorly, forming a mere line on posterior 0.25 of segment; segments 4-6 similar to segment 3 but with middorsal green progressively shorter posteriorly, lateral pale stripe white and forming a small quadrangular spot at anteroventral margin of segment; segment 7 with anterior 0.50 pale green, interrupted by black transverse carina, posterior 0.50 becoming red brown; segments 8-10 all red brown, often darker dorsoposteriorly; cerci pale grey green. Vulvar lamina (fig. 171) with plates broadly connected at basal 0.75, relatively unspecialized, cleft obtusely V- or U-shaped, about as wide as each lobe; postlamellar ridge with Y-juncture posterior to plates, base of stem well defined and with oval depression laterally. Abdomen 30-35 mm.

Diagnosis

Males of *E. constrictor* are easily separated from its closest allies, *E. tristani* and *E. sabaleticus*, by the shape of the cercus. This structure is concave ventrally in *E. constrictor*, not convex as in the other two species. It superficially resembles *E. schausi* in body colouration and is diagnosed under that species.

Females seem to be separable from the same two species by the width of the median trough of the vertex. This structure is slightly divergent anteriorly in *E. constrictor* (figs. 145), but is largely parallel in the other two species (fig. 146).

Remarks

Variation. – Venational details of lectotype male of *E. constrictor*. No marginal cells behind fore wing paranal cells; anx: fore wing 15/14, hind wing 11/11; pnx: fore wing 11/12, hind wing 12/13; cs under pterostigma: fore wing 7/7, hind wing 7/6; number of anal triangular cells: 4/3. Hind wing 29 mm.

Material I examined indicates that specimens from more southerly parts of its range (Guatemala, Honduras, Nicaragua) are more melanic than those from eastern Mexico. For example, black markings on the labrum, postclypeus, and thoracic striping are generally more extensive, further reducing or isolating green areas.

Two females, one from San Luis Potosí (El Salto Falls) and the paralectotype are unusual in having 5/3 and 4/3 marginal cells behind fore wing paranal cells in right and left fore wings, respectively. All other female specimens ranged from 0-1 marginal cells.

Biology. – E. González (*in litt.*) found this species to be abundant at the Rio Huichihuayan. Males perched on leaves, vines, and snags at the edge of the river. Judging from specimens in collections, *E. constrictor* is the northern counterpart of *E. tristani*, and appears to be common in certain areas.

Erpetogomphus constrictor appears to be a lowland species of wet tropical forest habitats along the east coast of Mexico south through Costa Rica (Guanacaste Prov.: Miravalles, 26 April 1991 (C. Esquivel), 3♂, A. Ramirez, *in litt.*). Altitudes range from near sea level (70 m, San Luis Potosí, km 410) to about 550 m (Nuevo Leon, entrance to Horsetail Falls). Collection dates range from 26 April to 4 October. One specimen was collected in an ultraviolet light trap.

Distribution (fig. 198). – This species occurs along the eastern Mexican states of Nuevo Leon, Tamaulipas, San Luis Potosí, Veracruz, south through Guatemala, Honduras, and Nicaragua, to Guanacaste Prov., Costa Rica. It is apparently parapatric or allopatric with *E. tristani* in Costa Rica.

Material

Type data. – Lectotype ♂ by present designation with the following data in Ris' hand: '15098' in green ink in an unknown hand, *Erpetogomphus* / n. sp. ♂ / *constrictor* Ris 1917/ Misantla, Vera Cruz / Mexico VI 1914 / W. Gugelmann. Two paralectotype males and one female with same data. One male is labelled '15092' in green ink, another male in poor condition (head partially fragmented, abdomen broken in several places) is labelled 'Type' probably by Ris. The left pair of wings is missing and probably served for figure 6 in the original description. The female is labelled '15096' in green ink. In SMF.

Other material (53♂, 15♀, including lectotype ♂ and paralectotypes). – MEXICO: Nuevo Leon: Cola Caballo, SW Monterrey, 6 July 1960 (W. B. Cutts), 1♀ (UMMZ); Rio Ramos, 3 km S of Allende, 500 m, 7 Sept. 1963 (T. W. Donnelly), 1♂ (RWG); south of Monterrey, Rio Elizondo, 19-20 June 1965 (O. S. Flint, Jr.), 6♂ (USNM, RWG); stream at entrance to Horsetail Falls, 550 m, 25 June 1965 (D. R. Paulson), 1♂ (DRP); Tamaulipas: Gomez Farias, Río Frio, 4 Oct. 1985 (F. Arias, L. Cervantes, M. Garcia), 'colectado en trampa U.V. en la noche', 1♂ (RWG); San Luis Potosí: El Salto, 4 June 1967 (O. S. Flint, Jr.), 1♀ (USNM); Palitla, N of Tamazunchale, 25 June 1965 (O. S. Flint, Jr.), 9♂ (USNM, RWG); Huichihuayan, rte 85, km 399, 7 Aug. 1966 (O. S. Flint, Jr.), 5♂ (USNM, CC, TWD); stream crossing Hwy 85 (1000'); 6 mi N of Tamazunchale, 4 Sept. 1957 (G. H. Beatty, III), 1♂ (FSCA); km 410, 'Sam Brown' Hacienda, 250 ft, 27 Sept. 1938 (L. J. Lipovsky), 1♂ (UMMZ); Route 85, km 399, Huehuetlán, 26 June 1965 (O. S. Flint, Jr.), 4♂, 1♀ (USNM); Rio Huichihuayan, Mpio de Huchuetlan, 100 m, 26 May 1987 (E. González-S, 2♂ (RWG); upstream Cascadas Micos just S of town N of Ciudad Valles off Hwy 85, 27 June 1990 (J. S. Daigle), 1♂ (RWG); GUATEMALA: Suchitepequez Dept., Cuyotenango, Finca San Rafael Olimpo, 1700 ft, 10-20 June 1966 (O. S. Flint, Jr., M. A. Ortiz-B.), 8♂ (USNM, RWG); HONDURAS*: Comayagua Dept.*, Rancho Chiquito, 11.8 mi SE Villa de San Antonio, 2-3 Aug. 1967 (O. S. Flint, Jr., M. A. Ortiz-B.), 3♂, 7♀ (USNM, CC, RWG); *Francisco Morazan Dept.*, 30 km E of Tegucigalpa, 13 June 1982 (Fernandez, Garcia), 1♀ (SWD); [no date], (Carlos Jaramillo), 1♀ (SWD); EL SALVADOR*: Ahuachapan Dept.*, Loma de Paya, Bosque El Impossible, San Francisco Menendez, 24 July 1987 (A. Campus), 1♂ (VH); 20 Aug. 1986 (V. Hellebuyck), 1♀ (VH) 4 Aug. 1987 (V. Hellebuyck), 1♀ (VH); NICARAGUA*: Chobales Dept.*, La Flor, rte 7, km 159, 4 mi W of Acoyapajit, 29 July 1967 (O. S. Flint, Jr., M. A. Ortiz- B.), 4♂ (USNM); *Managua Dept.*, stream along Pan American Hwy, 7 km S of Nandaime, 21 June 1962 (T. W. Donnelly), 1♂ (TWD).

Erpetogomphus sabaleticus **Williamson**

(figs. 2-thx, 48-hamules, 71-penis, 93-app, 172-vl, 198-distr)

Erpetogomphus sabaleticus Williamson, 1918: 1 (descr. holotype ♂, allotype ♀). – Williamson and Williamson 1930: 12 (summary of status); Paulson 1982: 255 (Panama, South America); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); De Marmels 1990: 338 (Venez.); Bridges 1991: VII.184 (cat.); Tsuda 1991: 95 (cat.); Belle 1992: 32 (descr. larva); Donnelly 1992: 85 (Panama); Belle and Quintero 1992: 99 (key, Panama).

Description

A thorough comparative description of the holotype male and allotype female is given by Williamson (1918). I illustrate the thorax (fig. 2), caudal appendages (fig. 93) and details of the accessory genitalia (fig. 48) of the holotype, and the vulvar lamina of the allotype (fig. 172).

Male (n=6, including holotype). – Venational statistics. Fifth (rarely sixth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 13-18/15-17, hind wing 10-12/9-12; pnx: fore wing 11-13/15-16, hind wing 11-14/11-13; cs under pterostigma: fore wing 5-6/6-7, hind wing 5-7/6-7; anal triangular cells 3-4/3-4. Hind wing 26-27 mm. Abdomen 30-33 mm.

Female (n = 4, including allotype). – Venational statistics . Fifth or sixth (rarely fourth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0-1; anx: fore wing 15-17/15-16, hind wing 11-12/9-12; pnx: fore wing 11-15/13, hind wing 10-12/11-13; cs under pterostigma: fore wing 6-7/6-7, hind wing 6-7/6-7. Hind wing 28-29 mm. Abdomen 31-32 mm.

Diagnosis

Erpetogomphus sabaleticus is diagnosed under *E. tristani.*

Remarks

Variation. – Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 15/16, hind wing 11/11; pnx: fore wing 13/13, hind wing 12/11; cs under pterostigma: fore wing 6/6, hind wing 6/6; anal triangular cells: 3/3. Hind wing 26 mm.

Venational details of allotype female: number of marginal cells behind fore wing paranal cells: 1/0; anx: fore wing 16/15, hind wing 12/11; pnx: fore wing 12/13, hind wing 10/11; cs under pterostigma: fore wing 6/6, hind wing 6/7. Hind wing 29 mm.

The living colours of the holotype male were recorded by Williamson (1918).

Biology. – Williamson (1918) collected the allotype female and holotype male along the upper San Juan near Maraquita in Colombia. The male was taken along the Quebrada Sabaleticus as it rested on a flat leaf about five feet above the water. Only one other specimen of this species was seen (but not collected) during their stay in Colombia. A description of the type locality is given by Williamson (1918).

Michael May collected one male and three female larvae of the species at the Quebrada Juan Grande, along Pipeline Road in the Panama Canal Zone on 28 January 1975 and 23 January 1977. These were brought back to Gainesville, Florida, where the adults emerged about three months later.

This species, like *E. tristani*, is apparently rare. Other odonatists and I have collected along Pipeline Road in Panama, but have failed to find the species.

Distribution (fig. 198). – *Erpetogomphus sabaleticus* is the most austral of the genus and is currently known from one locality in northwestern Venezuela, one locality in northern Colombia, and Panama. It is apparently the only member of the genus found in the first two countries. Its northern limit is unknown, but it is probably parapatric with the more northerly *E. tristani.* Collection dates range from 3 February (Maraquita, Colombia) through 24 June (Panama Canal Zone).

Material

Type data. – Holotype male: Colombia: Dept. Antioquia: Cristalina, 28 km on railroad above Puerto Berrio, 19 Feb. 1917 (J. H. and E. B. Williamson); allotype female: Colombia: Dept. Tolima: Maraquita, 3 Feb. 1917 (J. H. and E. B. Williamson). Both specimens in UMMZ.

Other material (6♂, 4♀, including holotype ♂ and allotype ♀). – Panama: *Canal Zone*: Quebrada Juan Grande, Pipeline Road, 28 Jan. 1975 (M. L. May), 1♀ larva, emerged 19 June 1975 (FSCA); same data but 23 Jan. 1977 (FSCA), 1♂, 2♀ larvae, male emerged 16 May 1977, females emerged 20, 26 May 1977; Pipeline Road, 1.7-4.8 mi NW of Gamboa, 2nd bridge, 24 June 1970 (E. S. Morton), 1♂ (TWD); Venezuela: *Tachira Dept.*: Tachira, 11 April 1920 (J. H. and E. B. Williamson, W. H. Ditzler), 3♂ (2♂ in UMMZ, 1♂ in FSCA).

Erpetogomphus tristani Calvert

(figs. 3-thx, 49-hamules, 72-penis, 94-app, 120-ept, 146-vertex, 173,174-vl, 198-distr)

Erpetogomphus tristani Calvert, 1912a: 290 (descr. of ♂, ♀). – Calvert 1912b: 384 (mentions mating adaptations); Williamson 1918: 1 (comparison with *E. sabaleticus*); Ris 1917: 154 (Panama); Ris, 1918: 154 (Panama); Calvert 1920b: 339 (mentions mating adaptations); Williamson and Williamson 1930: 12 (summary of status); Paulson 1982: 256 (Costa Rica, Panama); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.212 (cat.); Tsuda 1991: 95 (cat.); Belle and Quintero 1992: 100 (key, Panama).

Description

Male. – A thorough description of the holotype male and allotype female is given by Calvert (1912). I illustrate the caudal appendages of the holotype (fig. 94) and vulvar lamina of the allotype (fig. 173). In addition to Calvert's description, I add the following: A strong ventral tooth at base of cercus (plainly seen in lateral view, fig. 94), which in most specimens is partially hidden by lateroposterior margin of tergite 10; tips of epiprocts narrow in posterior view (fig. 120); anterior hamule black, divided at apical 0.25, lower branch a rounded shoulder; anterior (upper) branch well developed; posterior hamule pale, acutely triangular, with a prominent apical tooth; penis with well developed prepuce, which, when viewed laterally, is hidden by ventrolateral margin of segment 4; lateral lobe small, rudimentary, barely visible, and with spinulose margin; cornua rudimentary, forming an ental membranous plate with a quadrate margin (fig. 72). Abdomen 31-33 mm.

Venational statistics. – (n = 5, including holotype). Fifth antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0; anx: fore wing 13-15/14-15, hind wing 10-12/10-11; pnx: fore wing 11-13/11-13, hind wing 11-13/10-12; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/5-6; anal triangular cells: 3/3. Hind wing 25-27 mm.

Female. – Vulvar lamina (fig. 174, allotype; 173) broadly connected, relatively unspecialized, and with a gently U-shaped notch; basal plate poorly developed; juncture of Y-shaped postlamellar ridge posterior to posterior margin of lamina; well defined arcuate depression on either side of central stem. Abdomen 31-33.5 mm.

Venational statistics. – (n = 4, including allotype). Fifth antenodal thickened; number of marginal cells behind fore wing paranal cells: 0-1/0; anx: fore wing 15-16/15-17, hind wing 11-12/10- 12; pnx: fore wing 12-14/11-12, hind wing 12-13/12-13; cs under pterostigma: fore wing 5-7/6-7, hind wing 6-7/5-6. Hind wing 29 mm.

Diagnosis

Erpetogomphus tristani, E. sabaleticus, and *E. constrictor* form a compact group which is easily separable from all other congeners by the unique shape of the epiprocts of the male (figs. 92-94, 120) and by the morphology of the vertex of the female (figs. 145-146). Males of *E. tristani* differ from the other two species only in the shape of the cerci. The ventral margin is distinctly convex at the apical 0.60-0.80 in *E. tristani* (fig. 94) and *E. sabaleticus* (fig. 93), not smoothly concave as in *E. constrictor* (fig. 92). All three species have a prominent dorsal tooth near the distal end, but the tooth in *E. constrictor* is broader in lateral view and more vertical than in *E. tristani* and *E. sabaleticus.*

Males of *E. tristani* and *E. sabaleticus* approach one another closely. Williamson (1918: 4-5) found males of both species inseparable except by the male caudal appendages. Williamson sent a pair of *E. sabalecticus* to Calvert, who also supported the statement of differences between the males of both species. Calvert was unable to separate the females of these two species. I have found the females of these three species (*E. constrictor, E. tristani* and *E. sabaleticus*) to be extremely similar, more so than their males. The sides of the longitudinal trough of the vertex of *E. constrictor* are more parallel (fig. 145), than those of the other two species. Like Calvert and Williamson, I have not found any differences between females of the small series of *E. tristani* and *E. sabaleticus.*

Remarks

Variation. – Little variation is expressed among the small series (males, n = 5; females, n = 4, including holotype and allotype).

Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 14/14, hind wing 11/11; pnx: fore wing 12/12, hind wing 13/12; cs under pterostigma: fore wing 5/5, hind wing 5/5. Hind wing 27 mm.

Venational details of allotype female: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 15/15, hind wing 11/11; pnx: fore wing 14/12, hind wing 13/12; cs under pterostigma: fore wing 7/7, hind wing 7/6. Hind wing 29 mm.

Biology. – The species is relatively rare in collections, despite intensive collecting in Costa Rica in recent years. Collection dates are February, June, and July. Nothing else is known of its biology.

Distribution. (fig. 198). – *Erpetogomphus tristani* is thus far known from only two northwestern provinces of Costa Rica and Panama (Lino, Chiriqui Prov. at about 1600 m, 8°48'N, 82°26'W, 1♂, 1 ♀, Ris 1917). It is replaced to the north by *E. constrictor* (fig. 198) and to the south by *E. sabaleticus. Erpetogomphus tristani* will probably be found in southern Nicaragua, but its southernmost distribution is unknown.

Material

Type data. – Holotype male with following label data (all handwritten by P. P. Calvert unless otherwise noted): 'Oricuajo,/ Costa Rica./ July, 1911/ J. F. Tristan', '*Erpetogomphus*/ *tristani*/ ♂/ Calvert/ TYPE.', 'Needham/ fig' [in Needham's hand?], red label: '9244 TYPE [printed] 944/ *Erpetogomphus*/ *tristani* ♂/ Calvert.', '2nd ham-/ ules/ sheath of/ penis.' Allotype female with same label as holotype except for following: 'Labium &/ Maxillae.', '*Erpetogomphus*/ *tristani* ♀/ Calvert'. Both specimens were originally pinned, but each has been placed in a clear envelope. Both specimens in ANSP.

Other material (5♂, 4♀, including holotype ♂ and allotype ♀). – COSTA RICA: *Guanacaste Prov.*: Nicoga, Feb. 1912 (J. F. Tristan), 1♂ (UMMZ); Quebrada Azul, 2.5 mi W of Tilaran, 24 July 1967 (O. S. Flint, Jr., and Ortiz B.), 1♂, 1♀ (USNM); Rio Santa Rosa, 3.7 mi E of Las Canas, 25 July 1967 (O. S. Flint, Jr., and Ortiz B.), 1♀ (USNM); *Puntarenas Prov.*: 8 mi WNW of Esparta, 26 June 1967 (O. S. Flint, Jr., and Ortiz B.), 1♂ (USNM); stream 8.1 mi WNW of Esparta, 26 June 1967 (O. S. Flint, Jr., and Ortiz B.), 1♂ (DRP); *San Jose Prov.*: Res. Biol. El Rodeo, 7 km W of Villa Colon, 9°54'N 84°16'W, 800 m, 10-13 July 1990 (T. W. Donnelly), 1♀ (TWD).

Erpetogomphus ophibolus Calvert

(figs. 4-thx, 29-abd, 50-hamules, 73-penis, 95-app, 121-ept, 147-vertex, 175-vl, 198-distr)

Erpetogomphus ophibolus Calvert, 1905: 163 (Mexico: Atoyac in Veracruz, H. H. Smith, 2♂). – Calvert 1909: 489 (distr., Mex.); Muttkowski 1910: 87 (cat.); Calvert 1912a: 294 (comparison with *E. tristani*); Ris, 1917: 155 (comparison with *E. constrictor*); Williamson and Williamson 1930: 489 (summary of status); Kimmins 1969: 296 (type in BMNH); Montgomery 1973: 239 (derivation of name); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.154 (cat.); Tsuda 1991: 95 (cat.).

Erpetogomphus (Erpetocyclops) ophibolus. – Carle 1992: 148 (key to subgenera, type species of *Erpetocyclops* subg. n.).

Description

Male. – Labium, labrum, mandibles, anteclypeus brown; postclypeus entirely brown, or with small lateral green triangular spot; frons green except for brown along frontoclypeal suture, and at base of antefrons; vertex dark brown; area anterior to median ocellus undifferentiated, postocellar tubercles well developed, connected medially by a low transverse ridge, slightly tuberculate medially; occiput planar, trapezoidal, hind margin linear or slightly concave medially, crest covered with long brown hairs; postocciput brown, transversely concave; rear of head brown.

Prothorax brown, anterior lobe green, posterior lobe green brown; synthorax (fig. 4) with prominent well defined dark stripes on green background as follows: middorsal stripe slightly narrowing dorsally, antealar sinus and area along this structure connecting to humeral stripe, antehumeral stripe of same width as humeral connecting ventrally and (but not always) dorsally, and in some specimens broadly so, antehumeral not or just touching antealar sinus; second and third lateral stripes connecting at upper 0.75, isolating round green spot below subalar carina; posterior margin of metepimeron, metasternum and venter of thorax grey brown; venter of profemora grey green, remainder of femora dark brown, becoming black distally; tibiae, tarsi, armature black. Wings hyaline, venation and pterostigma black.

Venational statistics. Fifth (rarely fourth or sixth) antenodal thickened; number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 13-15/13-16, hind wing 10-12/10-12; pnx: fore wing 10-13/8-12, hind wing 9-12/9-12; cs under pterostigma: fore wing 4-7/5-8, hind wing 5-6/4-7; anal triangular cells: 3/3. Hind wing 25-27 mm.

Abdomen (fig. 29) with segment 1 brown, green posterolaterally and with a green middorsal stripe; segment 2 brown except for green auricles, ventral margin, and narrow middorsal stripe; annulus dark brown; segment 3 primarily dark brown, becoming black distally with green middorsal stripe extending from annulus of segment 2 and narrowing posteriorly to end, a pale grey anterolateral spot becoming narrower along ventral margin and disappearing at 0.25 to 0.50 of segment length; segments 4-6 similar to segment 3 but with pale middorsal stripe ending at posterior 0.10 to 0.75 of segment and anterolateral pale spot ending at transverse carina; segment 7 grey green on anterior 0.50 to 0.60, except for dark transverse carina, posterior part of segment brown to black; segments 8-10 red brown, becoming darker dorsally and ventrally, especially along foliate margins; posterior medial margin of segment 9 bluntly pointed or slightly so. Abdomen 30-33 mm.

Cercus (fig. 95) ivory brown, becoming brown distally, arcuate with a prominent laterally compressed dorsal tubercle on distal 0.75, extreme base with a black ventral tooth (mostly hidden by posterior margin of abdominal segment 10), though not as prominent as in *E. constrictor*; a ventral carina on distal 0.30 of cercus, tip of cercus with a black tooth; epiprocts brown, gently curved at distal 0.50, tips slightly diverging, each forming a blunt point (fig. 121), a well defined anterodorsally projecting tooth at middle of medial margin of epiproct.

Accessory genitalia. Hamules (fig. 50) small; anterior hamule brown, divided at distal 0.30, posterior branch a well developed shoulder; posterior hamule roughly triangular, its tip with a spine; penis (fig. 73) with cornuae slightly bilobate or transverse at base; a well developed prepuce, lateral lobe a small tooth.

Female. – Head markings similar to male but with some green on mediolateral areas of labrum, brown at base of antefrons with a median extension connecting with frontoclypeal suture, thus dividing frontal green into two spots. Morphology of vertex and occiput similar to male with following differences: transverse postocellar ridge (fig. 147) complete, slightly arcuate medially, with a slight shallow notch laterally before resuming at postocellar tubercle; occiput a narrow planar semicircle, crest covered with long brown hairs; postocciput tumid, brown; rear of head brown.

Pro- and synthorax as in male, with dark markings in some specimens less extensive.

Venational statistics (n = 11). Fifth (rarely fourth or sixth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-1/0-2; anx: fore wing 14-16/14-17, hind wing 10-12/10-13; pnx: fore wing 10-13/9-13, hind wing 10-13/10-14; cs under pterostigma: fore wing 5-8/5-8, hind wing 5-7/4-7. Hind wing 26-29 mm.

Abdomen with segment 1 brown, a green spot posterolaterally and a complete green middorsal stripe; segment 2 brown with following areas green: wide middorsal stripe narrowing posteriorly, incomplete lateral stripe extending from just anterior to auricle to black posterior annulus, a thin pale margin at venter of segment; segment 3 similar to segment 2 but brown becoming darker; middorsal stripe narrowing posteriorly and forming a mere line on posterior 0.25 of segment; lateral pale stripe ending posteriorly at transverse carina; segments 4-6 similar to segment 3 but middorsal green becoming increasingly smaller on successive segments, so that only a small middorsal spot occupies basal 0.10-0.50 of segment 6; segment 7 with anterior 0.50 pale green white, interrupted by brown transverse carina, posterior 0.50 becoming red brown to almost black; segment 8-10 all red brown to dark brown, darker dorsoposteriorly; cerci pale grey green. Vulvar lamina (fig. 175) with plates broadly connected at basal 0.75; relatively unspecialized, cleft obtusely V- or U-shaped, about as wide as each lobe; postlamellar ridge with Y- juncture posterior to plates, base of stem well defined and with oval depression laterally. Abdomen 30-33 mm.

Diagnosis

Males of *E. ophibolus* are unique in possessing an anterodorsal spine on the mediodorsal surface of the epiproct (fig. 95). The cercus of this species is most similar to that of *E. constrictor* (fig. 92). Morphology of the vertex and occiput serve to distinguish female *E. ophibolus* from similarly marked species. The median ocellus is in line with the lateral ocelli (fig. 147), separating this species from *E. sabaleticus, E. tristani* (fig. 146), and *E. constrictor* (fig. 145). Female *E. ophibolus* more closely resemble females of *E. schausi, E. agkistrodon,* and *E. eutainia.* However, *E. schausi* and *E. agkistrodon* have a transverse postocellar ridge which is medially bilobed (figs. 148-149), while *E. eutainia* lacks any postocellar ridge and has postocellar tubercles only. The postocellar ridge in *E. ophibolus* is arcuate and entire medially (fig. 147). *Erpetogomphus ophibolus* and *E. eutainia* are often sympatric, and the females superficially resemble one another. The second and third thoracic stripes in *E. eutainia* are always separate (figs. 7-9), but are connected at their upper 0.30 in *E. ophibolus* (fig. 4). Finally, females of *E. eutainia* lack the basal stem of the postlamellar ridge (fig. 178) present in *E. ophibolus* (fig. 175).

Remarks

Variation. – Most specimens of *E. ophibolus* that I examined are from southern Veracruz, and they show little variability in maculation. The single male from Chiapas has slightly more extensive black thoracic markings: the pale area between the dark humeral and antehumeral stripes is a narrow line. The two females from Belize have the apical dark brown on abdominal segment 7 laterally extending anteriorly separating the lateral pale area into one anterodorsal and one anteroventral spot. The acuminate condition of the posterior medial margin of abdominal segment 9 varies intraspecifically.

Biology. – This small green species often occurs with *E. eutainia* at small rivulets along the lowland Gulf of Mexico drainage systems of eastern Mexico. In 1976 I collected many by flushing them from agricultural stubble bordering trees and shrubs along the Rio Otapa in central Veracruz. Adults, when flushed, did not fly far and were consequently easy to collect. Six other gomphids collected at the same site under the same circumstances included *Phyllocycla breviphylla* Belle, *P. volsella* (Calvert), *Phyllogomphoides suasus* (Selys), *P. duodentatus* Donnelly, *Progomphus clendoni* Calvert, *Erpetogomphus eutainia*, and *E. bothrops*.

Raúl López (*in litt.*), from information given to him by Enrique González, writes that *E. ophibolus* is the most common gomphid in Veracruz, found yearround in the vicinity of the Los Tuxtlas Biological Station near Catemaco. Altitudinal range is from sea level to 615 m (Chiapas). Collection dates range from 8 June (Belize) to 13 September (Veracruz).

Distribution (fig. 198). – This species is thus far known from southern Veracruz (southeast of 19°N, 97°W), central Chiapas, Guatemala, and Belize. Tineke Boomsma (*in litt.*) collected a pair of this species in the Mountain Pine Ridge area of Belize (Cayo Distr.: Privassion Creek, 24 July 1993).

Material

Type data. Holotype male: [MEXICO] Vera Cruz, Atoyac, May (H. H. S[mith])/ Erpetogomphus ophibolus Calv. TYPE ♂. P. P. Calvert det. 1905. B. C. A. Neur., p. 164. Original of pl. 7, figs. 30-32, 46 (Kimmins 1969). In BMNH.

Other material (43♂, 12♀). – MEXICO: *Veracruz*: Rio Otapa, 8 km S of La Tinaja, 90 m, 13 Aug. 1976, (R. W. and J. A. Garrison), 18♂, 3♀, (RWG); 20 Aug. 1976, 12♂, 1♀ (RWG); Playa Escondida, 20-24 June 1981, (E. González), 1♀, (UNAM); Arroyo cerca de Playa Escondida, 17-24 July 1981, (E. González), 1♀, (UNAM); arroyo nr. Playa Escondida, about 30 km NE of Catemaco, 18°34-36'N, 95°04-09'W, 23 July-6 Aug., 9-13 Aug. 1982, (R. W. Garrison), 5♂, (RWG); Los Tuxtlas, arroyo despues de Laguna Escondida, 25 May 1980, (E. González), 1♂, (SWD); 11 June 1980, (R. Novelo), 1♂, (UNAM); Los Tuxtlas, stream nr. Jicacal Beach, 10 July 1979, (Gerado Jimenez), 1♀, (CC); Colonia Apachital, 16 km S, 10 km E of Tierra Blanca, 10 Sept. 1965, (T. W. Donnelly), 2♂, 1♀, (TWD, CC, UNAM); Rio Hondo, on rd. to 'Colonia la Apachital' 50 ft [15 m], 6 mi E of Hwy from Tierra Blanca to Cd. Aleman, 25-26 Aug. 1957, (G. H. Beatty III), 1♂, (FSCA); 3 km N of Santiago Tuxtla, 13 Sept. 1965, (T. W. Donnelly), 1♀, (CC); *Chiapas*: stream 20.1 mi N Ocozocoautla, 2000 ft [615 m], 25 Aug. 1967, (D. R. and M. L. Paulson), 1♂, (FSCA); BELIZE: *Toledo Distr.*: Blue Creek Village, EARTHWATCH Belize Expedition, 1981, 8 June 1981, (D. H. Messersmith, W.E. Steiner, *et al.*), 1♀, (USNM); *Cayo Distr.*: Mountain Pine Ridge, Rio Frio at Augustine, 16°58'N, 88°59'W, 500 m, 22-25 July 1983, (T. W. Donnelly), 1♀, (TWD); GUATEMALA: *El Progreso Dept.*: 6.5 km N of Est. de la Virgén, 29 Aug. 1965, (T. W. Donnelly), 1♂, 2♀, (TWD).

Erpetogomphus agkistrodon sp. n.
(figs. 5-thx, 30-abd, 148-vertex, 176-vl, 198-distr)

Type material. – Holotype ♀, MEXICO: Veracruz State, Parque Javier Clavijero, Jalapa, 23 Aug. 1982, 1300 m (R. López) in UNAM.

Description

Male. – Unknown.

Holotype female. – Labium pale grey, becoming dark grey medially; labrum, clypeus, base of mandible dark brown washed with dark olive green along median area of labrum, ante-clypeus, and above lateral lobes; pale green spot along lateral margin of labium; broad green stripe above frontoclypeal suture continuing to near base of vertex; antennae, vertex, occiput dark brown; transverse postocellar ridge (fig. 148) complete, emarginate medially; rear of occiput broadly semicircular; rear of head dark brown.

Prothorax entirely brown except for green anterior lobe; synthorax (fig. 5) with dark brown thoracic stripe well developed on green background; triangular middorsal stripe interrupting inverted green '7' at base, upper end of middorsal stripe connecting with antehumeral and humeral stripes, these two united leaving only pale spot below antealar sinus, and small green streak below; second lateral stripe connecting with humeral and third lateral stripes above and below, this stripe also connecting with third lateral below antealar sinus, thus isolating a green spot; metaspiracle black; posterior margin of metepisternum with a dark brown stripe; metasternum dark browngrey. Femora red-brown, becoming black distally; remainder of legs and armature black.

Wings hyaline, venation and pterostigma black.

Venational details. Sixth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 3/2; anx: fore wing 15/17, hind wing 12/11; pnx: fore wing 14/16, hind wing 15/15; cs under pt: fore wing 6/5, hind wing 5/6. Hind wing 31 mm.

Abdomen (fig. 30) predominantly black with vestiges of a narrow green middorsal stripe on segments 2-6; anterior 0.25 of segment 7 green, becoming white laterally; broad brown midlateral stripe on segment 2 becoming darker on segment 3 and more extensive on succeeding segments, thus encircling small white anterolateral spots; auricle on segment 2 green; segments 8-10 entirely black, cercus white. Vulvar lamina as shown in fig. 176. Abdomen 31 mm.

Diagnosis

Erpetogomphus agkistrodon belongs to the *E. tristani* group because of the simple condition of the vulvar lamina and the complete postocellar ridge. This species is distinguished from females of all other species by the emarginate condition of the postocellar ridge. That of *E. ophibolus* is entire. The female of *E. agkistrodon* is similar to the only known female of *E. schausi*, and is diagnosed under the latter species.

Remarks

I suspect the male of *E. agkistrodon* will have a penis similar to that of *E. ophibolus* or *E. schausi*; it should have a prepuce and the lateral lobes should be small, semi-circular and with or without spinules.

The thickened sixth antenodal in this species is an unusual condition: the fifth antenodal is usually thickened throughout the genus. However, this may be an anomaly of the holotype.

No conspicuous depressions or pits are present anterior to the median ocellus. This area, instead, forms a shallow transverse V. Based on female morphology, I suspect the male epiprocts will be relatively thick, gently curved at posterior 0.5, forming a 90° angle, tip broadly spatulate.

Biology. – The female was collected along a shaded creek in company with *Cordulegaster diadema godmani* McLachlan. *Erpetogomphus boa* were also taken at the locale, though they were flushed from low vegetation about 50 m from the stream.

Distribution (fig. 198). – Known only from the type locality.

Erpetogomphus schausi Calvert

(figs. 6-thx, 31-abd, 51-hamules, 74-penis, 96-app, 142-face, 149-vertex, 177-vl, 198-distr)

Erpetogomphus schausi Calvert, 1919: 33 (desc. holotype ♂). – Calvert 1920a: 113 (note on type); Williamson and Williamson 1930: 13 (summary of status); Paulson 1982: 255 (Guat.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.187 (cat.); Tsuda 1991: 95 (cat.).

Description

Male. – A thorough description of the holotype female accompanies the original description. I illustrate the thorax (fig. 6), abdomen (fig. 31), accessory genitalia (fig. 51), penis (fig. 74), head (fig. 142), and caudal appendages (fig. 96) of the holotype. The specimen has been skewered with a bristle. The cercus of the holotype (fig. 96) is strongly curved at distal 0.30, the ventral margin has a remnant of an inferior carina at its extreme base, but is well developed again on the distal 0.50.

Venational statistics (based on holotype ♂ and one ♂ from Costa Rica): number of marginal cells behind fore wing paranal cells: 3/2-3; anx: fore wing 16-18/16-20, hind wing 12-14/12-13; pnx: fore wing 15/14-15, hind wing 13-14/13-15; cs under pterostigma: fore wing 5-6/5-6, hind wing 6/5-6; anal triangular cells: 4/4. Hind wing 29-30 mm. Abdomen 32-33 mm.

Female. – Labium grey; labrum brown with indication of green mediolaterally, ante- and postclypeus brown with possible green medially on postclypeus; frons green with brown along frontoclypeal suture and base of antefrons, especially medially, with offshoot almost touching frontoclypeal suture, thus almost separating green; base of antefrons with a slight longitudinal raised area with a slight concavity on each side; antennae, vertex brown; transverse postocellar ridge (fig. 149) complete, emarginate medially; occiput brown, semicircular crest covered with long brown hairs; postocciput brown, convex, rear of head brown.

Prothorax entirely brown, paler on anterior and posterior lobes; synthorax as in holotype male (fig. 6); femora grey brown, tibiae and tarsi darker, armature black.

Wings hyaline, venation and pterostigma black.

Venational statistics (n = 1). Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 2/0; anx: fore wing 16/16, hind wing 12/11; pnx: fore wing 15/15, hind wing 14/14; cs under pterostigma: fore wing 6/5, hind wing 6/6. Hind wing 31 mm.

Abdomen compressed laterally with markings mostly unrecognizable, but probably similar to *E. agkistrodon* (fig. 30). Vulvar lamina simple (fig. 177), similar to that of *E. agkistrodon*. Abdomen about 32 mm.

Diagnosis

Erpetogomphus schausi is unique in possessing a combination of characters of the penis (with well developed prepuce) and caudal appendages (with gently decumbent cercus (fig. 96)). Although the morphology of its penis allies this species with *E. sabaleticus*, *E. tristani*, and *E. constrictor*, the penes of the other three species lack well developed cornuae and a spinulate lateral lobe, typical of *E. schausi*. The only known female differs from all other known species except *E.*

agkistrodon in possessing a complete transverse postocellar ridge which is notched medially. The only morphological difference that I have noted between these two species is the broader, more semicircular occiput (figs. 149) of *E. schausi,* compared with the narrower, more broadly semicircular condition found in the holotype of *E. agkistrodon* (fig. 148). The sixth antenodal crossvein is thickened in all four wings of *E. agkistrodon,* while the fifth is thickened in this female of *E. schausi*; but, as stated under *E. agkistrodon,* I suspect the condition in the holotype is atypical.

Remarks

Variation. – The male sex of this species is known from only two specimens, the holotype male described in detail by Calvert (1919), and another male from Costa Rica collected by J. Belle and loaned to me for inclusion in this paper. The Costa Rican male is slightly smaller (HW = 29 mm) than the holotype (HW = 30 mm) and differs as follows (condition for holotype in parentheses): small green triangle just lateral to medial area of anteclypeus (all dark brown); round green spot below antealar sinus of mesepisternum smaller (bigger); anterior pale abdominal spots extending well beyond transverse carina on segments 3-7 (these spots smaller and confined to anterior 0.25 of segments 4-6, to 0.5 of segment 7); sides of abdominal segments 8-10 light brown (dark brown); lateral lobe of penis more angulate (more rounded); second thickened antenodal in fore wing 5-5 (6-7) and in hind wing 5-6 (6-6).

The holotype appears to be a fully mature male: traces of pruinosity are present on the venter of its thorax. The Costa Rican male seems to be less mature: it lacks pruinosity, and the dark brown areas of the holotype are pale in this specimen. The green areas of the thorax of the Costa Rican male are slightly more restricted than for the holotype.

The teneral female described above seems to represent the female of this species. The combination of characters allying it with the *E. tristani* group and the occurrence of a male from Puntarenas Province, lead me to suspect that I have associated this specimen correctly.

Before the discovery of the two *E. schausi* from Costa Rica, I considered the possibility that *E. agkistrodon* might be the female of *E. schausi*: morphological considerations in light of the characters for other members of the *E. tristani* group (*e.g.*, vulvar lamina, shape of occiput) supported this view. However, the geographic distance (about 1700 km), coupled with the local occurrence of both forms, tend to discount this. It is possible that the morphological differences I detect in the occiput of female *E. agkistrodon* and *E. schausi,* though major, may be due to geographic variation, which would render *E. agkistrodon* a junior synonym of *E. schausi.*

Biology. – Nothing is recorded of the circumstances of capture of the holotype. Jean Belle records the following for the Costa Rican male: 'This gomphid was secured on the grass-covered bank of an almost impassable mountain rivulet where the insect alighted after a clash with a *Hetaerina* specimen. The colors when alive are as follows: compound eyes dark brown; head and thorax dark brown with light green; middorsal pale spots of abdominal segments 3 to 6 and pale spot of abdominal 7 yellow.'

Altitudinal data range from 1220 m to 1500 m; the female was collected 8-9 April, the Costa Rican male on 30 August.

Material

Type data. – Holotype male: GUATEMALA: Dept. Purulhá, Baja Vera Paz, 1220 m, forest stream (W. Schaus, J. Barns), 7 July [no date], in ANSP.

Other material (2♂, 1♀, including holotype ♂). – COSTA RICA: *Puntarenas Prov.*: Monte Verde, 1500 m, rivulet, 30 Aug. 1986 (J. Belle), 1♂ (RNHL); Rio Bellavista, *ca.* 1.5 km NW of Las Alturas (8.951 N, 82.846 W), elev. 1400 m, 8-9 April 1987 (Holzenthal, Hamilton, Heyn), 1♀ (USNM).

Distribution (fig. 198). – Known only from the type locality in Guatemala and Puntarenas Province, Costa Rica. It probably occurs in intervening Central American republics.

Erpetogomphus eutainia Calvert
(figs. 7, 8, 9-thx, 32, 33-abd, 52-hamules, 75-penis, 97-app, 122, 123, 124, 125-ept, 143, 144- face, 150-vertex, 178-vl, 199-distr)

Herpetogomphus menetriesii. – Selys, 1878: 429 (24 sep.) ('Guatemala. (Un mâle [*sic*, female] incomplet. Musée de Paris, une femelle. – Coll. Selys.')).

Erpetogomphus eutainia Calvert, 1905: 162 (1♂, Rio Papagayo in Guerrero, Mexico). – Calvert 1919: 35 (comparison with *E. schausi*); Kimmins 1969: 293 (type in BMNH); Paulson 1982: 255 (U.S., Mex., Guat.); Davies and Tobin 1985: 27 (cat.); Tsuda, 1986: 87 (cat.); Bridges 1991: VII.72 (cat.); Tsuda 1991: 95 (cat.).

Erpetogomphus diadophis Calvert, 1905: 167 (2♂, Texas). – Muttkowski 1910: 87 (cat.); Needham and Heywood 1929: 79 (descr.); Needham and Westfall 1955: 147 (descr.); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Kimmins 1969: 293 (type in BMNH); Paulson, 1982: 266 (synonymy of *E. diadophis* and *E. eutainia*); Bridges 1991: VII.60 (cat.).

Erpetogomphus ? diadophis. – Calvert 1919: 36 (Guat., possible conspecificity with *E. diadophis*)

Herpetogomphus diadophis. – Byers 1928: 5 (larva unknown).

Erpetogomphus (Calogomphus) eutainia. – Carle 1992 (key to subgenera, type species of *Calogomphus* subg. n.).

Description

Male. – Labium grey to dark grey, labrum all green with a small medial spot on anterior margin (fig. 144) to entirely brown with large central green spot (fig. 143), base of mandibles green, tips becoming black, anteclypeus all green to largely brown; postclypeus green with brown medially along frontoclypeal suture and descending laterally along lateral lobes, thereby isolating medial green spot; in more southerly specimens, brown expanding so that green confined to lateral margins; frons green with brown along frontoclypeal suture and at extreme base of antefrons; vertex brown with medial transverse area at postocellar tubercles green, to entirely brown; occiput brown, transverse triangular pits anterolateral to medial ocellus, postocellar tubercles low, incomplete medially; occiput trapezoidal, largely planar except for medial swelling; crest costate, linear to slightly concave, rimmed with long brown hairs; postocciput green medially to all brown, concave; rear of head brown.

Prothorax brown along middle lobe, remainder green or becoming entirely brown except for pale anterior lobe; synthorax (figs. 7-9) with prominent, well-defined dark brown stripes on green background as follows: middorsal stripe expanding toward collar, divided by pale middorsal thoracic carina, not touching collar, medial 0.5 or entire antealar crest, linear antehumeral, not touching upper margin; humeral, second and third lateral stripes, medial area of mesinfraepisternum; more southerly specimens with these stripes becoming thicker (figs. 8-9) so that antehumeral and humeral connect at lower and upper ends; a vestigial stripe along posterior margin of metepimeron; venter of thorax and metasternum pale grey green to grey. Coxae, trochanters pale green, venter of profemora green, remainder of profemora black; metafemora dark brown to black except for pale area ventrally; basal 0.40 to 0.60 of metafemora pale green to dark grey, becoming black apically; tibiae, tarsi and armature black.

Wings hyaline, venation and pterostigma black; more northerly specimens with pale, narrow line along costa disappearing proximal to pterostigma.

Venational statistics. Fifth, rarely fourth, antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-1/0-1; anx: fore wing 11-15/11-15, hind wing 8-11/8-10; pnx: fore wing 8-11/8-12, hind wing 8-11/8-11; cs under pterostigma: fore wing 4-6/4-6, hind wing 4-6/4-6; anal triangular cells: 3-4/3-4. Hind wing length 23-25 mm.

Abdomen (fig. 32) with segment 1 green and a pale brown dorsolateral stripe on each side; segment 2 brown except for green auricles, ventrolateral margin, and middorsal stripe; segment 3 with lateral brown stripe, interrupted medially just posterior to transverse carina, and with an irregular pale spot within anterior brown spot, posterior brown more prominent posteriorly and meeting dorsally on posterior 0.10 of segment; more southerly specimens with lateral brown not interrupted medially and with pale anterolateral spot reduced or almost absent; incomplete middorsal stripe blue green, pale areas becoming white laterally; segments 4-6 similar to segment 3 but with dark brown more prominent posteriorly and with anterolateral white spot confluent with ventral margin; segment 7 pale blue green on anterior 0.50-0.60, except orange brown transverse carina, posterior part of segment dark red brown; segments 8-10 red brown, becoming darker dorsally and ventrally, especially along foliate margins; posterior medial margin of segment 9 smoothly carinate, or with a moderately blunt point. Abdomen 29-32 mm.

Cercus (fig. 97) ivory, becoming brown distally, gently arcuate at distal 0.30, with a small black tooth, a ventral costate carina on basal 0.35-0.40 of cercus, often ending in a small, isolated, pebble-like tooth; in other specimens, the posterior part of this carina may be pebble- like; epiprocts (figs. 122-123) brown, moderately curved along posterior 0.50, tip of epiproct in lateral view thick, bluntly pointed, with lateral costate margin; tips in posterior view (figs. 124-125) planar, roundly divergent.

Accessory genitalia. Hamules (fig. 52) small, anterior hamule brown, distal 0.25 divided, the superior branch meeting the inferior branch, thus enclosing an oval space; posterior hamule small, digit-shaped, no apical hook; penis (fig. 75) with long pointed cornuae; dorsal membranous hood prominent, its ends parallel; lateral lobes large, frill-like, their margins with spinules; dorsal area of membranous third segment with a pair of mediolateral blunt chitinized tubercles.

Female. – Head as in male with following differences: brown at base of antefrons projecting anteriorly, partially isolating dorsal green; vertex morphology similar to male, postoccipital tubercles small, isolated medially, occiput trapezoidal as in male, planar with faintly convex arcuate crest; postocciput brown, planar.

Thorax as in male.

Venational statistics. Fifth, rarely sixth, antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-2/0-3; anx: fore wing 13-16/13-16, hind wing 9-11/8-11; pnx: fore wing 8-12/8-11, hind wing 8-12/8-13; cs under pterostigma: fore wing 4-7/4-7, hind wing 4-7/4-7. Hind wing 25-28 mm.

Abdomen (fig. 33) with segment 1 green with a brown dorsolateral stripe; segment 2 similar to segment 1, but with wash of brown along ventral margin of tergite; segment 3 with dorsolateral stripe darker, expanding posteriorly and connecting above at posterior 0.10 to 0.20 or separated by thin hairline of green, ventral margin with brown interrupted by white below brown dorsolateral stripe; in more northerly specimens, connecting above with middorsal green stripe; posterior part of brown connecting with dorsolateral stripe posteriorly, transverse carina dark brown; segments 4-6 similar to segment 3 but brown darker, more definite, connecting posterodorsally on 0.25-0.50 on progressive segments, lateral white confined to spots, one at anteroventral margin, another ventromedially, these two spots sometimes connected by narrow line of white ventrally; more northerly specimens with medioventral white connecting with middorsal green stripe; segment 7 with anterior 0.50 white except for darkened transverse carina, posterior 0.50 dark brown; segments 8-10 dark brown; cerci white, their tips black. Vulvar lamina (fig. 178) with plates small, almost digit-shaped; U-shaped cleft about as wide as or wider than each plate; postlamellar ridge with a costate semicircular ridge. Abdomen 29-33 mm.

Diagnosis

The characteristically shaped posterior hamules (fig. 52) and penile structures (short prepuce, wide spinulate lateral lobe [fig. 75]) separate males of this species from all others except *E. leptophis. Erpetogomphus eutainia* possesses a straight or pebble-like ventral carina on the basal 0.25 of the cercus (fig. 97); no such carina is present in *E. leptophis* (figs. 98).

Females of *E. eutainia* and *E. leptophis* are unique in possessing a semicircular postlamellar ridge; in all other congeners, this structure is a Y-shaped ridge. The posteriorly pointed occipital protuberance in *E. leptophis* (fig. 151) is distinct from the relatively unmodified condition present in *E. eutainia* (fig. 150).

Remarks

Variation. – Venational details of holotype male of *E. eutainia.* No marginal cells behind fore wing paranal cells; anx: fore wing 14/14, hind wing 10/10; pnx: fore wing 10/9, hind wing 10/10; cs under pterostigma: fore wing 5/5, hind wing 5/6; number of anal triangular cells: 4/4. Hind wing 24.5 mm.

Venational details of holotype female of *E. diadophis*: number of marginal cells behind fore wing paranal cells: 0/1; anx: fore wing 13/14, hind wing 10/10; pnx: fore wing 10/9, hind wing 10/11; cs under pterostigma: fore wing 6/7, hind wing 6/5. Hind wing 28 mm.

This small species has a widespread distribution and, consequently, exhibits some degree of clinal variation north to south. Specimens from southeastern Texas and northern Mexico are the palest: the dark transverse markings of the face are narrower, and green is often present medially on the vertex and occiput. The labrum is mostly green (fig. 144), the dark thoracic stripes are narrow, and none is present on the posterior margin of the metepimeron (fig. 7). Medial bands of white encircle abdominal segments 3-6 in both sexes. The dark somatic markings are darker, broader, and more definite in specimens from southern Veracruz. Vestiges of a stripe on the posterior margin of the metepimeron can be seen (fig. 8), and the pale white medial abdominal bands are obscured, entirely or almost entirely interrupted by the dorsolateral brown stripe. Specimens from Costa Rica are the most melanic (figs. 9, 143); no green is present on the vertex or occiput, and the middorsal green stripe of abdominal segments 3-6 is always separate from the medioventral white.

The ventral carina of the cercus is also variable. Some specimens have a continuous costate carina with a small, isolated, pebble-like tooth distally; but others may have several antepenultimate pebble-like teeth in addition to the longer ultimate one. The tips of the epiproct may also be variable. In most specimens, these structures are posteriorly flattened (fig. 122) with the outer margin slightly to strongly concave (fig. 123). The male from El Progreso, Guatemala, has the epiprocts similar to the condition described above, but they are narrower (fig. 125).

The clinal differences described above probably led Calvert (1905) to interpret the female of *E. diadophis* as a separate species from *E. eutainia.* Calvert (1919) later received another female from Guatemala, which he postulated may be the same as the paratype of *E. diadophis*; he made no mention of *E. eutainia.*

The large series of males and females examined from various parts of its range convince me that Paulson (1982) was correct in synonymizing the two names. The status of the two females (not male and female) described by Selys (1878) as *Herpetogomphus menetriesii* is discussed under the status of *E. menetriesii.* I also examined a female labelled '*Cyanogomphus*? / *mexicanus*/ n. sp. / coll. R. Martin / ♀', from Honduras, in the MNHP.

Biology

I collected this small, colourful species in southeastern Texas over several years. They were flushed from stubble bordering agricultural fields next to the Gonzales River. They were sympatric with the larger *E. designatus*, and were about as common. However, the former species behaved more like a damselfly, for they never flew far, rested on tips of stubble or barbs of barbed-wire fences, and were always easy to take with a net. I collected one male which was the prey of a robber fly (Asilidae); another, I rescued from an orb-weaver spider web. I was able to photograph a pair in copula in the late afternoon.

In southern Veracruz at the Rio Otapa, *E. eutainia* had similar habits, as described under *E. ophibolus.*

The female from El Salvador (Rio Palio) has the following by V. Hellebuyck: 'on bushes along a fast running river, clear water, rocky bottom & shady banks'. Altitudinal ranges are from near sea level (20 m, Medina Bank, Belize) to 615 m (Oaxaca). Collection dates range from 19 May (Costa Rica) through October (Veracruz, La Gloria; Guerrero, Rio Papagaio).

Distribution (fig. 199). – This species occurs southeast of the Edwards Plateau in southern Texas, south along the lowlands and foothills of the Sierra Madre Oriental in northern and central Mexico. The farthest western locality is El Sabino in Michoacan state. Specimens have been collected sporadically in Belize, Guatemala, Honduras, El Salvador, and northern Costa Rica.

Material

Type data. – Holotype male of *E. eutainia* [labels all printed unless otherwise stated]: 'R. Papagayo, / Guerrero, 1200 ft. / Oct. H. H. Smith.', 'Brit. Mus. / 1911-339.', 'ERPETOGOMPHUS/ *eutainia* Calvert [written]/ P. P. Calvert, det. 1905 [written]/ B. C. A. Neur., p. 162 [written]/ Original of Pl. 7, f. 24-27, 39 [all written]', small round label with red border: 'Holo-/ type', in BMNH. Holotype female (not male, as erroneously stated by Kimmins, 1969) of *E. diadophis*: [labels all printed unless otherwise stated]: 'Texas [written by an unknown hand]', pale violet label: 'McLachlan Coll./ B. M. 1938-674.', 'ERPETOGOMPHUS ♀ [written]/ *diadophis* Calv. TYPE [written]/ P. P. Calvert, det. 1905 [written]/ B. C. A. Neur., p. 167 [written]/ original of Pl. VII, ff. 35, 47 [all written]', in BMNH.

Material examined (74♂, 42♀, including holotypes of *E. eutainia* and *E. diadophis*). – U. S. A.: Texas: *Caldwell Co.*: San Marcos R. at Luling, (FSCA, CC); *Gonzales Co.*: Guadalupe River, 4 mi S of Gonzales, (CC, RWG); near Otting, Palmetto State Park, (FSCA); Palmetto State Park, 6 mi S of Luling, (RWG); Mexico: *Michoacan*: El Sabino, 20 mi SSE of Uruapan (UMMZ, RWG); *Oaxaca*: La Escondida, route 190, km 727, 2000', (USNM); *San Luis Potosí*: Tamazunchale, (USNM); *Tamaulipas*: 3 mi S of Ciudad Victoria, (USNM); *Veracruz*: Cardel, La Gloria, (USNM); pond 2.7 mi S of La Tinaja, 300 ft., (DRP); Rio La Palma, 25 km N of Catemaco, (RWG); Rio Otapa, 8 km S of La Tinaja, 90 m, (RWG); Sontecomapan, Coscoapan, (UNAM); Belize: *Toledo Dist.*: Medina Bank, 20 m, (TB); Guatemala: *El Progreso Dept.*: San Agustin Ac., (FSCA); *Zacapa Dept.*: Zacapa, (FSCA); unknown locality and date ('Rodig.' [illegible]) [labelled as *Herpetogomphus menetriesii*], (IRSN); unknown locality, date, and collector [labelled '*E. menetriesii*? Selys'], (MNHP); Honduras: Unknown locality, date, and collector [labelled '*Cyanogomphus?/ mexicanus*/ n. sp./ (Coll. R. Martin/ ♀'], (MNHP); El Salvador: *La Libertad Dept.*: Rio Palio, San Juan Opico, 400 m, (VH); Costa Rica: *Alajuela Prov.*: Quebrada Mina 0.2 mi S Hwy. 11 on Hwy, (FSCA); *Guanacaste Prov.*: Hda. Taboga, 100 ft., (DRP); Rio Santa Rosa, 3.5 mi N of Cañas, 300 ft (DRP).

Erpetogomphus leptophis sp. n.

(figs. 10-thx, 34, 35-abd, 53-hamules, 76-penis, 98-app, 151-vertex, 179-vl, 200-distr)

Type material. – Holotype male. Belize: Toledo District, I. Z. E. field station, Blue Creek, 25 June 1983 (M. L. May) (FSCA). Allotype female. Belize: Toledo District, Blue Creek Village (Earthwatch) Belize Expedition 1981, 8 June 1981 (D. H. Messersmith, W. H. Steiner, *et al.*) (USNM).

Description

Holotype male. – Labium light grey, becoming dark grey medially; labrum green with dark brown margin and medial line almost separating green into two spots; base of mandibles grey-green, anteclypeus green, postclypeus brown except for small green spots above lateral lobes; ventral margin of frons brown, joining brown of postclypeus, thus forming a large frontoclypeal stripe; remainder of frons green; a large transverse furrow at base of antefrons, this area with a pair of deeper pits, each anterolateral to median ocellus; postocellar ridge complete, but with medial part lower and at level of lateral ocelli; extreme base of frons, entire vertex, and occiput dark brown, occiput tumid medially, hind margin mostly straight but peaked medially so that hind margin seems slightly angularly convex; rear of head dark brown.

Prothorax entirely brown except for following green areas: anterior lobe, and two small midlateral spots (almost touching) on median lobe; synthorax (fig. 10) with dark brown thoracic stripes well developed on green background; dark middorsal stripe triangular, its wide base touching collar but not connecting with antehumeral; antehumeral and humeral connected along upper 0.25, thus isolating small green spot; second lateral as shown in fig. 10, a posterior branch connecting with third lateral along upper 0.30, isolating a green spot; posterior margin of metepimeron brown, all thoracic stripes connected by brown along antealar sinus; metasternum grey-brown. Venter of profemora grey-green, remainder of legs dark brown; tibiae, tarsi, armature black.

Wings hyaline, venation and pterostigma black.

Venational details. Fifth antenodal thickened in all wings; no supplementary marginal cells behind fore wing paranal cells; anx: fore wing 14/13, hind wing 10/10; pnx: fore wing 10/11, hind wing 10/10; cs under pterostigma: fore wing 6/5, hind wing 5/5; anal triangular cells: 4. Hind wing 29 mm.

Abdomen as in fig. 34. Segment 1 brown, green laterally and with a green middorsal spot; segment 2 brown except for green auricles, ventral margin, and narrow middorsal spot with a cordate expansion in the middle; segment 3 black with green middorsal stripe ending at basal 0.30 of segment and grey anterolateral spot; segment 4 black with anterior 0.2 white laterally, becoming green dorsally; segments 5-6 like segment 4; segment 7 with anterior 0.5 white laterally, becoming green dorsally, posterior 0.5 of segment dark red-brown; segments 8-10 red-brown, posterior medial margins of segments 8-9 slightly pointed. Abdomen 31 mm.

Cercus (fig. 98) light green, simple, with no ventral carinae, slightly arcuate, tip black; epiprocts brown, gently curved at distal 0.5, tips viewed posteriorly with parallel sides, forming bluntly rounded tips.

Accessory genitalia. Hamules (fig. 53) small; anterior hamule brown, distal 0.25 divided, the superior branch meeting the inferior branch, thus enclosing an oval space; posterior hamule small, finger-like, no apical hook; penis (fig. 76) with long, pointed cornuae, dorsal membranous hood long, its ends crossing (fig. 76); lateral lobes large, frill-like, their margins with spinules.

Allotype female. – Head as in male except on labrum, brown medial line separating green into two spots; base of antefrons as in male (fig. 151) with a raised bilobed ridge between lateral ocelli; posterior margin of occiput with a prominent, posteriorly directed, pointed protuberance, its base tumid so that entire raised area assumes shape of a plumbob.

Thorax as in male.

Wings hyaline, similar to male.

Venational details. No supplementary marginal cells behind fore wing paranal cells; anx: fore wing 14/16, hind wing 9/11; pnx: fore wing 11/13, hind wing 10/11; cs under pterostigma: fore wing 5/4, hind wing 5/6. Hind wing 25 mm.

Abdomen (fig. 35) with segment 1 brown, becoming dark green-brown laterally; segment 2 brown with a narrow green middorsal stripe and green lateral stripe encircling auricle and extending entire length of segment; segment 3 like segment 2, but brown becoming darker and green lateral stripe abbreviated, forming an elongate spot along basal 0.5 of segment; segments 4-6 all black with white basal band, extending ventroposteriorly along ventral margin of tergites; segment 7 with anterior 0.30 white, remainder dark red-brown; segments 8-10 dark red-brown, cercus white. Vulvar lamina (fig. 179) with plates connected anteriorly, plates wider than in *E. eutainia*; postlamellar ridge semicircular as in *E. eutainia*. Abdomen 30 mm.

Diagnosis

The structure of the hamules and penis ally *E. leptophis* with *E. eutainia*, but the superior appendages easily distinguish the two species (figs. 97-98). *Erpetogomphus eutainia* has a pebble-like ventral carina on the basal 0.25 of the cercus; but no such structure is present in *E. leptophis*. The posteriorly directed pointed occipital protuberance easily identifies the female of *E. leptophis*. The female shares with *E. eutainia* the semicircular postlamellar ridge, but *E. leptophis* possesses a bilobed ridge between the lateral ocelli. This surface is planar in *E. eutainia*.

Remarks

Although the types were taken by different collectors two years apart, the female characters indicate it is the female of *E. leptophis*.

Biology. – Michael May collected the male along a creek in the forest.

Distribution (fig. 200). – Known only from the type locality.

Erpetogomphus elaphe sp. n.

(figs. 11-thx, 54-hamules, 77-penis, 99-app, 180-vl, 200-distr)

Erpetogomphus elaps. – Calvert 1907: 398 (Costa Rica, figures anterior hamules).

Erpetogomphus sp. n. near *elaps*. – Dunkle 1988: 46 (Honduras).

Description

Holotype male. – Labrum pale grey green; anteclypeus, labrum, base of mandibles pale green, tips of mandibles dark brown; postclypeus and frons pale green, a slight wash of brown on lateral margins of frontoclypeal suture, antefrons pale green, slightly darker at base, vertex dark brown; a deep transverse trough in front of median ocellus; pedicel, scape, and flagellum brown; occiput trapezoidal, pale green, mostly planar, slightly tumid medially, crest slightly prominent, slightly emarginate medially and covered with long brown hairs; postocciput green, transverse when viewed dorsoposteriorly; rear of head yellow brown.

Prothorax green, becoming brown on middle lobe laterally and anteromedially. Synthorax (fig. 11) apple green with following dark areas: poorly defined middorsal stripe not extending to collar and interrupted medially by middorsal thoracic carina and antealar crest, well defined antehumeral stripe narrowing dorsally but touching antealar crest and extending ventrally to mesinfraepisternum, a small posterior offshoot from antehumeral stripe at upper 0.10 connecting with vestigial first lateral stripe which is abbreviated to upper 0.50; venter of synthorax green, coxae and trochanters grey green, femora pale green becoming dark brown on distal extensor surfaces, these dark markings occupying distal 0.80 of profemora, about distal 0.60 of mesofemora, and distal 0.30 of metafemora; tibiae and tarsi black; armature black.

Wings hyaline, anterior margin of costa yellow to pterostigma, thereafter black; yellow at base of costa darkening to brown at costal triangle, pterostigma brown, veins bordering it black.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1/1; anx: fore wing 13/13, hind wing 10/10; pnx: fore wing 9/9, hind wing 9/10; cs under pt: fore wing 6/5, hind wing 4/6; anal triangular cells: 4/3. Hind wing 26 mm.

Abdomen with segment 1 yellow green with a wash of brown dorsolaterally; segment 2 yellow green dorsally and ventrally, with a brown midlateral stripe expanding ventrally behind auricle, anterior 0.5 of this stripe poorly defined, annulus dark brown; segment 3 light yellow green dorsally interrupted laterally by a longitudinal brown stripe well marked at transverse carina, expanding again at posterior 0.25 of segment and connecting dorsally at black annulus; inferior margin of tergite probably ivory (post mortem preservation has partially obscured this area); segments 4-6 similar to segment 3, with anterior 0.10 of dark midlateral interrupted and with gradual dorsolateral expansion of stripe so that inverted dorsal pale green wedge-shaped middorsal stripe disappears at distal 0.40 of segment 6; segment 7 pale green brown becoming tawny on posterior 0.10 of segment; segments 8-10 red brown becoming darker dorsolaterally on segment 8; foliate expansion and denticles black. Abdomen 33 mm.

Cercus (fig. 99) pale ocher becoming dark brown at tip; linear, gradually narrowing distally, tips roundly pointed, a weakly defined ventral carina on distal 0.50 of cercus; epiprocts brown, gently curved at 90° angle; tips spatulate when viewed posteriorly.

Accessory genitalia (fig. 54). Anterior hamule green basally, becoming dark brown distally, branched at distal 0.50; superior (upper) branch greatly enlarged, as long as stem of hamule with resulting interval between branches small, semicircular; posterior hamule (fig. 54) almost digit-shaped, wider at base, with a poorly developed anterior shoulder, tip broadly rounded, without an apical tooth; penis with a prominent knife-like serrated lateral lobe; membranous hood well developed but lobes not overlapping, cornua pointed but with median shoulder as in fig. 77.

Allotype female. – Similar to male in markings and colouration. Head with transverse trough anterior to median ocellus as in male, but occipital region differing as follows: occiput small, erect, barely visible in dorsal view, convex medially; postocciput with median tumid area. Thoracic, leg, and abdominal patterns as in male, but dark areas more restricted; middorsal and antehumeral stripes faint, first lateral stripe vestigial, confined to upper 0.20 of thorax.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1/2; anx: fore wing 14/15, hind wing 10/10; pnx: fore wing 10/11, hind wing 11/12; cs under pterostigma: fore wing 6/5, hind wing 5/6. Hind wing 29 mm.

Vulvar lamina (fig. 180) with basal plate prominent, lobes narrow with medial margins distinctly concave, their bases not touching; distal part of lobe with a ventral flap bent under; its costate rim visible externally and disappearing medially near base of lobe (fig. 180); with resultant cleft forming a wide, U-shaped interval; Y-shaped juncture of postlamellar ridge not extending beyond posterior margin of plate, stem with diagonally ovaloid depression on each side. Abdomen 34 mm.

Diagnosis

Erpetogomphus elaphe males differ from males of the more northerly *E. elaps* by only two morphological characters (contrasting characters for *E. elaps* in parentheses): 1) The superior branch of the anterior hamule is robust and is as high as the basal 0.5 of the hamule so that the resulting gap between upper and lower branches is small (fig. 54), (superior branch less robust, thinner; resultant gap between hamular branches wider [figs. 55-56]), and 2) The tip of the posterior hamule is rounded, (tip of posterior hamule with a cephalad directed tooth). The posterior hamule of *E. elaphe* appears to be more digit-shaped and is reminiscent of those of *E. eutainia* and *E. leptophis*. The same structure appears more triangular in *E. elaps*. However, this last character is subtle and is best detected when specimens of both species are in hand: I do not consider it a good diagnostic character. I have found no significant differences in the penis or caudal appendages between the closely related and allopatric *E. elaphe* and *E. elaps*. I have been unable to find any differences between females of the two species.

Differences between *E. elaphe* and other similar species parallel those of *E. elaps* and are discussed under that species.

Remarks

Variation. – *Erpetogomphus elaphe* does not show as great variation in thoracic markings as does *E. elaps*. The holotype male is the most boldly marked of the series. All paratype males (n = 15), two of which are teneral, have an antehumeral stripe, although it is obscure in one male from Costa Rica. The humeral stripe in all but one of the paratypes is restricted to the upper 0.20 of the humeral suture, and the middorsal stripe is vestigial or absent.

Female paratypes of *E. elaphe* are similar in maculation to the allotype, although one female from Costa Rica has a poorly defined antehumeral stripe. The small humeral stripe is reduced to the upper 0.20 and barely visible.

Venational statistics for paratype males (n = 18); number of marginal cells behind fore wing paranal cells: 0-2/0-3; anx: fore wing 12-15/12-15, hind wing 9-11/9-11; pnx: fore wing 8-11/9-11, hind wing 9-11/9-11; cs under pterostigma: fore wing 3-6/4-7, hind wing 4-6/4-7; anal triangular cells: 3-5. Hind wing 25-28 mm. Abdomen 30-34 mm.

Venational statistics for paratype females (n = 6); number of marginal cells behind fore wing paranal cells: 0-4/0-3; anx: fore wing 11-17/14-16, hind wing 10-12/10-12; pnx: fore wing 9-12/10-12; hind wing 9-12/9-13; cs under pterostigma: fore wing 4-6/4-5, hind wing 5-6/4-6. Hind wing 27-30 mm. Abdomen 33-34 mm.

Biology. – Little is known of the biology of this species, though its habits probably mirror those of *E. elaps.* The female from Cartago Province was collected in a 'marshy area by grassy hillside'. Altitudinal gradients for *E. elaphe* range from about 900 m (nr. Camotán, Guatemala) to about 1700 m (SE of Cartago, Costa Rica). Collection dates range from 2 June (Agua Caliente, Guatemala) to 5 August (San Jose, Costa Rica).

Distribution (fig. 200). – *Erpetogomphus elaphe* is known only from Guatemala, Honduras, and Costa Rica, but it probably exists in El Salvador and Nicaragua. Its distribution is allopatric (or possibly parapatric) with the form of *E. elaps* with thin anterior hamules.

Material

Type data. – Holotype male: GUATEMALA, Guatemala Dept., El Fiscal, 6 June 1909 (E. B. Williamson). Allotype female: same data, but 4 June 1909. Both in UMMZ.

Paratypes examined (18♂, 7♀): GUATEMALA: *Chiquimula Dept.*: Alda dos Quebradas nr. Camotán, 900 m (T. W. Donnelly) , 1♀ (TWD); *Guatemala Dept.*: Agua Caliente, 2 June 1909 (E. B. Williamson), 1♀; El Fiscal, 4 June 1909 (E. B. Williamson), 1♂, 1♀; 5 June 1909 (E. B. Williamson), 1♂; 6 June 1909, 2♂ (all UMMZ); Finca El Rosario, 36.5 km SE of Guatemala City, 15 June 1975 (J. E. Hafernik, Jr.), 2♂ (RWG); HONDURAS: *Francisco Morazan Dept.*: 30 km ESE Tegucigalpa, 29 June 1985 (Pinto and Ranch), 1♀ (SWD); 24 July 1983 (L. Cordoba), 1♂ (SWD); COSTA RICA: [no locality data], 1920 (Paul Serre), 3♂ (MNHP); *Cartago Prov.*, 5 mi SE Cartago, 5500 ft, 14 June 1963 (F. G. Thompson), 1♀ (DRP); *San José Prov.*: (all collected by H. Schmidt), San José, 18 June [no year stated], 1♂ (H. Kahl Coll'n, Acc. 12676); 24 June, 1♂; 4 July, 1♂; 5 July, 2♂; 17 July, 1♂, 1♀; 18 July, 1♀; 21 July, 1♂; 5 August, 1♂ (FSCA).

Erpetogomphus elaps Selys
(figs. 12, 13-thx, 55, 56-hamules, 78-penis, 100-app, 152-vertex, 181-vl, 200-distr)

Erpetogomphus elaps Selys, 1858: 330 (70 sep.) (♂ descr. 'Le Mexique, d'après un exemplaire unique du Museum de Paris, rapporté par M. Sal[l]e.'). – Selys 1859: 538 (12 sep.) (descr. ♂); Selys 1869: 175 (12 sep.) (descr. ♂, ♀); Selys 1873b: 519 (75 sep.) (list); Calvert 1905: 163 (localities in Mex.); Calvert 1907: 399 (comparison with *E. boa*); Calvert 1909: 481 (distr. in Mex.); Muttkowski 1910: 87 (cat.); Ris 1917: 153 (mentions Calvert's [1907] comments on comparison with *E. boa*); Williamson and Williamson 1930: 13 (summary of status); Montgomery 1973: 239 (derivation of name); Paulson 1982: 255 (Mex., Guat., Costa Rica); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.68 (cat.); Tsuda 1991: 95 (cat.).

Gomphus elaps. – Hagen, 1861: 100 (descr. ♂)

Herpetogomphus elaps. – Hagen 1875a: 42 (cat.); Selys 1879: 64 (note on classification); Kirby 1890: 60 (cat.); Needham 1897: 182 (name mentioned); Calvert 1899: 386 (descr. ♂, comparison with *E. viperinus* auct.), 415 (gizzard); Higgins 1901: 128 (mentions Calvert, 1899).

Description

Male. – Labrum grey white with wash of brown around margin of median lobe; anteclypeus, labrum, base of mandibles pale grey green, tips of mandibles dark brown; postclypeus and frons light green, some specimens with brown at base; vertex dark brown; a deep transverse trough in front of median ocellus, a small tubercle behind each lateral ocellus; pedicel, scape and flagellum brown; occiput trapezoidal, light green, mostly planar; crest slightly prominent, straight, slightly notched medially, and covered with long brown hairs; postocciput green, transverse when viewed dorsoposteriorly; rear of head yellow brown, paler laterally.

Prothorax and median lobe red brown becoming pale apple green medially, especially on anterior and posterior lobes. Synthorax ranging from entirely apple green (fig. 13) with slight hint of dark antehumeral stripe to having following brown areas (fig. 12): poorly defined middorsal stripe divided by pale middorsal thoracic carina, well-defined antehumeral stripe just touching antealar crest dorsally and not touching mesinfraepisternum ventrally; a vestigial first lateral stripe confined to upper 0.30-0.40 of suture and sometimes with a small anterior offshoot touching antehumeral; venter of synthorax, coxae, trochanters, grey green; femora pale green, becoming dark brown on distal extensor surfaces; these dark markings occupying distal 0.80 of profemora, distal 0.50 of mesofemora, and distal 0.20 to 0.40 of metafemora; tibiae and tarsi dark brown to black; armature black.

Wings hyaline, anterior margin of costa yellow to pterostigma, thereafter black; yellow at base of costa darkening to brown costal triangle; pterostigma dark brown, veins bordering it black.

Venational statistics. Fifth antenodal (occasionally fourth or sixth) thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-2/0-3;

anx: fore wing 11-15/12-15, hind wing 9-11/8-11; pnx: fore wing 8-11/8-11, hind wing 8-11/8-11; cs under pt: fore wing 4-6/4-7, hind wing 4-6/4-7; anal triangular cells: 3-5. Hind wing 24-29 mm.

Abdomen with segment 1 yellow green with a wash of brown dorsolaterally; segment 2 yellow green dorsally with a large midlateral brown spot dorsoposteriorly to auricle, or, in well- marked specimens, a distinct dark brown midlateral stripe expanding ventrally behind auricle, annulus dark brown; segment 3 broadly light yellow green dorsally interrupted laterally by a longitudinal brown stripe well-marked at transverse carina and flaring again at posterior 0.25 of segment to annulus; in palely marked specimens, brown midlateral stripe interrupted behind transverse carina; in well-marked specimens, midlateral stripe broad and meeting dorsally on posterior 0.10 of segment; inferior margin of tergite ivory, in heavily marked specimens limited to a triangular spot an anterior 0.10 of segment; segments 4-6 similar to segment 3, but some specimens with dark midlateral stripe more prominent and not interrupted behind transverse carina; in heavily marked specimens, midlateral stripe almost black and covering entire segment, except for basal pale annulus at basal 0.10 of segment and dorsal inverted pale green wedge- shaped middorsal stripe gradually narrowing posteriorly and disappearing at distal 0.20 of segment 4; these dorsal pale areas lacking on segment 5 and 6; segment 7 pale green, becoming tawny on posterior 0.10 of segment, or with posterior 0.20 dark brown, becoming black dorsally, transverse carina brown; segments 8-10 generally red brown becoming darker dorsally; in darkly marked specimens becoming almost black dorsally; foliate expansion and denticles black. Abdomen 29-38 mm.

Cercus (fig. 100) pale ocher to light brown, linear, gradually narrowing distally, the tips roundly pointed, a weakly defined ventral carina on distal 0.50 of cercus; epiprocts brown, gently curved at a 90° angle, tips when viewed posteriorly slightly spatulate, broadly rounded, or obliquely truncate.

Accessory genitalia (fig. 55). Anterior hamule dark brown to black, branched at distal 0.30, superior branch larger than inferior branch; superior branch moderately thickened in specimens from northern Mexico south to Chiapas, Mexico; specimens south of Chiapas (fig. 56) with superior arm of hamule more slender (see remarks); posterior hamule (figs. 55-56) pale, roughly triangular, with an anterior shoulder, tip with a tooth pointed cephalad; penis with prominent, knife-like serrated lateral lobe; membranous hood well developed but lobes not overlapping, cornua pointed but with median shoulder as shown in fig. 78.

Female. – Similar to male in markings and colouration; head with transverse trough anterior to median ocellus as in male, but occipital region differing as follows: occiput small, planar, encompassed posteriorly by arcuate (convex) crest (fig. 152); postocciput with median tumid area. Thoracic, leg, and abdominal patterns as in male, but dark areas more restricted, especially on femora and abdomen; cerci pale. Abdomen 30-36 mm.

Venational statistics. Fifth (rarely sixth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 0-3/0-3; anx: fore wing 12-16/13-16, hind wing 9-12/9-12; pnx: fore wing 8-11/9-12, hind wing 8-12/9-12; cs under pt: fore wing 5-6/5-7, hind wing 5-7/5-7. Hind wing 26-30 mm.

Vulvar lamina (fig. 181) with basal plate prominent, lobes narrow with medial margin distinctly concave, their bases not touching, with resultant cleft forming a wide, U-shaped interval; apical 0.30 of plate with mesal margin folded ventrally, beneath main plate, the costate rim sometimes visible along lateral margin of plate (fig. 181); Y-shaped juncture of postlamellar ridge not extending beyond posterior margin of plate, stem with diagonally ovaloid depression on each side.

Diagnosis

Erpetogomphus elaps and *E. elaphe* are closely related species which are diagnosed under *E. elaphe.* In males, the linear cercus of *E. elaps* (fig. 100) easily distinguishes it from the decumbent cercus (fig. 102) of *E. bothrops.* Body colouration is similar in *E. elaps* and *E. bothrops,* but all *E. bothrops* have well-marked antehumeral and humeral stripes (fig. 15). Many specimens of *E. elaps* have these markings poorly developed or nearly absent (fig. 13).

With the exception of *E. elaphe,* whose females appear indistinguishable, females of *E. elaps* are most similar to *E. bothrops.* The differences in the vulvar lamina as discussed by Calvert (1899) are an easy way to distinguish them. Secondly, the occiput of *E. elaps* is small and convexly arcuate (fig. 152); in *E. bothrops,* this structure is wider (fig. 154) and not nearly as arcuate.

Remarks

Variation. – The description is based on 49 males and 21 females. The holotype is in fair condition, although most of dorsum of the prothorax and part of the mesepisternum have been eaten away by dermestids. It has a completely pale thorax and the black midlateral stripes on abdominal segments 3-6 are interrupted only on the basal 0.10 of each segment. The hamules (fig. 55) and cerci (fig. 100) show that this specimen is the apple-green species ranging from northern Mexico south through Guerrero and into southern Veracruz.

Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 12/12, hind wing 9/10; pnx: fore wing 9/8, hind wing 8/9; cs under pt: fore wing 4/4, hind wing 5/5; anal triangular cells: 3/4. Hind wing 24 mm. Abdomen 31 mm.

I consider *E. elaps* to be the most variable of any species in the genus. Calvert (1907) figured three forms of the anterior hamules of this species when he examined a male from San Jose, Costa Rica (= *E. elaphe*). His fig. 31 (Guerrero, Rincon) and fig. 32 (Morelos, Cuernavaca) correspond to the holotype of *E. elaps* (fig. 55), which is characterized by possessing a moderately thickened anterior branch whose tip almost overlaps the posterior branch when viewed laterally. Calvert's fig. 30 (Guerrero, Rincon) is typical of specimens I have seen from Chiapas, Mexico, and northern Guatemala (fig. 56). The anterior branch forms a slender hook which rarely overlaps the posterior branch when viewed posteriorly. Figures 33 and 34 of Calvert (1907) represent *E. elaphe* and are discussed under that species. Calvert (1907) stated that he was unable to find any other characters which varied correlatively, and I have found no other characters to separate *E. elaps* and the narrow hamular form. I have not found any intermediate conditions in the shape of the anterior hamule. Their distributions appear to be largely allopatric, although Calvert (1907) figures both forms from Rincon in Guerrero.

Interestingly, the distribution of the form with the thin anterior hamular branch lies between typical *E. elaps* and *E. elaphe.* Because I have been unable to find any other diagnostic characters, I am inclined to treat the Rincon male and others from Chiapas and northern Guatemala as a variant of *E. elaps.* The divergent morphology of southernmost *E. elaps* may represent character displacement between *E. elaps* and *E. elaphe.*

Both males and females show remarkable range in size and maculation patterns throughout its range. The smallest specimens examined are from Morelos (HW: males 23 mm, females 26 mm), the largest from the Rio Metlac region of Veracruz (HW: males 29 mm, females 31 mm).

Specimens collected at 1220 m in Sinaloa State are melanic, characterized by pale areas of abdominal segments 4-6 reduced to basal 0.10 laterally; pale areas on dorsum of segments 3-6 reduced laterally, this pale area a thin hairline on segment 5, a basal ring on segment 6.

I find no correlation of presence or absence of the dark thoracic stripe to locality. A series of specimens from Palapita, Nayarit, ranges from an entirely pale thorax to possessing antehumeral and humeral stripes. All specimens from Veracruz that I have examined lack dark thoracic stripes, but all southern variants with the thin anterior hamular branch from Chiapas and northern Guatemala possess them.

Biology. – This small species has habits similar to those described for *E. bothrops.* The following field notes accompany specimens collected by E. B. Williamson: Nov. 6 (Tepic): '♀ Gomphine – from brushy vegetation between road and river at rapids above mill'; Nov. 7: 'Gomphine ♂ – Have seen these only in bushes along bank of Rio de Tepic – usually not over foot above ground – resting or flying. One ♀ was ovipositing in rather still water below the rapids'; Nov. 14 (Jalisco: San Diego Rancho): 'Very hard to catch in net. Sits tight on rock and lets it [net] pass over and then flies. Easily approached and I finally began catching them by dropping the net over their rock & letting them rise into the bag.'; and Nov. 16 (Jalisco: San Diego Rancho): '[♂, ♀] caught in grass in banana patch early in AM, sluggish'.

López (*in litt.*) records it as one of the most common members of the genus in Mexico, having a wide tolerance for diverse stream habitats. I have seen no records of this species taken near sea level, unlike *E. bothrops.* Altitudinal records range from 670 m (Nayarit, Palapita) to about 1500 m (Cuernavaca), dates of capture from 9 June (Veracruz, Teocelo) to 23 November (Jalisco, San Diego Rancho).

Distribution (fig. 200). – Both this species and *E. bothrops* appear to be the most widespread members of this genus in Mexico. *Erpetogomphus elaps* occurs in mesic areas on either side of the Sierra Madre Oriental and Occidental. It has been collected as far north as Nuevo León in the east, and southern Sinaloa in the west, southward through Jalisco, Morelos, Guerrero, and Veracruz.

Material

Type data. – Holotype male with following data: small round white label with handwritten '2/44'; rectangular manila label with handwritten (in R. Martin's hand) 'Ophiog. elaps/ ♂ De Selys/ Mexique? a renvoyer.'; large green label with black border with handwritten 'E. elaps, Selys/ Mexique'; small white label with printed 'MUSEUM PARIS'; narrow red label with printed 'HOLOTYPE'; white printed label with '*E. elaps* HOLOTYPE/ Det. J. Belle, 1977/ No. 2, 1844. Insects [sic] de/ [reverse side] differents Ordres envoyes/ de Mexique par/ *Mr. Ghresbreght* !' and in lower right hand corner 'ne pas/ Sal[l]e!' In MNHP. The caudal appendages and accessory genitalia are shown in figs. 55, 78, 100.

Other material (49♂, 21♀). – MEXICO: *Chiapas*: Pacific slope, 800-1000 m), (USNM); stream 20.1 mi NE Tapanatepec, Oaxaca, 2700 ft., (FSCA); San Geronimo, Volcan Tacana, 450 m (UMMZ); Distrito Soconusco, Finca Juarez, (UMMZ); Guerrero: Chilpancingo, 4600', (FSCA, BMNH); Tepetlapa, 3000 ft., (BMNH); Jalisco: San Diego Rancho nr. Cocula, (ummz); 15 mi on road to Tequila, (ummz); Michoacan: El Sabino, 20 mi SSE of Uruapan, (ummz); Morelos: Alpuyeca, S of Cuernavaca on Rt. 95, (fsca); Cerro de Higuerón, Jojutla, (unam); Cuautla, (ummz); Cuernavaca, ca. 1200-1500 m, (ummz, usnm, rwg); 5 mi S of Cuernavaca, (ummz); 16 mi S of Cuernavaca, (ummz); Itzamatitlan, 5 km SW of Yautepec, (rwg); Nayarit: Acaponeta, (bmnh); Jumatán, (unam); Tepic, (ummz, usnm); Jalisco: Palapita, 670 m (unam); Nuevo León: Municipio de Monterrey, Cerro El Mirador, (fsca); Sinaloa: stream 27.9 mi NE of Concordia, 4000 ft., (drp, fsca, cc, rwg); Veracruz: Barranca de Cayoapa, Teocelo, (unam); Jalapa, (usnm); 4.9 km N of Coscomatepec by Mex. Hwy 156 (rwg); Rio Metlac, 2 km WNW of Fortin, 900 m, (rwg); Guatemala: Suchitepequez Dept.: Finca Moca Grande, Rio Bravo, (fsca).

Erpetogomphus liopeltis sp. n.
(figs. 14-thx, 36-abd, 57-hamules, 79-penis, 101-app, 117-cercus, 126-ept, 140, 141-occiput, 153-vertex, 182-vl, 201-distr, 227-wings)

Erpetogomphus elaps. – Novelo & Peña, 1991: 130 (misidentification).

Type material. – Holotype male: Mexico: Nuevo Leon State, Municipio de Monterrey, La Estanzuela, 2 July 1987 (M. J. Westfall, Jr., H. Quiróz, A. Contreras). In fsca. Allotype female: Nuevo Leon State, Monterrey, El Diente, 5 mi SE, 2 July 1960 (W.B. Cutts). In ummz.

Paratypes examined (15♂, 3♀, including holotype ♂ and allotype ♀). – Mexico: *Hidalgo*: Pemuxtitla, Rio Zacuala, 1000 m, 22 April 1984 (R. Novelo), 1♂ (rwg); *Michoacán*: 12 km W Apatzingán, 369 m (1200 ft.), 4th Hoogstraal Mexican Biological Expedition, 12 Aug. 1941 (Harry Hoogstraal), 1♀ (ummz); *Nuevo Leon*: Chipingue, 12 July 1960 (W.B. Cutts), 1♀ (rwg); Municipio de Monterrey, Cerro El Mirador, 9 Aug. 1984 (A. Contreras), 2♂ (iori); same data as holotype, 3♂ (fsca); Municipio de Santiago, El Cercado, Arroyo Dolores, 17 Aug. 1984 (A. Contreras), 2♂ (iori); Municipio de Santiago, Rancho Los Pinos, 3 July 1987 (M. J. Westfall, Jr., Jr., G. Luna, A. Contreras), 5♂ (fsca, rwg); *San Luis Potosí*: La Conchita (Camino a Xilitla), 7 May 1950 (no collector), 1♂ (cc).

Description

Holotype male. – Entire head pale green, labrum dull grey green, base of mandible, anteclypeus dull green, tip of mandible black; basal 0.25 and all of vertex brown, a transverse trough at anterior margin of vertex at juncture of base with antefrons, this trough with two slightly deeper pits, one each anterolateral to median ocellus; occiput with slightly medial tumid area, occipital crest distinctly emarginate medially (figs. 140-141), dark brown, rimmed with long dark brown hairs; postocciput green, becoming black laterally, concave medially; rear of head brown, becoming yellow brown laterally; antennae dark brown.

Prothorax brown, anterior and posterior lobes and small dorsolateral area of median lobe pale green. Thorax (fig. 14) entirely green (probably blue green in life) with following dark brown: obscure middorsal stripe ending before collar, becoming darkest near middorsal thoracic carina, lateral margins of this stripe gradually fading to green on mesepisternum; posterolateral rim of antealar crest; lateral 0.40 of mesepisternum except for dorsal emargination, with no indication of pale green separating coalesced humeral and antehumeral stripes; this stripe narrowing slightly ventrally but connecting with lateral margin of collar and anterior 0.50 of mesinfraepisternum; rim below subalar carina at obsolete second lateral suture; narrow partial third lateral stripe extending ventrally to 0.50 of suture before merging with green. Metasternum pale grey brown, tawny anteriorly. Coxae, trochanters grey; base of femora brown, becoming black distally; tibiae and armature black.

Wings hyaline, anterior margin of costa dark brown at base, becoming yellow distally to proximal level of pterostigma, remainder of venation and pterostigma black.

Venational details. Fifth antenodal thickened in all wings; no supplementary marginal cells behind fore wing paranal cells; anx: fore wing 14/15, hind wing 10/10; pnx: fore wing 8/9, hind wing 9/9; cs under pterostigma: fore wing 7/6, hind wing 6/5; anal triangular cells: 4/3. Hind wing 31 mm.

Abdomen (fig. 36) with segment 1 green dorsally, paler laterally with a midlateral stripe of brown expanding anteriorly at base and darkening posteriorly at articulation point; segment 2 similar to segment 1 but with a ventral stem of brown behind auricle from dark midlateral stripe, midlateral brown becoming wider and darker along posterior 0.50 of segment, annulus black; segment 3 with pale green middorsal stripe acuminate and disappearing at posterior 0.10 of segment, black midlateral stripe expanding slightly at transverse carina and again widening at posterior 0.10 of segment, this area with a ventral offshoot terminating anteriorly at 0.20 of segment; segments 4-6 similar to segment 3, but with middorsal pale green stripe shorter and narrower on each succeeding segment, thus black midlateral stripe connecting dorsally at posterior 0.40 of segment 6, these midlateral stripes interrupted at anterior 0.10 of each segment with small longitudinal wedge-shaped white area along ventral margin of tergite behind transverse carina; segment 7 with basal 0.60 pale grey green, except for irregular diffuse black spot at transverse carina, remainder of segment red brown, becoming black dorsally; segments 8-10 red brown, becoming darker dorsally; carinae and lateral foliations black, posterior medial margin of segment 9 pointed.

Cercus (fig. 101) pale ocher, decumbent at posterior 0.30, largely parallel in lateral view except for distal 0.20, tip with a shiny black tooth; black inferior carina on distal 0.25; epiproct brown, about 0.45 as long as cercus, U-shaped in lateral view, tip of epiproct when viewed posteriorly (fig. 126) broadly truncate. Abdomen 40 mm.

Accessory genitalia (fig. 57). Anterior hamule dark brown, branched at distal 0.30, superior branch larger than inferior branch; posterior hamule pale, roughly triangular with a well developed anterior shoulder, distal 0.75 curved posteromedially with a well developed black tooth twisted laterally from broad axis of hamule; penis with cornuae acuminate as shown in fig. 79, lateral lobe prominent, knife-like, serrated posteriorly.

Allotype female. – Similar to male with following differences: labrum slightly darker (possibly due to post mortem effects); transverse trough at juncture of antefrons and vertex well defined with slightly larger and deeper pit anterolateral to median ocellus; occiput strongly reduced to a small, gently convex, largely perpendicular medial arch; postocciput tumid medially, dark middorsal stripe vestigial, with only a wash of brown on either side of lower arms of antealar sinus, a narrow poorly defined incomplete green stripe separating dark brown antehumeral and humeral stripes up to dorsal 0.75. Abdominal segment 3 with acuminate black spot posterolateral to black dorsolateral stripe projecting anteriorly to black transverse carina; dorsolateral black stripes on segments 4-7 more extensive; pale middorsal stripe reduced to basal 0.75 (segments 4-5) to basal 0.50 (segment 7), and anteriorly touching annulus on each segment; segments 8-9 black dorsally, red brown laterally. Abdomen 38 mm.

Vulvar lamina (fig. 182) small, cleft larger than each plate, each plate connected basally, each with a raised shelf occupying anterior 0.5, postlamellar ridge with Y-shaped juncture posterior to hind margin of lamina, central stem with a well defined circular depression on either side.

Venational details. Fifth antenodal thickened in left fore wing; the sixth in remaining wings; Number of marginal cells behind fore wing paranal cells: 2/3; anx: fore wing 16/17, hind wing 13/11; pnx: fore wing 10/12, hind wing 12/11; cs under pterostigma: fore wing 6/7, hind wing 6/7. Hind wing 34 mm.

Diagnosis

This remarkable species approaches *E. viperinus* in size, colour, and maculation, but is most closely related to *E. bothrops* in morphology. Males of *E. liopeltis* and *E. bothrops* are similar in possessing epiprocts with broadly truncate tips (figs. 126-128); but those of *E. bothrops* are usually, but not always, bidentate (fig. 128). In lateral view, the epiprocts of *E. liopeltis* are more strongly curved and extend about 0.5 or less the length of the cercus; the same structures in *E. bothrops* extend 0.75 or more the length of the cercus (fig. 102). The apical tooth of the posterior hamule of *E. liopeltis* is longer and not as tightly recurved as in *E. bothrops* (figs. 57-58). Abdominal segments 1-3 in *E. liopeltis* (fig. 36) are more heavily marked than in *E. bothrops* (fig. 37); and the dark thoracic markings are also more extensive (fig. 14) than in *E. bothrops* (fig. 15).

In size and overall colouration, *E. liopeltis* seems indistinguishable from *E. viperinus*; but differences in the tips of the epiproct (figs. 126, 129) and structure of the area anterior to the vertex in both sexes (figs. 136 [as for *E. bothrops*], 137) easily distinguish the two species. Subtle differences between these two species exist in the morphology of the distal 0.5 of the cercus. In *E. liopeltis*, these structures are thicker and more cylindrical when viewed dorsally (fig. 101) and mediodorsally (fig. 117). The cercus of *E. viperinus* is more laterally compressed (fig. 119). The tip of the cercus in *E. liopeltis* terminates in a sharp black tooth; this tooth is lacking in *E. viperinus*.

Females of *E. liopeltis* and *E. bothrops* can be separated by overall size (*E. liopeltis* hind wing 32-34 mm; *E. bothrops* hind wing 28-31 mm) and thoracic maculation and colouration, as stated for males. Structural differences of the occiput and postocciput easily distinguish these species. The occiput of *E. liopeltis* is rudimentary, with only a gently rounded vertical medial crest. The medially tumid postocciput is easily visible in dorsal view (fig. 153). In *E. bothrops*, the occiput is narrow, but the anterior and posterior margins are roughly parallel except for the angulate lateral margins (fig. 154). In *E. bothrops*, the crest is vertical and the exposed postocciput is easily visible; but its posterior margin is planar or only slightly tumid. Receptacles for the tips of the male cerci differ slightly between the females. The transverse trough located anterior to the median ocellus narrows laterally in *E. bothrops* (fig. 136); but the lateral area of the greater U-shaped trough tends to curve lateroposteriorly around the anterior margin of the median ocellus in *E. liopeltis* (as in fig. 139).

Like males, females of *E. liopeltis* and *E. viperinus* can show striking similarities, but greater morphological differences manifest themselves in structures of the head and vulvar laminae. The trough anterior to the median ocellus of *E. liopeltis* is unlike the anterolateral pits of *E. viperinus* (fig. 137). The occiput of *E. viperinus* (fig. 155) is much broader, and the anterior margin of the occiput and curvilinear occipital crest are roughly parallel. The median postoccipital swelling of *E. liopeltis* is absent in *E. viperinus*. The vulvar laminae of the two species are similar, but the Y-shaped postlamellar ridge generally arises at or just before the posterolateral margins of the lamellar plates in *E. liopeltis*; the postlamellar ridge usually surpasses the vulvar lamina in *E. viperinus*. The median cleft between the vulvar lamellae is more obtuse in *E. viperinus* (fig. 184) than in *E. liopeltis* (fig. 182).

Erpetogomphus liopeltis and *E. viperinus* are allopatric and *E. viperinus* generally has more dense venation, despite wing lengths (*E. liopeltis* hind wing 29-31 mm [n = 13 males, 3 females], *E. viperinus* hind wing 29-31 mm [n = 20 males, 20 females]). The number of marginal cells behind fore wing paranal cells in male *E. liopeltis* ranges from 0-2 (only one wing has 3), compared with 1 (in 4 wings only) to 4 in *E. viperinus*.

Both sexes of *E. liopeltis* and *E. elaps* are easily diagnosed in the key by differences in body colouration, shape, and position of the posterior hamular tooth and shape of the cercus (males) and shape of the vulvar laminae (females). The occiput of females of *E. elaps, E. elaphe*, and *E. liopeltis* are similar in being reduced to a perpendicularly raised medial area (figs. 152-153) and a medial tumid area on the postocciput.

Remarks

Variation. – I found little variation among the 12 paratype males and 2 paratype females. The hind margin of the occiput (crest) is medially concave in the holotype (fig. 140), but ranges to almost linear (fig. 141) in other specimens. A poorly defined narrow green stripe is present between the coalesced dark antehumeral and humeral thoracic stripes in 7 males, but this condition varies from a short, narrow mark to one occupying the medial 0.50 of the lateral margin of the mesepisternum.

Wing variation among paratypes: Males: anx: fore wing 13-15/13-16, hind wing 9-12/10-12; pnx: fore wing 8-10/8-10, hind wing 9-13/9-12; cs under pterostigma: fore wing 5-7/4-6, hind wing 4-6/5-7; anal triangular cells: 3-4/3-4. Hind wing 29-31 mm. Abdomen 37-40 mm.

Females: Anx fore wing 16/14-15, hind wing 10/10; pnx fore wing 8-10/9-10, hind wing 11/9-11; cs under pterostigma fore wing 6-7/6, hind wing 6-7/7-8.

Other aspects of wing venation variability are characterized under the diagnosis for *E. liopeltis* and *E. viperinus*.

Some (n = 5) males have no marginal cells behind fore wing paranal cells, while two others (fig. 227) have one marginal cell in only one wing. All females have at least two such cells, except for the left fore wing of the Chipingue female. The fifth antenodal is almost always thickened; but the sixth is thickened in two males from La Estanzuela and in the right fore wing of the Apatzingan female.

One male from La Estanzuela has aberrant hind wing venation and was not included in the measured samples. Most specimens, including the holotype, had been preserved in acetone; and their resultant preservation leads me to believe that the pale colouration is similar to the blue green of *E. viperinus*.

Biology. – Novelo (pers. comm.) misidentified this species as *E. elaps* in Novelo and Peña (1991). They collected *E. liopeltis* in Hidalgo state from 22 April to 25 July (Rio Zacuala, Pemuxtitla) and 27 July (Calnali). They were taken as they perched on rocks along narrow, shaded, shallow, rocky streams. *Erpetogomphus liopeltis* was collected at Cerro El Mirador with *E. elaps*. Data for the female collected in Michoacan indicate that it was collected on 'side of stream'. Collection dates range from 22 April (Rio Zacuala) to 17 August (Arroyo Dolores).

Distribution (fig. 201). – *Erpetogomphus liopeltis* is only known from the states of Hidalgo, Michoacan, Nuevo Leon, and San Luis Potosi in northeastern Mexico.

Erpetogomphus bothrops sp. n.

(figs. 15-thx, 37-abd, 58-hamules, 80-penis, 102-app, 118-cercus, 127, 128-ept, 136-base of postfrons, 154-vertex, 183-vl, 201-distr, 228-wings)

Erpetogomphus viperinus. – Calvert 1899: 385 (described as *E. viperinus* Selys); Calvert 1905: 163 (described as *E. viperinus* Selys); Calvert 1909: 35 (misidentified as *E. viperinus*, compared with *E. schausi*); Muttkowski 1910: 87 (in part, cat.); Williamson & Williamson 1930: 11 (in part, refers to true *E. viperinus* but specimens in E. B. Williamson Coll. misidentified); Calvert 1947: 608 (status of Tepic specimens); Paulson 1982: 256 (in part, as *E. viperinus* from Mex., Guat.); Davies and Tobin 1985: 28 (in part, cat.); Tsuda, 1986: 87 (in part, cat.); Maes *et al.* 1988: 36 (as *E. viperinus* from Nicaragua); Tsuda 1991: 95 (in part, cat.).

Type material. – Holotype male: Mexico: Veracruz: Rio Otapa, 8 km S of La Tinaja, elev. 90 m, 13 Aug. 1976 (R. W. Garrison). Allotype female: same data, but 20 Aug. 1976. In usnm.

Paratypes examined (61♂, 28♀). – Mexico: *Guerrero*: Dos Arroyos, 1000 ft., Sept. 1888 (H. H. Smith), 1♀ (bmnh); *Jalisco*: San Diego Rancho near Cocula, 14 Nov. 1923 (J. H. Williamson), 1♂ (bmnh); *Michoacan*: El Sabino, 20 mi SSE of Uruapan, 27 July, 1 Aug. 1936 (H. Devlin Thomas), 8♂, 3♀ (ummz, fsca); *Morelos*: Puente de Ixtla, 3

July 1900 (C.C. Deam), 1♀ (UMMZ); Cerro del Higuerón-Jojutla, July 1983 (C. Deloya), 1♂ (UNAM); *Nayarit*: Acaponeta, 1-2 Nov. 1923 (J. H. Williamson), 9♂, 1♀ (UMMZ); Tepic, 7 Nov. 1923 (J. H. Williamson), 1♂ (UMMZ); Jumatán, 10 Sept. 1980 (G. Jiménez), 2♂ (UNAM); *San Luis Potosí*, Cascadas Micos nr. aqueduct, 27 June 1990 (K. J. Tennessen), 1♂ (KJT); El Salto, 400 m, 6 Sept. 1963 (T. W. Donnelly), 1♂, 1♀ (TWD); Huichihuayan, km 410, S of Valles, 'Sam Brown' Hacienda, 25 Sept. 1938 (L. J. Lipovsky), 1♂, 2♀ (UMMZ); *Tamaulipas*: Rio Corona, 20 mi N of Ciudad Victoria, nr. Mex. Hwy 101, 1000 ft., 26 July 1968 (R. W. Garrison), 1♂, 2♀ (RWG); *Veracruz*: Atoyac, 400 m, (Schumann), 1♀ (BMNH); 16.5 mi S of Catemaco, by Hwy 180, 25 June 1985, (I. S. Askevold), 2♂ (CC); Cordoba 12-25 July 1964 (E. Fisher, D. Verity), 1♀ (LACM); Isla, 17 July 1969 (R. Wind), 1♂ (CC); K375-390 Cordoba Rd., 11 Aug. 1961 (R. and K. Dreisbach), 1♂ (USNM); 4.9 km N of Coscomatepec, by Mex. Hwy 156, 11 Aug. 1976 (R. W. and J. A. Garrison), 1♀ (RWG); Rio Otapa, 8 km S of La Tinaja, 90 m, 13, 20 Aug. 1976 (R. W. and J. A. Garrison), 10♂, 2♀ (RWG); Rio Hondo, on road to 'Colonia la Apachital' (50'), Soteapan, 500 m, July-Aug. 1990, (collector unknown), 6♂, 4♀ (PM, RWG); 6 mi E of Hwy from Tierra Blanca to Ciudad Aleman, 25-26 Aug. 1957 (G. H. Beatty, III), 1♂ (FSCA); Salto Eyipantla, 8 km S of San Andres Tuxtla and Mex. Hwy 180, 15 Aug. 1976 (R. W. and J. A. Garrison), 2♂ (RWG); Tierra Colorada, nr. Veracruz, 17 July 1932 (H. M. Smith), 1♀ (UMMZ); *Oaxaca*: Candelaria Loxicha, 500 m, 7 Sept. 1973, (E. C. Welling-M.), 1♂ (CC); 5 July 1974, (E. C. Welling-M.), 1♂ (SWD); *Chiapas*: river 26.1 mi NE Tapanatepec, 2100 ft., 2 Aug. 1965 (D. R. Paulson), 1♂ (DRP); stream 15.4 mi NE Arriaga on Mex. 195, 2300 ft., 24 July 1965 (D. R. Paulson), 2♂ (DRP); El Aguacero, nr. Ocozocoautla, 26 Oct. 1986 (E. Fisher), 1♂ (RWG); GUATEMALA: *Baja Vera Paz Dept.*: San Geronimo, 1879-80 (G. C. Champion), 1♂ (BMNH); *Chiquimula Dept.*: streams vic. Tierra Colorado, 800 m, 20 July 1962, (T. W. Donnelly), 1♂, 2♀ (TWD); small stream vic. Veguitas, 600 m, 10 July 1962 (T. W. Donnelly), 1♂, 1♀ (TWD); *Dept. Zacapa*: Gulan, 16-17 June 1909 (E. B. Williamson), 2♂ (UMMZ); La Union, 850 m, 31 Aug. 1972 (E. C. Welling M.), 1♀ (UMMZ); EL SALVADOR: *Anuachopan Dept.*: (all collected by V. Hellebuyck): Bosque El Imposible, San Francisco Mendez, 16 Aug. 1987, 3♂ (VH, RWG); May 1987, 1♂, 1♀ (VH); 12 July 1987, 2♂ (VH); 25 July 1987, 1♂, 1♀ (VH); 16 Aug. 1987, 1♂ (VH); 3 Sept. 1987, 3♂, 1♀ (1 pair in copula) (VH); El Coyolar, El Imposible, 2 Aug. 1987, 2♂ (VH); Valle de la Puerta, Bosque El Imposible, 3 Sept. 1987, 3♂ (VH).

Description

Holotype male. – Labium grey-white with wash of brown around margin of median lobe; entire face including vertex and occiput yellow green, a transverse trough in front of median ocellus, lateral ends slightly deeper than medial area; a small tubercle behind each ocellus; pedicel, scape, flagellum brown; occiput yellow green, mostly planar, slightly tumid medially, crest green, slightly prominent, straight, slightly notched medially and covered with long brown hairs; postocciput green, transverse when viewed dorsoposteriorly; rear of head yellow brown, paler laterally; lateral margins of labrum and base of mandible ocher; rear of head yellow brown.

Prothorax yellow green except for brown on anterior margin of median lobe and posterior area of anterior lobe. Synthorax (fig. 15) entirely yellow green except for following brown areas: slight vague stripe lateral to middorsal carina; antehumeral stripe; spot on upper end of humeral suture connected anteriorly to antehumeral, and gradually disappearing basally toward mesinfraepisternum; line bordering antealar crest; metasternum pale yellow green. Coxae, femora pale yellow green, becoming dark brown dorsodistally; tibiae, tarsi and armature black.

Wings hyaline, anterior margin of costa yellow, remainder of venation black, pterostigma brown.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1/3; anx: fore wing 15/15, hind wing 11/11; pnx: fore wing 11/13, hind wing 13/13; cs under pterostigma: fore wing 6/6; hind wing 7/6; anal triangular cells: 4. Hind wing 27 mm.

Abdomen (fig. 37) with segment 1 yellow green with a wash of brown dorsally; segment 2 yellow green with diffuse brown spot posterodorsally to auricle; segment 3 broadly light green dorsally, interrupted laterally by a longitudinal brown stripe flaring at transverse carina, inferior margin of tergite ivory; segments 4-6 similar to segment 3, but lateral brown stripes progressively more extensive and each meeting its neighbor dorsally at posterior end of segment; segment 7 with anterior 0.66 pale green white except for black transverse carina, posterior 0.30 of segment red brown; segments 8-10 red brown, darker dorsally, carinae and lateral foliations black; posterior medial margin of 9 pointed. Abdomen 35 mm.

Cercus (fig. 102) pale ocher, gently decumbent at posterior 0.30, gradually narrowing toward end, tip with a shiny black tooth; epiproct brown, gently curved as is characteristic for the genus, tip of epiproct when viewed posteriorly (fig. 128) bidentate.

Accessory genitalia. Anterior hamule dark brown, branched at distal 0.30, superior branch larger than inferior branch; posterior hamule (fig. 58) pale, roughly triangular with an anterior shoulder, tip with a black tooth twisted laterally from broad axis of hamule; penis with cornuae pointed but each with median shoulder as shown in fig. 80; lateral lobe prominent, knife- like, serrated posteriorly.

Allotype female. – Similar to male with following differences: synthorax with definite dark triangular middorsal stripe, its base not touching collar; broad, diffuse brown dorsolateral stripe on abdominal segment 2, brown lateral stripes on segments 3-6 with their anterior ends ending at basal 0.20 of each segment so that lateral white connects with dorsal yellow-white middorsal stripe; cercus pale.

Vulvar lamina (figs. 183) small, cleft about as large as each plate; each plate connected basally, each with a raised shelf occupying anterior 0.5; postlamellar ridge with Y-shaped juncture posterior to hind margin of lamina; central stem with a well defined circular or oval depression on each side. Abdomen 32 mm.

Venational details. Fifth antenodal thickened in all wings; no marginal cells behind fore wing paranal cells; anx: fore wing 12/13, hind wing 9/9; pnx: fore wing 8/9, hind wing 10/10; cs under pterostigma: fore wing 4/5, hind wing 5/5. Hind wing 27 mm.

Diagnosis

Selys' (1868) description of *Erpetogomphus viperinus* was too brief and inexact for Calvert (1899) to detect a specific difference between his specimens of *E. viperinus* (= *E. bothrops*) and the true *E. viperinus.* Examination of the lectotype male and female of *E. viperinus* shows that the *Erpetogomphus viperinus* of Calvert and all subsequent authors is referable to the new species *E. bothrops.*

E. bothrops is most similar to *E. liopeltis* and is diagnosed under that species. *Erpetogomphus bothrops* also resembles *E. viperinus,* but in life, the pale colouration of *E. bothrops* is yellow green (deep green in *E. viperinus*). *Erpetogomphus viperinus* is generally larger (hind wing male 29-31 mm) and darker. In males, the cercus of *E. bothrops* is pale with a distinct black tooth; while in *E. viperinus* this structure is dark red brown with no apical tooth. In *E. bothrops,* the distal 0.5 of the cercus gradually narrows, so the distal 0.5 of the cercus in lateral view is not as thick or robust as the base (fig. 102). In *E. viperinus,* the distal 0.5 of the appendage is robust and is as thick as its base (fig. 103). In dorsoposterior view, the posterior 0.30 of the cercus of *E. bothrops* gradually narrows (fig. 118), and is not as laterally compressed as in *E. viperinus* (fig. 119). The inferior distal margin of the cercus of *E. viperinus* is strongly carinate, not so in *E. bothrops.* The tip of each epiproct of *E. bothrops* in posterior view is bidentate (fig. 128) or truncate (fig. 127), not bluntly pointed as in *E. viperinus* (fig. 129). Other characters are given in the key.

Females of these species are easily distinguished by overall body colouration in life, and thoracic maculation. Two structural characters separate *E. bothrops* from *E. viperinus*: the anterior margin of the vertex of *E. viperinus* contains two well defined pits, each dorsolateral to the median ocellus. Each pit is the receptacle for the bluntly pointed tip of the male epiproct when in copulation. In *E. bothrops,* these pits are replaced by a continuous groove deepest medially, which accommodates the explanate tips of the male epiprocts. Secondly, the V-shaped notch of the vulvar lamina in *E. bothrops* is more acute (fig. 183) than the more widely divergent notch of *E. viperinus* (fig. 184). The shape of the vulvar lamina of *E. bothrops* (fig. 183) distinguishes it from similarly marked females of *E. sipedon* (figs. 187, 188) and *E. elaps* (fig. 181).

Remarks

Variation. – Venational variation among the paratype series of males (fig. 228): number of marginal cells behind fore wing paranal cells: 0-3; anx: fore wing 14-16/13-16, hind wing 9-12/10-12; pnx: fore wing 9-11/8-13, hind wing 10-13/10-13; cs under pterostigma: fore wing 5-7/5-7, hind wing 5-7/5-7; number anal triangular cells: 3-4. Hind wing 21-28 mm.

Variation exists in the direction of the apical tooth of the posterior hamule. It is present in all males and, in most, is twisted so that its tip is directed laterally (*i.e.,* distally) to the direction of the planar surface of the hamule. In a few males, the tooth, though rotated, points in a more lateroanterior direction.

The tip of the epiproct, when viewed posteriorly, is planar and bidentate (*e.g.,* fig. 128); but in some, the distal and mesal teeth are reduced. In rare cases, the tip is almost straight (fig. 127); variations link these extremes. I have found no correlation of the posterior hamular condition with the epiproct condition; nor do these conditions seem to vary according to altitude or locality. For example, of 5 males from Nayarit, Jamatan, only one has hamular teeth pointing predominantly cephalad. This same specimen has a bidentate condition of tips of the epiprocts. Another male has a bidentate condition, another has an intermediate condition, and two others have truncate tips. Of another series of 9 males (including holotype) from the Veracruz, Rio Otapa, two have the hamular tooth pointing predominantly cephalad. These two specimens have bidentate epiprocts, although the right epiproct of one male is intermediate. The remaining 7 males have bidentate epiprocts, but one has an intermediate condition of its right epiproct.

The membranous hood of the penis is variable among and within populations. Most specimens, including the holotype, possess a short hood, exposing a subcutaneous membrane (fig. 80); but a male from

San Luis Potosi, Cascadas Micos, has a long, acute, non-overlapping hood. Another two males, one from Guatemala (Dept. Chiquimula, small stream, vic. Veguitas), and all specimens I examined from El Salvador (Dept. Anuachopan, Bosque El Imposible, San Francisco Mendez), have long, overlapping hood membranes similar to that illustrated for the holotype male of *E. leptophis* (fig. 76). With the exception of the San Luis Potosí male, specimens with long, acuminate hoods seem to typify most southerly specimens. I can find no other characters differentiating these specimens from others.

Venational variation among the paratype series of females (n = 18): number of marginal cells behind fore wing paranal cells: 1-3; anx: fore wing 12-16/12-16, hind wing 9-11/8-11; pnx fore wing 8-12/9-12, hind wing 9-13/9-13; cs under pterostigma: fore wing 4-7/5-7, hind wing 5-8/5-7. Hind wing 27-31 mm.

Biology. – I have often seen this species along margins of cut agricultural fields bordering streams and canals. Its apple green colouration renders it difficult to detect among vegetation, but when disturbed, it does not fly far. The type locality is a wide, shallow stream bordered by trees in extensively cultivated farmland. I collected *E. bothrops* next to cut fields along with six other gomphids: *Erpetogomphus eutainia, E. ophibolus, Phyllocycla breviphylla* Belle, *P. volsella* (Calvert), *Phyllogomphoides duodentatus* Donnelly, and *Progomphus clendoni* Calvert. Twenty-five other species of Odonata were collected there.

R. Novelo (pers. comm.) observed a pair in copula in Morelos state (Cerro del Higuerón) at 1250 m at 18.20 hr on 14 Sept. 1988.

Williamson records the following on two Acaponeta males: 'Eas[il]y caught while sitting in brushy weed patch on bank of river, sun behind cloud,' and 'Quite common flying over water just above the real rapids and lighting on willow-like stems and twigs along the bank. Saw no ♀ gomphine today.' López (*in litt.*) writes that they perch along sides of streams or on exposed rocks in the middle of streams. He states that they do not remain long at a spot, moving constantly along the length of the stream.

Elevation gradients range from near sea level (50 m, Veracruz, Agua Caliente) to 1250 m (Morelos, Cerro del Higuerón). Collection dates range from May (El Salvador) to November (Mexico, Jalisco).

Distribution (fig. 201). – This species and *E. elaps* are the most widely distributed species in Mexico and Guatemala. *Erpetogomphus bothrops* ranges from Tamaulipas in eastern Mexico (24°N) south to El Salvador (14°N). It also occurs in mesic areas in western Mexico from Nayarit (22°N) south. Its distribution indicates an avoidance of the xeric areas in northwestern Mexico and the high mountain plateau in northern Mexico.

Erpetogomphus viperinus Selys

(figs. 16-thx, 38-abd, 59-hamules, 81-penis, 103-app, 119-cercus, 129-pet, 137-base of postfrons, 155-vertex, 166-postocciput, 184-vl, 201-distr, 229-wings)

Erpetogomphus viperinus Selys, 1868: 68 (3 sep.) (descr. of ♂, ♀, 'D'Orizaba'). – Selys 1869: 176 (13 sep.) (redescription of ♂ and ♀ from Orizaba); Selys 1873b: 519 (75 sep.) (list); Muttkowski 1910: 87 (in part, cat.); Williamson & Williamson 1930: 14 (summary of status); Paulson 1982: 256 (Mex.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.220 (cat.); Tsuda 1991: 95 (cat.).

Herpetogomphus viperinus. – Hagen 1875a: 42 (cat.); Selys 1879: 64 (2 sep.) (status of classification); Kirby 1890: 60 (cat.).

Description

Male. – Entire head pale green (blue green in life), slightly darker on anterior of ante- and postclypeus and labrum, lateral margins of labrum ocher, base of mandible and labium dull grey green; basal 0.25 of postfrons and all of vertex brown, a pair of pits at anterior margin of vertex at juncture of base of antefrons (fig. 137), one each anterolateral to median ocellus; antennae dark brown; occiput with well developed medial tumid area, green, occipital crest slightly emarginate medially, dark brown to black, rimmed with long dark brown hairs; postocciput brown, green medially, transverse, with a slight vertical depression medially; rear of head yellow brown.

Prothorax brown, anterior and posterior lobes green. Synthorax (fig. 16) entirely green (blue green in life) with following dark brown: obscure middorsal stripe ending before collar, becoming darkest at base of antealar crest and extending as narrow wash of brown below rim of antealar crest and joining wide stripe along lateral 0.30 of mesepisternum; this stripe coalescing with normal humeral stripe; often with a narrow isolated stripe of green separating these two stripes; combination antehumeral and humeral stripe reaching collar; all of mesinfraepisternum and ventral part of thorax; rim below subalar carina, often with small extension on obsolete second lateral suture, which in some specimens may form an indistinct second lateral stripe; narrow but well defined third lateral stripe. Metasternum pale grey green. Coxae, trochanters grey, becoming brown exteriorly; base of femora brown, becoming black distally; tibiae and armature black.

Wings (fig. 229) hyaline, anterior margin of costa dark brown at base, becoming yellow distally to proximal level of pterostigma, remainder of venation and pterostigma black.

Venational statistics. Fifth (occasionally sixth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1-4/1-4; anx: fore wing 13-18/13-18, hind wing 9-12/10-13; pnx: fore wing 8-13/10-12, hind wing 10-14/10-13; cs under pterostigma: fore wing 5-7/4-7, hind wing 5-7/5-7; anal triangular cells: 4 (rarely 5). Hind wing 29-31 mm.

Abdomen (fig. 38) with segment 1 green with brown dorsolaterally except for green on posterior dorsal 0.50 of segment; segment 2 with middorsal green stripe; brown dorsolaterally surrounding green auricle; ventrolateral area pale green, annulus black; segments 3-6 primarily black with following pale areas: basal 0.10 of each segment, dorsally forming an incomplete blue green middorsal stripe extending to posterior 0.20 of each segment; ventrolateral wedge shaped white spot at middle of each segment, connecting in some specimens to basal pale ring; segment 7 with dorsal 0.50 light green, posterior 0.50 red brown, black along transverse carina; segments 8-10 predominantly red brown, darker dorsally, denticulated posterior margin of these segments black; posterior margin of segment 9 often forming a posteriorly directed point. Abdomen 36-40 mm.

Cercus (fig. 103) pale ocher, slightly darker ventrally, robust and strongly curved at posterior 0.30, inner margin of posterior 0.30 of cercus planar (fig. 119); same structure in posterodorsal view narrow, inferior carina along posterior 0.30 of cercus; epiproct brown, becoming black posteriorly, gently curved as is characteristic for the genus; tip of epiproct, when viewed posteriorly (fig. 129) forming a narrow, blunt point.

Accessory genitalia. Anterior hamule (fig. 59) black, divided at distal 0.30; smaller posterior branch almost as large as anterior branch, its pointed tip almost meeting tip of anterior (larger) branch; posterior hamule (fig. 59) pale, roughly triangular, swollen at distal 0.25 to 0.50 of appendage, tip with a black tooth twisted laterad from broad axis of hamule; penis with cornuae pointed but each with well developed median shoulder (or median lobe in some specimens), as shown in fig. 59; lateral lobe prominent, knife-like, arcuate laterally, its outer margin strongly serrated.

Female. – Similar to male, with following differences: Vertex (fig. 155) without postocellar ridge, a well defined pit anterolaterad to median ocellus as in male; occiput green, narrow, mostly planar, or with only a slight tumid area medially, hind margin slightly sinuate, barely emarginate at middle; postocciput green, transverse; synthorax with no vestige of second lateral stripe; abdomen with dorsolateral dark stripe on segment 1 reduced or vestigial, middorsal dark stripe on segments 2-6 narrower, anteriorly touching black annulus, widened at transverse carina, constricted near center and widening at distal 0.25 of each segment, ventral white narrow but expanded near center of segment, sometimes a longitudinal wedge-shaped spot isolated by narrow posterior and anterior lateral offshoots of black dorsolateral stripe, white lateral wedge- shaped spots largest on segments 2 and 3, dividing or partially dividing dorsolateral brown stripe; segment 7 similar to segment 6, but dorsal pale orange green connecting anteriorly with lateral white at basal 0.10 of segment; segments 8-10 dark brown, becoming black dorsally and posterolaterally to all black with ill-defined white lateral spot on each segment; cercus, paraproct brown. Abdomen 37-41 mm.

Vulvar lamina (fig. 184) small, cleft as large as each plate; each plate broadly connected basally, each with a well developed raised shelf occupying anterior 0.50; medial margin of each plate slightly concave, its tip falcate; postlamellar ridge with Y-suture posterior to hind margin of lamina; central stem short with a well-defined circular or oval depression on each side.

Venational statistics. Anx: fore wing 15-20/15-21, hind wing 10-14/11-14; pnx: fore wing 10-13/10-15, hind wing 10-15/9-14; cs under pterostigma: fore wing 5-8/5-8, hind wing 5-8/6-7. Hind wing 31-34 mm.

Diagnosis

Erpetogomphus viperinus is most closely related to *E. bothrops*, and is diagnosed under that species. It is also superficially similar to *E. liopeltis* and is diagnosed under that species. The thoracic pattern of *E. viperinus* is superficially similar to that of *E. sipedon*, but is easily separated by characters listed under that species and in the key.

Remarks

Variation. – The description is based on 49 males and 38 females from Veracruz State, Mexico. The lectotype and paralectotype are in reasonably good condition, but post mortem preservation is poor and would yield an inadequate description. Venation characters for this pair are as follows:

Lectotype male: number of marginal cells behind fore wing paranal cells: 3/1; anx: fore wing 16/17, hind wing 12/12; pnx: fore wing 13/12, hind wing 11/13; cs under pterostigma: fore wing 6/6, hind wing 6/5; anal triangular cells: 4/4.

Paralectotype female: number of marginal cells behind fore wing paranal cells: 4/3; anx: fore wing 15/18, hind wing 12/11; pnx: fore wing 10/12, hind wing 12/13; cs under pterostigma: fore wing 7/8; hind wing 7/6.

Examination of 20 males shows variability is some venational characters. All specimens have marginal cells behind the fore wing paranal cells, ranging from 1-4 cells. The fifth antenodal is most often thickened, but rarely the fourth (one wing) or sixth (7 wings). The sixth antenodal is thickened on both wings of the lectotype.

Little variation exists in body colouration. The second lateral thoracic stripe is incomplete or vestigial in most males. It is complete on only one male from Rio Metlac. Females show a greater tendency toward a dense venation than do males. Marginal cells behind the fore wing paranal cells were present in all 20 females I examined, ranging from 1 (one wing) to 8 (two wings). The fifth antenodal is generally thickened, but it is the fourth on the left wing of the paralectotype, sixth in 17 wings (including right wing of paralectotype) and seventh in four wings.

Biology. – Although of restricted distribution, *E. viperinus* can be common during certain years. I collected a few specimens of both sexes in the mostly shaded understory at the Rio Metlac. The locality consists of a fast running river in a steep canyon. The narrow valley contained many coffee plants. I flushed various specimens, and they alit on low vegetation, where their deep blue green colour made them difficult to detect unless the eye followed closely where each specimen landed. Once approached they were easy to take with a net. Other Odonata taken at the same site were *Hetaerina cruentata* Rambur, *Argia* sp. nr. *fissa* Selys, *Argia extranea* Hagen *in* Selys, *Aeshna psilus* Calvert, *Brechmorhoga pertinax* (Hagen), *B. vivax* Calvert, *Cannaphila vibex* Hagen, *Erythrodiplax fusca* (Rambur), and *E. umbrata* (Linnaeus).

The species has been collected more frequently farther north at Teocelo under similar circumstances. The Odonata assemblage there is more varied and consists of *Palaemnema* sp. n., *Paraphlebia zoe* Selys, *Argia extranea*, *Argia* sp. n., *Brechmorhoga pertinax*, *B. rapax* Calvert, *B. tepeaca* Calvert, *Cannaphila vibex*, *Libellula herculea* Karsch.

This species has been taken at elevations of 800-1300 m (Teocelo and vicinity). Collection dates range from 6 June through 18 September (Teocelo and vicinity).

I have abstracted the following biological notes from López (*in litt.*): Tenerals and adults travel far from the stream, hiding in vegetation in open areas, where they feed by making short sallies from perches. They capture primarily small flies and butterflies (Lycaenidae) passing by. Copulation takes place in open fields away from streams, as males grab females which fly by. The copulating pair then retires to the dense forest. Females oviposit while flying above water, dropping their eggs from about 30 cm. At dusk, males return to feeding sites, often in considerable numbers, where threat display patterns among males and females have been observed when two or more individuals try to occupy the same perch. Specimens are often preyed upon by spiders (Araneidae).

Distribution (fig. 201). – *Erpetogomphus viperinus* is apparently restricted to central Veracruz. As stated under the species account for *E. bothrops*, all published records of this species since Calvert's redescription of *E. viperinus* refer to the widespread *E. bothrops*. I examined one male from the Paris Museum with a handwritten label, 'N. Carolina', but I have seen no specimens of *E. viperinus* from the United States. I believe that locality is in error.

Material

Type data. – Lectotype male by present designation with following data: small green handwritten label 'Mex/B[ouchard]'; white handwritten label '*Herp. / viperinus* /S.[elys]/ ♂'; two manila coloured labels each with '26' handwritten in pencil in an unknown hand; rectangular red label with printed 'LECTOTYPE'/and handwritten: '*Erpetogomphus*/ *viperinus* Selys 1869/ ♂/des. [printed] R. W. Garrison 1984'. The caudal appendages are shown in fig. 103. Paralectotype female: small green handwritten label 'Mex./B[ouchard]'; white handwritten label '*Herp./ viperinus*/ S[elys]/ ♀', two manila coloured labels, each with '28' handwritten in pencil in an unknown hand; rectangular white label with printed 'LECTOTYPE'/ and handwritten '*Erpetogomphus*/ *viperinus* Selys 1869/ ♀/ des. [printed] R. W. Garrison 1984'. Both specimens in IRSN.

Other material (48♂, 32♀, including lectotype ♂ and paralectotype ♀). – MEXICO: *Veracruz*: nr. Municipio Teocelo at Puente Teocelo, *ca.* 1150 m, (UNAM, RWG); Barranca de Cayoapa, Teocelo, 750-890 m, (UNAM, JB, CE, PSM, DALD); Barranca de Cayoapa, Tejeria-Teocelo, 800 m, (UNAM); road to Monte Blanco, Teocelo, (UNAM); El Trapiche, Teocelo, 1100 m (UNAM); road to Santa Rosa, Teocelo, (UNAM); Santa Rosa, Teocelo, (UNAM); Cascada de Xico, Teocelo, 1100 m, (UNAM); Cascada Texolo, (UNAM); Parque Javier Clavijero, Jalapa, 1300 m (UNAM); Fortín de las Flores, 1010 m (RWG); Rio Metlac, *ca.* 3.5 km WNW of Fortín de las Flores, 900 m (RWG); km 327 W of Cordoba, (FSCA); Cordoba, (USNM).

Erpetogomphus designatus **Hagen *in* Selys**

(figs. 17, 18-thx, 60-hamules, 82-penis, 104-app, 130, 131-ept, 156, 157-vertex, 185, 186-vl, 202-distr)

Erpetogomphus designatus Hagen in Selys, 1858: 661 (401 sep.) (descr. ♂, ♀, 'Pecos River, Texas'). – Hagen in Selys 1859: 536 (10 sep.) (descr. ♂, ♀); Selys 1873b: 519 (75 sep.) (list); Calvert 1899: 386 (mentioned); Calvert 1905: 166 (Ohio, Ind., Mexico); Muttkowski 1910: 86 (cat.); Calvert 1912a: 289 (Mex., distr.); Hine 1913: 96 (Ohio); Williamson 1914b: 447 (Tex.); Kennedy 1917a: 544 (larva, notes); Williamson 1917: 8 (Ind.): Kennedy 1917b: 137 (Kans.); Kennedy 1918: 298 (notes); Williamson 1923: 8 (Kentucky); Montgomery 1925: 386 (Ind., habits); Montgomery 1927: 289 (Ind.);

Kennedy 1928: 373 (seasonal distribution); Montgomery 1929: 340 (Ind.); Needham & Heywood 1929: 80 (key, descr.); Byers 1930: 53 (Fla. Key, descr., habits); Williamson & Williamson 1930: 12 (summary of status); Byers 1931: 51 (Tenn.); Bird, 1932: 51 (Okla.); Williamson 1932: 23 (Mo., habits); Tinkham 1934: 216 (Tex.); Montgomery 1935: 234 (Ind.); Borror 1935: 453 (Ohio); Borror 1937: 186 (Ohio); Montgomery 1937: 207 (Ind., habits); Ahrens 1938: 11 (Mo., predation); Wright 1938: 27 (Tenn.); Ferguson 1940: 5 (Tex.); Montgomery 1940: 289 (S. C.); La Rivers 1940b: 63 (Nev.); Montgomery 1941: 230, 238 (Ind.); Ferguson 1942: 146 (Tex.); Montgomery 1947: 165 (distr.); Bick 1951: 179 (Okla.); Montgomery 1951: 207 (Ind.); Needham and Westfall 1955: 146 (key, descr.); Cross 1955: 11 (S. C.); Montgomery 1955: 133 (Ind.); Cross 1956: 4 (Fla.); Bick and Bick 1957: 2 (Okla.); Kormondy 1957: 108 (Tenn.); Bick 1957: 80 (La.); Gloyd 1958: 8 (Tex.); Bick and Bick 1958: 240 (Okla.); Bick 1959: 131 (Ark.); Donnelly 1961: 7 (Md. Va., D. C.); Alrutz 1961: 23 (Ohio); Borror 1963: 104 (common name); Macklin and Cook 1967: 120 (Ky.); Montgomery 1967: 127 (distr.); Roback & Westfall 1967: 114 (water quality data); Montgomery 1968: 134 (distr.); Pinhey 1969: 189 (tandem linkage); Resener 1970: 37 (Ky.); Huggins *et al.* 1976: 16 (Kans.); Harp & Rickett 1977: 50 (Ark.); Huggins 1978: 2 (Kans.); Young & Bayer 1979: 90 (larva, key, Tex.); Carle 1979: 322 (status in Virginia); White *et al.* 1980: 26 (S. C.); Carle 1982: 339 (W.Va.); Dunkle & Westfall 1982: 32 (status in Fla.); Paulson 1982: 255 (U.S., Mex.); Huggins & Brigham 1982: 4: 39 (N. C., S. C.); Harp & Rickett 1985: 132 (Ark.); Davies & Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat., attributes authorship to Selys); Bridges 1991: VII.60 (cat.); Tsuda 1991: 95 (cat.); Dunkle 1992: 39 (Fla).

Gomphus designatus. – Hagen 1861: 99 (descr. ♂, ♀).

Gomphus sp.. – Cabot,1872: 4 (descr. larva as *Gomphus* sp. No. 6, Poles Creek, Tex.).

Herpetogomphus designatus. – Walsh 1862: 389 (compared with *Ophiogomphus rupinsulensis*); Hagen 1875a: 42 (cat.); Selys 1879: 64 (2 sep.) (characters of genus); Hagen 1885: 255 (larva of Cabot identified); Kirby 1890: 60 (cat., attributes authorship to Selys); Banks 1892: 179 (Kans.); Calvert 1899: 386 (characters of genus); Adams 1900: 622 (Ark.); Williamson 1903: 226 (Tenn.); Van der Weele 1906: 177 (mentioned); Tucker 1907: 79 (Kans.); Tucker 1908: 99 (Tex.); La Rivers 1938: 76 (Nev., habits); La Rivers 1940a: 112 (Nev.).

Description

Male. – Entire face pale green, more vivid on postclypeus and frons, vertex with wash of brown around ocelli or entirely dark brown, scape dark brown, pedicel light brown, flagellum dark brown; anterior margin of vertex forming a trough at junction of antefrons, this trough with a pair of deeper pits anterolateral to median ocellus; occiput green, wide, tumid medially, crest slightly sinuate, barely emarginate medially or straight, its hind margin covered with long brown hairs; postocciput not visible dorsally, green; rear of head brown, darker toward occipital foramen.

Prothorax predominantly brown, becoming green dorsally; anterior and posterior lobes green; synthorax (fig. 17) green with following dark brown: well defined middorsal stripe widening to collar, its upper end extending along antealar sinus connecting with narrow humeral stripe; an isolated antehumeral stripe not touching dorsal or ventral margin (except in specimens from Durango and Chihuahua – see remarks); lower part of humeral stripe extending posteriorly to form a fragmented second lateral stripe, though in some specimens a vestige of a complete stripe exists; narrow third lateral stripe. Coxae, trochanters pale green, femora green becoming brown posterolaterally at distal 0.20; distal 0.05 of metafemora green with narrow brown line extending distally from subapical brown area; tibiae dark brown with yellow along lateral carinae of basal 0.5 of mesotibiae, a vestige of yellow or none on metatibiae; tarsi dark brown, armature black.

Wings hyaline with wash of yellow basally, venation dark brown, basal wing venation light brown, especially anteriorly, anterior margin of costa yellow, except for anterior margin of pterostigma; pterostigma dark brown, veins bordering it black.

Venational statistics. Fifth (rarely fourth) antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 2-5/1-4; anx: fore wing 11-14/11-14, hind wing 8-11/8-11; pnx: fore wing 7-10/8-11, hind wing 7-11/8-12; cs under pterostigma: fore wing 5-7/5-7, hind wing 4-7/4-7; anal triangular cells: 3-5/3-4. Hind wing 28-31 mm.

Abdomen. Segment 1 green with dorsolateral brown stripe occupying basal 0.75 of segment; segment 2 similar to segment 1, but dark brown expanding ventrolaterally behind auricle, contracting again and connecting with dark brown annulus; segment 3 similar to segment 2 but dark brown dorsolateral stripe interrupted at anterior 0.25 and again at distal 0.50 to 0.75 of segment, dark brown prominent at transverse carina, posterior 0.25 to 0.30 of segment with dorsolateral brown expanding laterally to encircle segment at posterior 0.10 of segment; segments 4-6 similar to segment 3 but dorsolateral brown interrupted only at anterior 0.25 to 0.30 of segment and expanding abruptly at transverse carina; segment 7 with narrow dark brown on transverse carina and poorly defined brown on lateral 0.50 of segment; segments 8-10 yellow brown with dorsolateral red brown occupying basal 0.40 to 0.75 of segments; pale areas of segments 2-6 orange green dorsally, becoming white below. Abdomen 35-37 mm.

Cercus (fig. 104) yellow brown, strongly angulate near middle; tip of cercus beyond angulation narrow, drawn out into a fine point; ventral margin with inferior carina at basal 0.45. Epiprocts yellow brown, gently curved dorsally at 90°, tips obliquely truncate (fig. 130) or spatulate (fig. 131).

Accessory genitalia (fig. 60). Anterior hamule black, divided at upper 0.50; lower branch forming a small, posteriorly directed truncate appendage; posterior hamule pale green, triangular, with anterior basal shoulder, tip evenly round, black; penis with long, decumbent lanceolate lateral lobe, its posterior end serrated; cornuae separated, tips narrowly rounded, with no medial lobe; membranous hood moderately long but usually with ends not overlapping.

Female. – Head as in male, but median swelling of occiput more prominent; prothorax and synthorax as in male; wings with yellow at base more extensive, often with markings at base of arculus, to cubitoanal crossvein; abdomen with definite pale orange dorsally, white to orange white laterally, these areas separated by brown dorsolateral stripes as in male; these stripes on each segment may be narrower, especially so between transverse carina and posterior 0.20 to 0.30 of segment; segments 8-9 mostly dark brown dorsally, sides tawny, annulus pale; segment 10 yellow brown, cercus ocher. Abdomen 33-36 mm.

Vulvar lamina (figs. 185-186) with prominent basal plates; quadrangular laminar plates acuminate posteriorly, meeting at medioanterior margin; cleft between plates broadly U-shaped; juncture of Y-shaped postlamellar ridge at or before level of posterior margin of lamina. Abdomen 33-36 mm.

Venational statistics: number of marginal cells behind fore wing paranal cells: 2- 5/1-5; anx: fore wing 12-15/11-15, hind wing 8-12/8-11; pnx: fore wing 7-12/7-12, hind wing 8-12/7-12; cs under pterostigma: fore wing 5-7/5-7, hind wing 4-8/5-7. Hind wing 28-32 mm.

Diagnosis

Little difficulty should be encountered in identifying either sex of this species. The strongly angulate cercus superficially allies it with *E. sipedon, E. heterodon,* and *E. lampropeltis,* but the structure of the occiput and the penile characters easily separate males of these species. The broadly defined occiput, with the large medial tumid area characteristic of *E. designatus,* is not present in the other three species. Male *E. lampropeltis* have a broad occiput, as do male *E. designatus,* but the medial area of the occiput is only slightly tumid.

The long, recumbent lateral lobe of the penis is unique to this species (fig. 82). In *E. lampropeltis* and *E. sipedon,* this structure forms a spinulose semicircle (figs. 83-85).

As in males, females of *E. designatus* are distinguished from all other similar species by the tumid median area of the occiput (fig. 156). The vulvar lamina in *E. designatus* (figs. 185- 186) more closely approaches that of *E. bothrops* (fig. 183) than of *E. sipedon* (figs. 187-188), *E. heterodon* (fig. 193), or *E. lampropeltis* (figs. 189-190). Each lamellar plate of *E. designatus* is smaller and the notch in the medial margin is more concave than in the other species.

Remarks

Variation. – Calvert (1907) described a specimen from San Pedro, Coahuila, Mexico, which differed from typical *E. designatus* in the following characters (typical condition in parentheses): 1) dark antehumeral stripe reaching down to mesinfraepisternum (lower part of stripe isolated), and 2) darker, more pronounced markings on abdominal segments as follows: segment 7 with a black spot on each side of posterior 0.50 of segment (like area red brown, blending anteriorly with ocher pale area); segment 8 with a black stripe on each side for almost its entire length (this area red brown); segment 9-10 with black at basal dorsolateral 0.50 to 0.75 (this area red brown with some black on dorsal 0.50 of segment). Calvert (1907) considered the San Pedro male to represent *E. designatus.* This specimen is indicated as in the ANSP, but it could not be found (Azuma *in litt.*, 1984). However, I have seen three males (Durango and Chihuahua) and a female (Durango) whose markings agree with Calvert's San Pedro male. I also find the following other differences: 1) no wash of yellow present on wing bases, 2) dark thoracic stripes thicker and more pronounced (fig. 18), 3) a black spot anteroventrally to auricle of abdominal segment 2, and 4) tip of epiproct, viewed posteriorly, is spatulate (fig. 131), not obliquely truncate (fig. 130) as is typical of other specimens. The single female has a more arcuate occiput (fig. 157) than typical *E. designatus* (fig. 156), but the dark anteroventral spot on segment 2 is small and inconspicuous.

Specimens from Durango, Chihuahua, and Coahuila could be a well-defined subspecies characterized by overall darker colouration and slight morphological modification of the female occiput (if typical for this form) and male epiproct. I detect no morphological differences in the penes, hamules, or cerci and, like Calvert, I am inclined to treat these specimens as *E. designatus.* Further evidence to support their conspecificity comes from a male from Nuevo Leon (in foothills of the northernmost range of mountains) in which the antehumeral stripe extends to the mesinfraepisternum but is in all other characters typical of *E. designatus.*

One male from McLennan Co., Texas, has the tips of the posterior hamules with a small, anteriorly recurved hook. This male and another from the same locality have vestiges of an anteroventral dark spot on abdominal segment 2.

I have not seen sufficient material of this species throughout eastern parts of its range to render any conclusions about geographic variability. Numerous specimens, primarily from Gonzales and Williamson counties, Texas, show little variability.

Although the type locality for *E. designatus* and many other species collected by Capt. John Pope of the Smithsonian Institution and described by Hagen, is said to be the Pecos River in western Texas (32°N, 104°W), Needham and Cockerell (1903), citing Scudder and Cockerell (1902), argue that the type locality was probably at or near Roswell, Chaves Co., New Mexico, as follows (Needham and Cockerell 1903: 138-139): 'In Proc. Davenport Acad. Sci. vol. 9 (1902), p. 51, it is inferred that Pope collected his material at very different localities above the river, since he obtained both *Melanoplus bivittatus* and *M. differentialis*, which inhabit different life-zones. However, in 1902 it was observed that these two grasshoppers do actually occur together at Roswell. As it is not very likely that their ranges overlap very much, it thus seems likely that Pope's collections, if all from one place, were from the vicinity of the present town of Roswell, rather than from Lat. 32° (the present boundary between New Mexico and Texas), as Hagen indicates. In all probability, however, the collections were made in several places.'

No year is indicated on the data of any of the type material, nor have I found any reference to the year of Capt. Pope's expedition. However, a public display on the recent human history of the caverns at the visitor center at Carlsbad Caverns National Park, Eddy Co., New Mexico, states that Pope's expedition occurred in 1854-1855.

Venational details of lectotype male: number of marginal cells behind fore wing paranal cells: 1/2; ; anx: fore wing 12/13, hind wing 10/10; pnx: fore wing 8/9, hind wing 9/9; cs under pterostigma: fore wing 6/6, hind wing 7/6; anal triangular cells: 3/4.

Biology. – The synonymy indicates that more is known about this species than any other congener. *Erpetogomphus designatus* seems to be a species of mesic deciduous forests where there are clear streams and rivers. Montgomery (1925) writes of its habits in Indiana: 'This species was common in a well-cultivated orchard near Vincennes on August 7, 1924, resting on the ground with wings spread out against the soil but taking flight so readily that only three specimens were taken in two hours although I saw 20 or more.' In Hamilton Co., Indiana, Montgomery (1937) records it as '...rather numerous at ripples in the river, flying just above the surface of the water, and alighting on rocks. However, it was exceedingly difficult to capture...'. Williamson (1932) observed this species flying back and forth near the surface over ripples in Missouri. Others alighted on vegetation or on tips of mullein heads. La Rivers (1938) described the flight of *E. designatus* at Hiko Springs in the Pahranagat Valley, Nevada, as 'low, swift, and change of position rapid...' Ahrens (1938) describes the capture of a male along with a male *Hagenius brevistylus* Selys near Lebanon, Missouri: 'The *H. brevistylus* had struck and seized the *designatus* with such force that both were carried into the water. Both were dipped from the river an instant after they struck the surface.'

Dunkle and Westfall (1982) assign *E. designatus* as 'threatened' in Florida, because it is thus far known only from Liberty and Gadsden counties in the panhandle. In 1975 and 1977, I found this species abundant along cultivated stubble bordering trees next to the Guadalupe River in Gonzales County, Texas. It was more abundant than *E. eutainia*; and both species were easily flushed from low or cut vegetation. Members of both sexes did not fly far, and I could easily photograph and capture specimens.

Collection dates range from 6 May in Texas (Williamson, 1914b) to 5 October in Tennessee (Wright, 1938).

The larva has been described by Cabot (1872), Needham and Heywood (1929) and Needham and Westfall (1955).

Distribution (fig. 202). – *Erpetogomphus designatus* and *E. compositus* are the most boreal of the genus, with *E. designatus* generally replacing the western *E. compositus* in the eastern United States. *Erpetogomphus designatus* occurs as far north as Maryland and Washington, D. C., west through West Virginia, Ohio, Indiana, Missouri, Kansas, southeastern Colorado, eastern New Mexico, into western Texas. Sidney Dunkle (*in litt.*, 1991) mentions one female from South Dakota (Fall River Co., 9.7 mi SW Hot Springs, 29 July 1976, G. and J. Bick, L. Hornuff), erroneously published as *Stylurus intricatus* (Selys) (Bick *et al.*, 1977: 151), which is the northernmost record for this species. It occurs generally throughout the southeastern United States, but does not penetrate peninsular Florida (Dunkle and Westfall, 1982). Farthest western records include Hiko Springs, Lincoln Co., Nevada (La Rivers, 1938) and Arizona (Maricopa Co., Salt River at Corn Bluff Campground, 15 mi NE of Mesa). *Erpetogomphus designatus* is found as far south as Nuevo Leon (24-26°N, 100°W) and west to Coahuila (Calvert, 1907), Durango, and Chihuahua, Mexico.

It is partially sympatric with *E. compositus* in Arizona, Nevada, New Mexico, and western Texas. I collected it with *E. eutainia* in Gonzales Co., Texas.

Material

Type data. – Lectotype male by present designation with following data: 'July/ 16' [handwritten], '*designatus*' [handwritten], 'Hagen' [printed], small white label with printed 'Type' with red label glued to lower edge with handwritten '1864'; red rectangular label with printed 'LECTOTYPE'/ and written

'*Erpetogomphus designatus*/ Hagen ♂/ des. [printed] R. W. Garrison 1984'. Another ♂, a paralectotype, has the handwritten labels, '*Erp. designatus*/ ♂/ Pecos River' [in Hagen's hand] and 'Pecos River/ Uhler 1860.' in an unknown hand. A female paralectotype, collected 'July/ 15' has the additional label: [all printed unless otherwise stated] 'ERPETOGOMPHUS/ DESIGNATUS HAGEN [stamped] / P. P. Calvert, det [written] 1905/ B. C. A. Neur., p. [written] 166.' Type locality herein restricted to vicinity of Roswell, Chaves Co., New Mexico (see remarks).

Other material (84♂, 53♀, including lectotype ♂ and ♂ ♀ paralectotypes). – U. S. A.: FLORIDA: *Gadsden Co.*, Apalachicola River, Aspalaga Landing, Hwy I-10 (JD, RWG); GEORGIA: *Houston Co.*, Ocmulgee River at 96, (RWG); VIRGINIA: *Louisa Co.*, South Anna River, Rte 657, (CSUC); North Anna River, Rte 601, (CSUC); KANSAS: *Chatauqua Co.*, Big Caney River, 1 1/2 mi W of Elgin, (CSUC); TEXAS: *Caldwell Co.*, Plum Creek at US Hwy 90 (RWG); *Goliad Co.*, 3 mi N of Goliad, (RWG); *Gonzales Co.*, Guadalupe River, 4 mi S of Gonzales (RWG); Palmetto State Park, 6 mi S of Luling, nr. US Hwy 183, (RWG); *Hidalgo Co.*, Bentsen, Rio Grande State Park, (CSUC); *McLennan Co.*, Hog Creek, (RWG); *Real Co.*, Nueces River at Tex Hwy 55, S of Barksdale, (RWG); *Reeves Co.*, roadside irrigation ditch W of Balmorhea (RWG); *Williamson Co.*, 3 mi SW of Taylor, (RWG); Mustang Creek by Carlos G. Parker Blvd (= Loop 427), Taylor, (RWG); COLORADO: *Las Animas Co.*, Purgatory River, Bent Cyn nr. Delphi (CSUC, RWG); NEW MEXICO: *Guadalupe Co.*, Santa Rosa, 4600 ft. (UMMZ); ARIZONA: *Maricopa Co.*, Salt River at Corn Bluff Campground, 15 mi NE Mesa, (-FSCA); MEXICO: *Nuevo Leon*: in foothills of the northernmost range of mountains, (UMMZ); Apodaca, just NE of Monterrey, near course on Instituto farm, (-UMMZ, RWG); Chihuahua: La Cruz, (RWG); Naica (UMMZ); Durango: 3.7 mi NW of Gomez Palacio on Hwy 49, 3700 ft., (UMMZ); 8.2 mi N of Gomez Palacio on Hwy 49, (UMMZ); Rio Nazas at Mex. Hwy 49, 3.4 mi S Ciudad Leon Guzman, 4200 ft. (DRP).

Erpetogomphus sipedon Calvert

(figs. 19-thx, 39, 40-abd, 61-hamules, 83-penis, 105, 106-app, 158, 159-vertex, 168-leg, 187, 188-vl, 203-distr)

Erpetogomphus sipedon Calvert, 1905: 165 (descr. ♀ Jalisco: Guadalajara). – Calvert 1907: 399 (♀ 'Las Bocas in Durango...'); Calvert 1908c: xxx (*Erpetogomphus sipedon*, type ♀, Guadalajara, found by Schumann); Calvert 1909: 481 (Cuernavaca, Mexico); Williamson and Williamson 1930: 13 (summary of status); Kimmins 1969: 297 (type in BMNH); Paulson 1982: 256 (Mex.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.195 (cat.); Tsuda 1991: 95 (cat.).

Description

Male. – Entire face light green; this colour more vivid on frons, post- and anteclypeus; base of mandible, labrum light green, vertex with brown around and on ocellar prominences, remainder light green; antennal pedicel dark brown dorsally, light green ventrally; second segment and flagellum dark brown; occiput light green, crest slightly emarginate medially, its hind margin covered with long brown hairs; rear of head brown, darker toward occipital foramen, becoming light green laterally.

Prothorax predominantly dark brown, becoming light green dorsally; anterior and posterior lobes light green. Synthorax entirely light green (probably a vivid apple green in life) with following dark brown: antehumeral stripe ending dorsally before antealar sinus, narrow stripe along humeral suture, this stripe widening at dorsal 0.30 of suture and with anterior margin just touching upper part of antehumeral stripe, anterior 0.50 of mesinfraepisternum. Coxae, trochanters ivory, femora light green with black along external surfaces, more so on mesofemora; most of lateral surface of mesofemora dark brown, these markings more restricted and limited to apical 0.30 of metafemora; tibiae black with small lateral ivory stripes along basal 0.30; tarsi and armature black.

Wings hyaline, venation dark brown, basal wing venation brown, anterior margin of costa yellow; pterostigma brown, black along margins.

Venational statistics (n = 13). Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 1; anx: fore wing 12-13/12-15, hind wing 9-10/9-10; pnx: fore wing 7-10/7-9, hind wing 9-11/8-10; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/6; anal triangular cells: 4. Hind wing 28-31 mm.

Abdomen (fig. 39). Segment 1 light green with dorsolateral brown stripe; segment 2 similar to segment 1 but dark brown expanding posteriorly behind auricle, contracting again and interrupted just before brown annulus; segment 3 similar to segment 2 but with dark brown at transverse carina, anterior end of dorsolateral not on or just touching segment 2, its posterior end broadly connecting with dark brown annulus; segments 4-6 similar to segment 3 with posterior 0.40 wider than anterior 0.60; segment 7 largely pale except for brown along transverse carina, becoming red brown posteriorly, especially so laterally; segment 8 largely red brown with ill-defined light yellow brown middorsal and ventrolateral stripes; segment 9 similar to segment 8; segment 10 red brown basally, becoming pale yellow brown distally. Abdomen 33-37 mm.

Cercus (figs. 105-106) ivory, strongly angulate near middle; tip of cercus beyond angulation narrow, drawn out to a fine point; ventral margin with inferior carina at basal 0.30. Epiprocts yellow brown, typical of genus.

Accessory genitalia (fig. 61). Anterior hamule black, divided at upper 0.30, lower branch forming a small, truncate appendage; posterior hamule white, triangular, with anterior basal shoulder, tip with small, anteriorly recurved tooth; penis with small serrated lateral lobes, membranous hood short, exposing a subcutaneous membrane which forms posterior margin of segment (fig. 83); cornuae (fig. 83) moderately long, widely separated, medial lobe present, usually 0.5 to 1.0 length of outer lobe.

Holotype female. – Face entirely pale except for small black area at base of mandible, occiput (fig. 159) dark brown around ocelli, remainder pale. Prothorax mostly pale, darker along pleura. Synthorax (fig. 19) mostly pale except for brown margin around antealar sinus and incomplete antehumeral stripe, its upper end joined with narrow humeral stripe. Coxae, trochanters, and femora pale with apical 0.30 black, especially mesofemora, metathoracic legs with black less extensive (fig. 168), forming black streaks externally; tibiae entirely black except for pale line laterally, tarsi and armature black.

Abdomen (fig. 40) similar to male but with dark brown dorsolateral stripe of uniform width on segment 2, segments 8-9 mostly black dorsally, sides tawny, annulus pale, cerci lacking. Abdomen 35 mm.

Venational details: number of marginal cells behind fore wing paranal cells: 2/2; anx: fore wing 13/13, hind wing 9/11; pnx: fore wing 9/9, hind wing 10/12; cs under pterostigma: fore wing 6/7, hind wing 7/6. Hind wing 31 mm.

Vulvar lamina (fig. 187) with broadly rectangular flaps meeting at anterior margin; juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Diagnosis

Males of *Erpetogomphus sipedon* are most similar to *E. heterodon* but are easily distinguished by the structure of the penis and cercus. The cornua in *E. sipedon* has a medial lobe (fig. 83), which is lacking in *E. heterodon* (fig. 87), and the tip of the cercus in *E. sipedon* are slender and finely attenuate (figs. 105-106), not robust and short as in *E. heterodon* (figs. 110-111). *Erpetogomphus heterodon* and *E. sipedon* are the only two species of the *E. designatus* group which share a similar thoracic design. However, *E. sipedon* lacks any dark thoracic stripes on the second and third lateral sutures; a vestigial incomplete second lateral stripe and complete narrow third lateral stripe exist on *E. heterodon*. The thoracic pattern of *E. boa* is also similar to *E. sipedon*, but *E. boa* is well differentiated by genital characters given in the keys. Although the difference in somatic patterns between *E. lampropeltis* and *E. sipedon* is great, these two species are separable by the structure of the penis. In *E. sipedon*, the hood is abbreviated, exposing a subcutaneous membrane, which latter forms the posterior margin of the segment. In *E. lampropeltis*, the hood is of normal length and it forms the posterior margin of the segment.

Although females of *E. sipedon* are easily differentiated from all other similar species by differences in colour and pattern, their separation from the same species using only structural characters is more difficult. Species morphologically similar to *E. sipedon* include *E. crotalinus, E. compositus, E. viperinus, E. bothrops*, and *E. heterodon*.

The occiput of *E. sipedon* is straight or, at most, weakly notched, (notch in *E. crotalinus* not clearly seen in the paralectotype female, [fig. 161]). The longitudinal distance of the occiput (hereafter called width) is narrower in *E. sipedon* than in *E. crotalinus*, and the posterolateral ocellar tubercle is less pronounced in *E. sipedon* than in *E. crotalinus*.

The occipital crest of *E. compositus* is sinuous (mostly linear in *E. sipedon*) and the postocciput is easily visible in dorsal view (fig. 163); the same structure is barely visible in *E. sipedon* (fig. 159).

The structure of the postlamellar ridge provides the best means of separation between *E. sipedon* and sister taxa *E. bothrops* and *E. viperinus*. In *E. sipedon*, this Y-shaped structure is short: the juncture of the lateral arms meets at or near the hind margin of each vulvar plate. The longitudinal stem also does not possess any circular or oval depressions on either side (figs. 187-188). In *E. bothrops* and *E. viperinus*, the juncture of the Y-stem is well posterior to the hind margin of each vulvar plate, and a well-defined oval or circular depression exists on either side of the longitudinal ridge (figs. 183-184).

I have been unable to find any morphological differences between females of *E. sipedon* and *E. heterodon*. Body pattern (figs. 19, 23) and distribution (figs. 201-204) will serve to separate females of these closely related species.

Remarks

Variation. – The male description is based on 11 males from Jalisco, Morelos, and Durango states, Mexico. The four from Durango are slightly larger (hind wing 30-31 mm); and their thoracic pattern is similar to that of the holotype female (fig. 19). The other seven males are smaller (hind wing 28-29 mm), and the lower 0.60 of the dark humeral stripe is narrower. The Durango males, though larger, have a sparser venation. For example, three have no marginal cells behind fore wing paranal cells, one has one marginal cell in both wings; and all other specimens have one marginal cell, except for the left fore wing of one Acatlipa male, which has no marginal cells. Two of the Durango males have a 3-celled anal triangle in both hind wings, while all others possess 4 cells. The cerci of the Durango males are less angulate and the tips more robust (fig. 106) than the other males, but other characters of the body and penis leave no doubt that they represent *E. sipedon.*

Variability for females is less pronounced than for males, and I can find no overall differences in venational patterns among the 12 females examined.

Female venational statistics (n = 12, including holotype): number of marginal cells behind fore wing paranal cells: 1-3/0-3; anx: fore wing 12-14/12-15, hind wing 9-12/9-11; pnx: fore wing 8-10/8-10, hind wing 9-11/8-12; cs under pterostigma: fore wing 5-7/5-7, hind wing 5-7/4-6. Hind wing 30-34 mm. Abdomen 36-37 mm.

When Calvert (1905) described this species, he had only 6 females available; and he noted differences in the condition of the occiput between the holotype and a paratype from Matamoros, Puebla (figs. 158-159). Both forms were represented in his key. I cannot consider the differences noted by Calvert as useful, as much variation seems to exist in the shape of the occipital ridge in females of this and other species.

At the time of the original description, Calvert (1905) postulated that the female of *E. sipedon* could be *E. boa*, which was then known only from one incomplete teneral male. The discovery of more specimens of both species, and especially the capture of both males and females of *E. sipedon* in Durango, leaves no doubt that both are valid species.

Biology. – González (*in litt.*) collected this species at Palo Bolero, where adults perched on herbaceous vegetation on the banks of the Rio Sabinos. Its known distribution suggests that it is more widely distributed, but specimens are rare in collections. Specific ecological requirements may restrict its occurrence to certain sites, but a more likely answer to its apparent rarity is a lack of thorough collecting within its range. Collection dates range from 21 May (Cuernavaca) to 13 August (Nombre de Dios).

Distribution (fig. 203). – *Erpetogomphus sipedon* is known from northern Durango (Las Bocas [Calvert, 1907] settlement on the Rio Florida in extreme northern Durango near Villa Ocampo, approx. 26°25'N 105°25'W, [Selander and Vaurie 1962]) south through Morelos and Puebla (approx. 18°50'N, 99°W) and seems restricted to the highland area of central and western Mexico from altitudes of 1000 m (Palo Bolero) to about 2073 m (Las Bocas). González (*in litt.*) collected this species in Mexico state (Tonatico) during July, 1992.

Material

Type data. – Holotype female: white printed label: '[Mexico] Guadalajara,/Jalisco,/July. Schumann:', white, partially printed label: '*Erpetogomphus* ♀/*sipedon* Calv. TYPE /P. P. Calvert, det. 1905/B. C. A. Neur., p. xxx, 166/orig. of Pl. VIII, ff. 34, 40' with '(form/*a*)' handwritten on left side; printed label 'Brit. Mus./1911-339.'; small round label with red margin: 'Holo-/type'.

Other material (11♂, 12♀, including holotype ♀). – MEXICO: *Durango*: Nombre de Dios, just SE of Durango on Mex. Hwy 45 (23°51'N, 104°14'W), 5900 ft. (1800 m), 13 Aug. 1947 (W. Gertsch, M. Cazier), 4♂, 7♀ (AMNH, RWG); Morelos: Cuernavaca, 21 May 1898 (no collector), 1♀ (CUIC); Cuernavaca, 7 July 1900 (C.C. Deam), 2♀ (UMMZ); Palo Bolero, km. 18.3, route 95, 5 km. S. Acatlipa, 1000 m (approx. 18°45'N, 99°15'W), 26 June 1985 (E. González), 2♂ (UNAM); 18 June 1986 (E. González), 2♂ (UNAM), 12 July 1986 (E. González, V. Garcia), 3♂ (RWG); Morelos: Pueblo Cocyotla, Hwy 421, about 30 km SW of Cuernavaca, 23 July 1992 (J. Daigle), 1♂ (JD); Puebla: Matamoros, no date, (Otis W. Barrett), 1♀ (ANSP).

Erpetogomphus lampropeltis Kennedy

Description

Male. – Face entirely pale with dark markings as follows: along basal margin of labium, along frontoclypeal suture (less developed in *E. l. natrix*), base of antefrons; vertex all dark brown; antennae dark brown; anterior margin of vertex with an arcuate pit, one each anterolaterad to median ocellus; area between these pits tumid (fig. 138), occiput white green, wide, slightly tumid medially, crest entirely black, slightly raised, linear or slightly convex posteriorly, some with a small median notch, its hind margin covered with pale brown hairs; postocciput slightly concave, pale; rear of head dark brown.

Prothorax largely brown with pale green or grey green areas on anterior and posterior lobes, and with two small median spots on median lobe; contrasting dark/pale areas more prominent in nominotypic subspecies; pale colours of synthorax grey or grey green (*E. l. lampropeltis*) to green (*E.l. natrix*) with following dark brown areas: middorsal stripe, widening basally to collar, its upper end covering antealar sinus, extending posteriorly and connecting with broad, well defined antehumeral and humeral stripes; well defined sinuate second lateral stripe; third lateral stripe. Coxae, trochanters pale grey green with slight wash of brown posteriorly; tibiae pale grey green with defined superior surfaces brown, becoming dark brown distally; tibiae black with narrow strip of pale grey green along basal 0.30 to 0.50 of lateral margin; base and armature black.

Wings hyaline, basal wing venation brown; anterior margin of costa yellow up to pterostigma; pterostigma black; fifth antenodal thickened in all wings (with rare exceptions).

Abdomen. Abdominal segment 1 pale grey green to green with basal 0.25 brown and with dorsolateral brown stripe; segment 2 with dorsolateral stripe sending a ventral stem posterior to auricle and (often) an isolated spot on anteroventral margin of segment, dorsolateral stripe often connecting with black annulus or ending just before; segment 3 with isolated black dorsolateral spot surrounding lateral carina; its anterior end tapering and sometimes touching anterior margin of segment, distal 0.25 of segment with dorsolateral black increasing in width posteriorly and touching dorsally near black annulus; segment 4 similar to segment 3, but two black spots broadly connected forming a continuous dorsolateral stripe occupying distal 0.80 of segment, this stripe often constricted in middle; segments 5 and 6 similar to segment 4, but with middorsal pale areas becoming darker; segment 7 with anterior 0.50 pale, except for black transverse carina, becoming entirely tawny to black posteriorly; segments 8-10 yellow brown, becoming black dorsally in most specimens; foliar extensions dark brown to black.

Cercus (figs. 107-108) ocher, in lateral view slightly concave dorsally near base, posterior 0.25 moderately angulate, the short tips slightly recumbent; cercus enlarged ventrally at basal 0.40 to 0.50 with inferior carina along same area, remainder slightly concave with tip forming a blunt point. Epiprocts yellow brown, gently curved dorsally at 90°, tips (fig. 132) dorsoventrally flattened and divergently bluntly pointed.

Accessory genitalia (figs. 62-63). Anterior hamule dark brown, divided at basal 0.50, lower branch forming a small, posteriorly directed truncate appendage; posterior hamule grey white, triangular, with anterior basal shoulder, tip bluntly rounded and armed with a small anteriorly directed tooth on posterior border; penis with lateral lobe small, roughly semicircular, serrate; cornuae (figs. 84-85) moderately widely separated, tips broadly rounded with well developed median lobes.

Female. – Head as in male, but with crest of occiput slightly more erect and convexly arcuate; posterior margin of postocciput slightly concave; prothorax and thorax as in male, but with pale areas generally more extensive; wings hyaline or with saffron infusion at base in some *E.l. natrix*; abdomen in well preserved specimens with pale colours primarily white with dull orange dorsally; black dorsolateral stripes and spots more reduced than in male, these stripes sometimes separated or greatly constricted on segments 4 and 5; cercus ocher.

Vulvar lamina (figs. 189-190) with prominent basal plates, quadrangular laminar plates acuminate posteriorly, meeting at anteromedial margin; cleft between plates forming a 90° angle; V juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Diagnosis

This species is most similar to its congeneric relatives, *E. sipedon* and *E. compositus*, and is diagnosed under those species.

Remarks

The original description of *E. lampropeltis* is brief and is based on an unspecified number of males and females from Sespe Creek, Fillmore, Ventura County, California. Williamson and Williamson (1930) originally described *E. natrix* in detail from 21 males and two females from Baja California, Mexico. An abstract of their diagnosis of males *E. natrix* from *E. lampropeltis* is as follows:

> 'The head and thorax of *lampropeltis* are duller and paler than in *natrix*.... the rear of the head is brown in *lampropeltis* and black in *natrix*; the thoracic brown is paler in *lampropeltis* and the pale areas are grayer, giving much less contrast in the thoracic pattern; the two lateral dark stripes are always joined, often very broadly in *lampropeltis*, and are not joined in.....*natrix*,....the femora are brown in *lampropeltis*.....black in *natrix*; and the inferior dilated edge of abdominal segments 8 and 9 is black in *lampropeltis* and, in *natrix*, is colored light vivid brown like the sides of the segment adjacent to the edge.....'

The apparent differences in morphology described above fall well within the latitude of individual and geographic variation and do not, in my opinion, constitute specific differences. Further, several specimens of *E. natrix* from various parts of its range have maculation patterns more closely approaching those of *E. lampropeltis*. For example, the antehumeral and humeral stripes are briefly connected, the dorsum of abdominal segments 7-10 have black as in *E. lampropeltis*, and the inferior dilated margin of abdominal segments 8 and 9 is black. I can also detect no differences in the shape of the vulvar lamina between females of *E. lampropeltis* and *E. natrix*.

The forms are allopatric, separated by the Colorado Desert. The large series of *E. lampropeltis* (mostly topotypes) that I examined does show consistent differences in pale thoracic colouration and minor differences in thoracic maculation. I consider the forms to represent subspecies separable as follows:

1. Pale thoracic colouration grey green, antehumeral and humeral stripes broadly connected on dorsal 0.25, after isolating a small pale spot below antealar sinus; second lateral stripe about twice as wide on dorsal 0.5 and often connecting with narrow third lateral stripe; dark thoracic stripes,

especially second and third, often not well defined (fig. 20); Ventura, San Diego, Los Angeles, and western San Bernardino counties, California *E. lampropeltis lampropeltis*

- Pale thoracic colouration vivid green, antehumeral and humeral stripes not connected, or only narrowly so; second lateral stripe narrower than in *E. l. lampropeltis*, not connecting with third lateral stripe (fig. 21); central Baja California, Arizona, New Mexico, western Texas, south through Durango, Mexico .... *E. lampropeltis natrix*

Erpetogomphus lampropeltis lampropeltis Kennedy (figs. 20-thx, 62-hamules, 84-penis, 107-app, 132-ept, 138-base of postfrons, 160-vertex, 189-vl, 204-distr)

Erpetogomphus lampropeltis Kennedy, 1918: 297 (descr. ♂ Sespe Creek, Fillmore, Ventura Co., California). – Needham and Heywood 1929: 80 (descr. ♂, ♀); Williamson and Williamson 1930: 13 (summary of status); Needham and Westfall 1955: 147 (descr.); Pritchard and Smith 1956: 116 (key); Musser 1962: 14 (notes on larva); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Paulson and Garrison 1977: 157 (Calif.); Paulson 1982: 255 (U.S.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.115 (cat.).

Herpetogomphus lampropeltis. – Byers 1928: 5 (larva unknown).

Erpetogomphus lampropeltis lampropeltis. – Tsuda 1991: 95 (cat.).

Description

Male. – Colouration and maculation as given under species account, key and in fig. 20.

Venational statistics: number of marginal cells behind fore wing paranal cells: 0-3/1-3. – anx: fore wing 9-14/10-14, hind wing 8-10/8-10; pnx: fore wing 7-9/5-10, hind wing 7-12/7-12; cs under pterostigma: fore wing 4-5/4-5, hind wing 3-5/3-6; number of anal triangular cells: 3-4/3-5. Hind wing 28-31 mm. Abdomen 34-37 mm.

Female. – Venational statistics (n = 6): number of marginal cells behind fore wing paranal cells: 0-4/1-3; anx: fore wing 13-15/12-16, hind wing 9-11/9-11; pnx: fore wing 9-11/9-10, hind wing 9-12/9-12; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/5-6. Hind wing 32-36 mm. Abdomen 33-36 mm.

Diagnosis

See account under *E. compositus* and key to subspecies of *E. lampropeltis*.

Remarks

Variation. – Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 1/2; anx: fore wing 12/12, hind wing 9/9; pnx: fore wing 8/9, hind wing 9/9; cs under pterostigma: fore wing 5/5, hind wing 5/4; number of anal triangular cells: 4/5. Hind wing 28 mm.

The large series of specimens primarily from the type locality shows little somatic colour and/or pattern variation, due, possibly, to its limited distribution. The fifth antenodal in the fore wings is generally thickened, but 7 of 40 wings of 20 males examined have the fourth antenodal thickened; and one wing has the sixth antenodal thickened. A 3-celled anal triangle is common in this subspecies, as almost half (19/40) of the wings possess this condition.

The female from Matillija Hot Springs has flavescent wing bases.

Biology. – At the type locality, this species was abundant during early September, 1982. I collected 54 males within about two hours. All preferred to sit on exposed rocks and were easily collected with a net. Hundreds of cast skins were attached to the exposed rocks. I did not find the species in smaller rivulets emptying into Sespe Creek. The only female I saw and collected was found dead in the water.

I returned to the locality in September, 1984, but the entire area had been fenced off. Five males were collected in the general vicinity, below Matillija Hot Springs, but they were rare and more wary.

This is a late summer species: the specimens from San Bernardino Co. collected in June are all teneral. Flight dates for specimens from Ventura Co. range from 10 July to 8 September.

Distribution (fig. 204). – The nominotypic subspecies has been collected only at three localities in Ventura County one in San Bernardino County, one in Los Angeles County, and one in San Diego County, California. It has the most restricted distribution of any Odonata form in southern California.

Material

Type data. – Holotype male: CALIF: Ventura Co., Sespe Creek, Fillmore, 7 Aug. 1915 (C. H. Kennedy); in USNM. I have illustrated the thorax (fig. 20), caudal appendages (fig. 107), and penis (fig. 84) of the holotype.

Other material (70♂, 6♀, including holotype ♂). – U. S. A.: CALIFORNIA: Los Angeles Co., San Gabriel Mtns., jct of N and W Fork of San Gabriel River, E of Hwy 39, 11 Aug. 1986 (D. Swinney), 1♂ (RWG), *Ventura Co.*, Sespe Creek, 4.0 mi N of Fillmore, 600 ft., 8 Sept. 1971 (D. Paulson), 2♂ (CC, RWG); 5 Sept. 1982 (R. W. and J. A. Garrison), 54♂, 1♀ (RWG); Matillija Hot Springs, 14 Aug. 1927 (T. Craig), 1♂, 1♀ (FSCA); just below Matillija Hot Springs, 1400 ft., 2 Sept. 1984 (R. W. and J. A. Garrison), 5♂ (RWG); Wheeler Hot Springs, 10 July 1927 (T. Craig), 4♂, (FSCA); *San Bernardino Co.*, Deep Creek Public

Camp, 15 June 1957 (A. Menke, L. Strange), 1♂, 4♀
(LACM); *San Diego Co.*, La Jolla, La Jolla Indian Res. Campground, San Luis Rey River, 25 Aug. 1991 (W. F. Mauffray), 1♂ (RWG).

Erpetogomphus lampropeltis natrix Williamson and Williamson **stat. n.**
(figs. 21-thx, 63-hamules, 85-penis, 108-app, 1990-vl, 204-distr)

Erpetogomphus natrix Williamson & Williamson,1930: 19 (-descr. ♂, ♀ Baja Calif. Sur, Purissima, 12 October 1923). – Byers 1939: 50 (quotes Williamson & Williamson, 1930); Fraser 1940: Pl. 6 (penis); Needham & Westfall 1955: 148 (descr. ♂); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Paulson 1982: 255 (U.S., Mex.); Davies and Tobin 1985: 28 (cat.); Tsuda 1986: 87 (cat.).

Erpetogomphus lampropeltis. – Tinkham 1934: 215 (Tex.), Needham & Westfall 1955: 147 (Tex.); Gloyd 1958: 8 (Tex.); Kormondy 1960: 122 (Ariz.); González & Novelo 1991: 97 (Mex.); Novelo & González 1991: 154 (descr. larva, Mex.).

Erpetogomphus lampropeltis natrix. – Bridges 1991: VII.144 (cat.); Tsuda 1991: 95 (cat.). [Demotion of *E. natrix* to subspecies status was advised by me *in litt.* to Bridges and Tsuda.]

Description

Male. – Colouration and maculation as given under species account, key, and fig. 21.

Venational statistics: number of marginal cells behind fore wing paranal cells: 0-3/0-2; anx: fore wing 11-15/11-14, hind wing 9-11/9-11; pnx: fore wing 6-11/7-10, hind wing 8-14/7-12; cs under pterostigma: fore wing 4-6/4-6, hind wing 4-6/4-6; number of anal triangular cells: 3-4/2-4. Hind wing 24-33 mm. Abdomen 30-37 mm.

Female. – Venational statistics (n = 17, including allotype): number of marginal cells behind fore wing paranal cells: 0-6/0-5; anx: fore wing 12-15/12-15, hind wing 9-11/9-11; pnx: fore wing 7-11/7-12, hind wing 9-12/9-12; cs under pterostigma: fore wing 4-6/4-7, hind wing 4-7/5-7. Hind wing 30-35 mm. Abdomen 36-41 mm.

Diagnosis

See comments under *E. compositus* and key to subspecies of *E. lampropeltis.*

Remarks

Venational details of holotype male: number of marginal cells behind fore wing paranal cells: 2/1; anx: fore wing 13/13, hind wing 9/9; pnx: fore wing 9/9, hind wing 10/9; cs under pterostigma: fore wing 4/4, hind wing 5/4; number of anal triangular cells: 4/3. Hind wing 30 mm.

Venational details of allotype female: number of marginal cells behind fore wing paranal cells: 2/1; anx: fore wing 13/13, hind wing 9/10; pnx: fore wing 7/8, hind wing 10/9; cs under pterostigma: fore wing 6/5, hind wing 5/5. Hind wing 30 mm.

Variation. – Intrapopulational variation of body maculation appears to be as great as interpopulational variation. The antehumeral and humeral stripes may be connected or separate in any small series from a given locality: 1 of 3 specimens from Cane Springs, Mojave Co., 3 of 12 specimens from Cave Creek, Maricopa Co. (4 have these stripes barely connected), and 2 of 11 specimens from 15 mi E of Douglas, Cochise Co., Arizona, all have connected antehumeral and humeral stripes. Similar degrees of variation exist for the dorsal and dorsolateral darkening of abdominal segments 7-10. Some specimens have little black on these segments (as noted by Williamson and Williamson, 1930, for their type series of *E. natrix*), but others have various degrees of darkening, and some specimens are as dark as I have observed for nominotypic *E. lampropeltis.*

A male I collected at Las Parras, Baja California, has the posterior 0.5 of the dorsum of abdominal segments 7 and all of segments 8-9 with black. The male from 'Corralitos' is unusual in having narrow second and third lateral thoracic stripes. The upper 0.5 of the second lateral stripe is also lacking, but in all other aspects, this specimen is *E. lampropeltis natrix* by morphology and overall body colouration and maculation.

Biology. – Williamson and Williamson (1930) described the type locality. González (*in litt.*) collected this subspecies with *E. crotalinus* in Durango state (La Michiliá). I collected one male of the species at Las Parras in September, 1985 (Garrison, 1986) as it sat upon an exposed rock in the middle of the small stream. It was the only individual I saw.

This subspecies can be common at certain sites in Arizona and New Mexico. Jo A. Garrison and I collected *E. lampropeltis natrix* on the East Fork of the Gila River at Grapevine Campground, where it was equally as common as *E. heterodon.* Adults landed on exposed rocks, exposed bleached logs in the center of the stream, or on the gravel shores. I have also taken it on sandy-bottomed desert streams, often in company with *E. compositus.* Novelo (pers. comm.) found this subspecies with the more common *E. crotalinus* in Durango state (La Michiliá).

I observed oviposition on 1 August 1992 at the Agua Fria River, Yavapai County, Arizona. Females appeared over the stream surface in the late afternoon (about 6: 15 p.m.), and flew rapidly over the water, dispersing their eggs by dipping the abdomen briefly into the water. This behaviour continued until sundown (about 7: 30 p.m.). A few males were still present, sitting on emergent rocks near oviposition sites. No copulations were observed.

Altitudinal gradients for the species range from near 923 m (Tangle Creek, Yavapai Co., Ariz.) to 1754 m in New Mexico and southeastern Arizona (W of Portal). Like *E. l. lampropeltis, E. l. natrix* is primarily a late summer to autumn species. Flight dates range from 27 June to 10 October.

Distribution (fig. 204). – Though originally described from Baja California, *E. lampropeltis natrix* is widely distributed throughout the southwestern United States. It has been collected as far east as western Texas (Tinkham, 1934, Gloyd, 1958) and Durango and Chihuahua, Mexico. The most northerly records are from northcentral Arizona. I have seen no specimens from central or eastern New Mexico, although it probably occurs in those areas. The species apparently does not penetrate north of the Mogollon Rim in Arizona northwest into the Colorado Desert.

Material

Type data. – Holotype male: Mexico: Baja California Sur: Purissima, 12 Oct. 1923 (J. H. Williamson); allotype female, same data but 6 Oct. 1923 (both examined), in UMMZ. I have illustrated the thorax (fig. 21), hamules (fig. 63), caudal appendages (fig. 108), and penis (fig. 85) of the holotype, and vulvar lamina (fig. 190) of the allotype.

Other material (101♂, 22♀, including holotype ♂ and allotype ♀). – U. S. A.: Arizona: *Cochise Co.*: Bear Creek, Rte 61, 6 mi SE Parker Lake, Coronado National Forest (CSUC); mouth Miller Canyon, Huachuca Mtns., (FSCA, UMMZ), pond N of Slaughter Ranch, 15 mi E of Douglas, 3800 ft, (RWG); springs just E of Slaughter Ranch, 17 mi E of Douglas, (RWG); Bear Creek, Rte 61, 6 mi SE Parker Lake, Coronado Nat'l Forest, (CSUC), San Pedro River at Hwy 90 (FSCA); San Pedro River, jct. Charleston Rd., (BYUC); San Pedro River, 9 mi SW of Tombstone (BYUC); San Pedro River at Hereford Rd., (RWG); Southwestern Research Station, 5 mi W of Portal at John Hands Picnic Grounds, 5400 ft, (FSCA); *Gila Co.*, Tonto Natural Bridge (RWG); Webber Creek at Camp Geronimo, 8 mi ENE of Payson, (RWG); *Maricopa Co.*, Cave Creek by Ocotillo Rd, Cave Creek, (RWG); Camp Creek by Cave Creek Rd., 12 mi NE of Scottsdale Rd., 2700 ft., Tonto Nat'l. Forest, (RWG); Sycamore Cyn., 3.3 mi WNW of Hwy 87 (RWG); *Mojave Co.*, irrigation ditches E of Cave Springs, (DRP); *Pima Co.*, Sabino Cyn, N of Tucson (FSCA); Lower Sabino Cyn, (RWG); Upper Sabino Cyn, *ca.* 3 mi N of visitor center, N of Tucson (RWG); *Santa Cruz Co.*, Sonoita Creek Ranch (on way to Salero Cyn), along Santa Cruz River, along Ariz. Hwy 82, 2 mi SW of Patagonia, (RWG); White Rock Campground, Peña Blanca Lake, 4200 ft, (RWG, JD); *Yavapai Co.*, Agua Fria River at Black Canyon City, (RWG); Tangle Creek, nr Tangle Creek cabin, *ca* 33 mi N of Carefree, T9N-R5E, sec. 1, 2800 ft (RWG); on limestone rim of Montezuma's (*sic*) Well (National Monument) (RWG); Sycamore Canyon, Atasco Mtns (LACM); New Mexico: *Catron Co.*, Gila Cliff Dwellings, (RWG); West Fork Gila River at Gila Cliff Dwellings Nat'l Mon., 5700 ft, (RWG); *Grant Co.*, Gila River at Cliff (FSCA); Mangus Springs Creek, Hwy 180, Mangus Springs, (RWG); Grapevine Campground, East Fork of Gila River at N. Mex. Hwy 15, 5600 ft, (RWG); Texas: *Jeff Davis Co.*, Ft. Davis, (FSCA); Limpia Creek, 2-3 mi N of Ft. Davis, (UMMZ); Musquiz Creek, 6 1/2 mi SE Ft. Davis (FSCA); Mexico: Chihuahua: Cascada de Basaseachic National Park, (CSUC, BYUC); San Diego Canyon, (BYUC); Durango: Arroyo El Temazcal (camino a El Aleman), Reserva de la Biosfera La Michiliá, (UNAM); km 21 Camino Suchil-Reserva de la Biosfera La Michiliá, 'Corralitos', (UNAM); Sonora: Maycoba River, (BYUC); Maycoba River, W of Maycoba, (BYUC); 8 mi W of Maycoba River, (CSUC); Maycoba River, Hwy 16, 13 mi W of Maycoba at San Francisco Bridge, (CSUC); Rio Magdalena, Hwy 15 S of Immuris, (BYUC, CSUC); small river W of Vecora, Rte 15, (CSUC, BYUC); Baja California Sur: Purissima (FSCA); Las Parras, about 18 km W of Hwy 1 on route to San Javier, SW of Loreto, (RWG).

Erpetogomphus crotalinus (Hagen *in* Selys)

(figs. 22-thx, 41-abd, 64-hamules, 86-penis, 109-app, 133-ept, 161-vertex, 169-leg, 191, 192-vl, 205-distr)

Ophiogomphus crotalinus Hagen *in* Selys, 1854: 40 (21 sep.) (♂, ♀ descr. from Mexico).

Erpetogomphus crotalinus. – Hagen *in* Selys 1858: 332 (72 sep.) (descr. ♂, ♀, relationship with *E. menetriesii*); Walsh 1863: 253 (mentioned); Selys 1869: 174 (11 sep.) (Mex., attributes authorship to Selys); Selys 1873b: 519 (75 sep.) (list, attributes authorship to Selys); Kirby 1890: 61 (cat., attributes authorship to Selys); Calvert 1899: 38 (Tepic, Mex.); Calvert 1905: 165 (Mex.); Calvert 1907: 399 (Mex.), Calvert 1909: 481 (distr. in Mexico); Muttkowski 1910: 86 (cat.); Ris 1917: 153 (comparison with *E. boa*); Kennedy 1918: 298 (comparison with *E. lampropeltis*); Byers 1939: 50 (quotes Calvert 1907); Williamson and Williamson 1930: 12 (summary of status); Montgomery 1968: 133 (distr.); Paulson 1982: 255 (cat.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat., attributes authorship to Selys); Bridges 1991: VII.54 (cat.); Tsuda 1991: 95 (cat.); Cannings and Garrison 1991: 478 (Mex.); González and Novelo 1991: 97 (Mex.); Novelo and González 1991: 150 (descr. larva, Mex.).

Herpetogomphus crotalinus. – Hagen 1875a: 43 (cat.); Selys 1879: 64 (2 sep.) (characters of genus); Kirby 1890: 61 (cat.).

Description

Male. – Labium grey white, base of mandibles pale green becoming red brown distally, lips black, remainder of face pale green except for narrow wash of brown at base of antefrons, vertex mostly dark brown with green medially behind postoccipital tubercles; antennae dark brown; anterior margin of vertex with two lanceolate pits, each anterolateral to median ocellus; occiput bright green, broad, gently tumid medially, crest black, linear to emarginate medially, its rim covered with row of long brown hairs; postocciput green, smoothly concave or somewhat angulate medially, rear of head light green with brown near occipital foramen.

Prothorax predominantly green, most of middle lobe and posterior of frontal lobe marked with dark brown, a small middorsal green spot longitudinally divided by narrow dark brown line medially on middle lobe. Synthorax (fig. 22) entirely green with brown along margins of antealar crest in a few specimens with a hint of a dark brown antehumeral stripe. Coxae, trochanters pale green, femora green with streak of dark brown becoming wider distally, these streaks restricted to lateral surface of femora (fig. 169) and brown reduced to apical 0.50 of metafemora; a supplementary narrow, linear streak of dark brown more posteriorly placed on femora and, in some specimens, touching lateral streaks of brown distally; tibiae ranging from all yellow green except dark brown laterally, to all brown with yellow on lateral carinae; tarsi and armature black or with some yellow on exterior surfaces of second and third tarsomeres.

Wings hyaline, venation dark brown, anterior margin of costa yellow to base of pterostigma, this structure brown, veins bordering it black.

Venational statistics. Fifth, rarely fourth or sixth, antenodal thickened in all wings; marginal cells behind fore wing paranal cells: 1-3/1-3; anx: fore wing 11-13/11-13, hind wing 8-9/8-10; pnx: fore wing 7-10/7-10, hind wing 8-10/8-10; cs under pterostigma: fore wing 4-6/4-7, hind wing 4-7/4-6; anal triangular cells: 3-4/3-5. Hind wing 26-31 mm.

Abdomen (fig. 22). Segment 1 green, slightly fuscous basally, with small line of black at posterior articulation point; segment 2 all green with narrow dorsolateral streak of black above auricle and with poorly defined dorsolateral brown spot on posterior 0.25 of segment, dorsal 0.75 to 0.50 of annulus black; segment 3 pale green, becoming white ventrally with black along transverse carina and elongate black dorsolateral spot on posterior 0.25 of segment connecting to black annulus; segments 4-7 similar to segment 3, but with narrow anterior offshoot of black laterally on transverse carina and with posterior midlateral black occupying posterior 0.50 of segments, middorsal pale area of these segments becoming progressively more tawny posteriorly, especially so on posterior 0.50 of segment 7; segments 8-9 ocher yellow with well defined dark brown dorsolateral stripe; segment 10 ocher becoming red brown at basal 0.50. Abdomen 31-36 mm.

Cercus (fig. 109) yellow, strongly to moderately angulate dorsally at distal 0.50-0.30; tip of cercus beyond angulation attenuate, drawn out to a blunt point, ventral margin with inferior carina at basal 0.40 to 0.50. Epiprocts yellow brown, gently curved dorsally at 90°, extending to distal 0.25 or almost to level of tip of cercus, tips forming divergent points, dorsoventrally flattened (fig. 133).

Accessory genitalia (fig. 64). Anterior hamule black, divided at upper 0.50, lower branch forming small posteriorly directed truncate appendage; posterior hamule pale green, triangular, with anterior basal shoulder, tip rounded with a small anteriorly directed tooth on posterior margin; penis with semicircular spinose lateral lobe, cornuae separated; with medial lobe, and a long narrow flap at outer distal margin, membranous hood present but not overlapping. Abdomen 31-37 mm.

Female. – Head as in male but with crest of occiput (fig. 161) more emarginate medially, in some specimens with lateral margin arcuate; prothorax and synthorax as in male; legs with black areas more reduced than in male; wings with slight wash of yellow at base (more so in tenerals); abdomen as in male but with black areas more reduced on abdominal segments 1-3; dorsolateral brown stripes almost complete on segments 4-7 except for basal 0.05 of each segment, these stripes complete on segments 8-9; cercus ocher. Abdomen 30-36 mm.

Vulvar lamina (figs. 191-192) with broadly rectangular flaps meeting at anterior margin, juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Venational statistics: number of marginal cells behind fore wing paranal cells: 1-4/1-3; anx: fore wing 11-13/11-13, hind wing 8-10/8-10; pnx: fore wing 7-10/7-9, hind wing 8-10/8-10; cs under pt: fore wing 4-7/4-6, hind wing 4-6/4-6. Hind wing 26-32 mm.

Diagnosis

Erpetogomphus crotalinus is unique in having the extensor surfaces of the tibiae yellow (fig. 169). Some specimens have largely brown tibiae, but the lateral costate ventral margins are always yellow; all other congeners have dark brown to black tibiae. The almost immaculate synthorax is shared by only two other species: *E. cophias* (fig. 27) and some *E. elaps* (fig. 13), but the male cerci of these two species (figs. 100, 116) are never angulate as in *E. crotalinus* (fig. 109). The cornua of the penis (fig. 186) has a well developed median lobe and a long, acuminate tip, a condition unique to this species. This species is superficially similar to *E. heterodon* and is diagnosed under that species.

Females of *E. crotalinus* differ from other species by three characters of the head, the presence of anterolateral pits at the base of the frons, the relatively broad occiput, and the medial notch of the crest. The vulvar lamina (figs. 191-192) provides no discriminatory characters, and is similar to those of *E. lampropeltis* (figs. 189-190), *E. compositus* (fig. 194), *E. heterodon* (fig. 193), and *E. sipedon* (figs. 187-188).

Remarks

The description is based on 91 males and 43 females. The lectotype male is reasonably well preserved, although it lacks the accessory genitalia. I illustrate the cercus (fig. 109) and right hind leg (fig. 169) of the lectotype, and the vertex, occiput (fig. 161), and vulvar lamina (fig. 191) of the paralectotype.

Venational details for lectotype male: number of marginal cells behind fore wing paranal cells: 2/3; anx: fore wing 13/13, hind wing 9/8; pnx: fore wing 10/10, hind wing 10/10; cs under pt: fore wing 6/6, hind wing 6/6; anal triangular cells: 4/5. Hind wing 31 mm. Abdomen 36 mm.

Venational details for paralectotype female: number of marginal cells behind fore wing paranal cells: 1/1; anx: fore wing 11/11, hind wing 9/9; pnx: fore wing 9/9; hind wing 9/9; cs under pt: fore wing 5/4, hind wing 4/5. Hind wing 29 mm. Abdomen 33 mm.

Variation. – Two teneral males of *E. crotalinus* reared in Arizona are superficially similar to *E. heterodon* in the blunt shape of the cercus, the vestige of an isolated antehumeral stripe in one specimen, and the fuscous condition of the extensor surfaces of the metafemora. However, the penis structure of both specimens is unmistakably that of *E. crotalinus.* Because the two Arizona specimens are teneral, I cannot determine if dark thoracic stripes similar to those of *E. heterodon* would have developed, or whether the maculation would have been the same as observed when mature.

The male described by Hagen *in* Selys (1858) has the darkest and most distinct antehumeral stripes that I have seen for any specimen of this species. The tibiae of a majority of specimens I examined are entirely dark brown with the lateral costae yellow; others, including the lectotype, have the entire ventral margin yellow.

Biology. – Specimens are apparently common at favored localities. Boris Kondratieff (*in litt.,* 1990) states that adults of this species were 'on every [exposed] rock [in Rio Macoba] – hundreds and hundreds of them.' During a two-day stay at Ajijic near Laguna Chapala, Oliver S. Flint, Jr., and M. A. Ortiz collected 28 males and 23 females. Calvert (1907) records the following concerning its habits: '[*Progomphus borealis*] and *Erpetogomphus* were found on sand- or mud-banks, hardly above water-level, along sides of an irrigating ditch into which the water from the baths of Santa Rosalia empties. On alighting on these banks, *P. obscurus borealis* held its abdomen slanting upward to form an angle of 45°-60° with the bank, while *E. crotalinus* held it nearly horizontal.' The male collected at Lago de Patacuaro in Michoacan is noted as taken on 'stream flowing into lake', the two males and one female from the pyramids at S. Juan Teotihuacan as 'on high grassy plains far from water'. González and Novelo (1991) record the following about *E. crotalinus* (in translation): 'This is the most abundant gomphid in the area [the Biosphere Reserve of La Michiliá, Durango]. Like other members of the family, the adults of *E. crotalinus* have a seasonal flight pattern that, although it has not been exactly established, apparently is restricted to the months of May to October. The individuals of this species are characteristic inhabitants of both seasonal and permanent streams, easily recognized in the field by the bright green colour of the thorax. Males have the habit of resting on emergent rocks, a position they defend aggressively from other conspecific males.'

Erpetogomphus crotalinus has been collected with *E. designatus, E. lampropeltis,* and *E. heterodon.* Collection dates range from May through October (Calvert 1905).

Distribution (fig. 205). – *Erpetogomphus crotalinus* is restricted to the higher xeric areas of central and western Mexico. The species was reared from larvae collected by Minter Westfall, Jr., from the Slaughter Ranch, 15 mi W of Douglas, Cochise Co., Arizona; but no other collectors have encountered it there. I have also seen a pair from New Mexico (Eddy Co., Sitting Bull Falls), which may be strays from Mexico; its occurrence in the southwestern United States appears sporadic, and other odonatists have failed to find the species during their work in Arizona and New Mexico. Altitudinal data show a range of 1225 m (Mexico: Chihuahua: Santa Rosalia Springs) to 2290 m (Mexico: Mexico: Pyramids, S. Juan Teotihuacan). In the Paris Museum is a male labelled, 'Veracruz', which is probably in error.

Material

Type data. – Lectotype male by present designation with following data: white handwritten label by Hagen, '*G. lineatus* / Mexico'; white handwritten label, '*crotalinus*' in an unknown hand; white, black-bordered printed label: 'Mus. Berol.'; two small printed labels, 'Hagen'; red label with 'Type [printed]/12334' (written by N. Banks); rectangular label [all printed unless otherwise stated]: 'ERPETOGOMPHUS / CROTALINUS HAGEN [stamped]/ P. P. Calvert, det. 1905 [written]/ B. C. A. Neur. p. 165 [written]'. In MCZC. The penis and hamules are missing and probably served as the basis for the free-hand illustrations of these structures for Hagen *in* Selys (1858). Paralectotype female with following data: green printed label: 'Mexico/ Deppe.'; red printed label 'Typus'; yellow printed label, 'Zool. Mus./ Berlin', on reverse side written in ink, 'cat nr./ 2314; white label: 'syntypus ♀ von: / *Ophiogomphus* / *crotalinus* Hagen' [written in an unknown hand]; yellow label (handwritten except as noted), 'PARALECTOTYPE [printed] ♀/ *Ophiogomphus* / *crotalinus* Hagen/ des.

[printed] R. W. Garrison 1984'. In ZMHB.

There is a male in the ZMHB with the same data as the paralectotype female, except as follows: green label, 'Mexico Deppe'; green label, '*crotalinus* / Hag.' [both handwritten by Selys]; printed label, '2314'; and 'Syntypus ♂ von / *Ophiogomphus* / *crotalinus* Hagen'. Although the specimen is labelled as a type, I believe it is not a syntype and, in fact, that it represents the second male described by Hagen *in* Selys, 1858. I decided that the male in the MCZC and the female in the ZMHB represent the original syntypes for the following reasons: The original (1854) description of *Ophiogomphus crotalinus* is brief and was based on a male and female. Hagen gave measurements for both sexes (abdomen: male 36 mm, female 33 mm; hind wing male 31 mm, female 29 mm). These measurements and the description of the male ('Front of thorax yellow, with indication of two median stripes and a pale red humeral stripe...') correspond to the MCZC male and the ZMHB female. Hagen *in* Selys (1858) described this species in greater detail and had access to a second, smaller male (abdomen 33 mm, hind wing 29 mm). He stated, 'In the other specimen [*i.e.*, the second male], the stripes are brown and straight, quite visible...' The original male is again characterized as follows, 'Thorax yellow green without spots and...one can scarcely see the appearance of two median stripes and a thick antehumeral stripe...', which tallies with the earlier description of 1854. The male from the ZMHB corresponds with the smaller of the two measurements given by Hagen in 1858; and it also has a pair of easily visible antehumeral stripes, an apparently rare feature for this species. The ZMHB male is unique in this respect. Even though the original description by Hagen gives 'Musée de Berlin' as the repository of the types, I strongly suspect that Hagen took the male with him when he was invited to join the faculty at the Museum of Comparative Zoology in 1867.

Other material (97♂, 44♀, including lectotype ♂ and paralectotype ♀). – U. S. A.: ARIZONA: *Cochise Co.*, San Bernardino Ranch, 15 mi E of Douglas (FSCA); NEW MEXICO: *Eddy Co.*, Sitting Bull Falls, Guadalupe Mtns., (RWG, WM); MEXICO: Chihuahua: Chihuahua Creek, 4 mi SW of Col. Juarez, (CSUC); Rio Pacheco, (CSUC); Santa Rosalia Springs, 1219 m, (ANSP); Durango: Durango City, (ANSP); Rio Dalita and marshes, 6 mi E of Durango, 1890 m, (DRP); Jalisco: Jopopau, 1667 m, (ANSP); Guadalajara, (ANSP, MCZC); Laguna de Chapala (nr. Mex. Hwy 15), 75 mi SE of Guadalajara, (RWG); Ajijic nr. Laguna Chapala (USNM, CC, TWD); Ajijic, (FSCA); Rio La Sanguijuela, Degollado, (UNAM, RWG); route 15, km 206, San Lorenzo, 9 mi W Tuxpan, (USNM, CC); Jalisco [no other locality], (BMNH); Michoacan: Arrollo W of La Piedad, (UNAM); Lago de Patzcuaro, 2.6 mi W of Quiroga, 2042 m, (FSCA); Route 15, km 206, San Lorenzo, 8 mi W of Tuxpan, (USNM); Route 15, km 431, Carapan, (USNM); Route 15, km 291, near Morelia, Parque Nacional Insurgente Morelos, (USNM); stream 0.5 mi S of Tuxpan, 1798 m, (DRP); Hidalgo: ditches around Tasquillo, 1700 m, (DRP); Rio Tula at Puente Tasquillo, (USNM); Tecozautla, Rio San Juan, 1710 m, (RWG); Tecozautla, Rio Tecozautla, 1750 m (RWG); Tecozautla, arroyo San José del Desierto, 1730 m (RWG); Mexico: Route 15, km 125, El Salitre, (USNM); Pyramids, S. Juan Teotihuacan, 2290 m, (FSCA, CUIC); Morelos: Cuernavaca (BMNH, ANSP, CUIC); Puebla: ditch just NW of Tehuacan, 1700 m, (DRP, TWD); Veracruz: Veracruz [probably erroneous locality], (MNHP); MEXICO [no other locality], (ZMHB).

Erpetogomphus heterodon sp. n.
(figs. 28-thx, 42, 43-abd, 65-hamules, 87-penis, 110, 111-app, 162-vertex, 170-leg, 193-vl, 206-distr, 230-wings)

Type data. – Holotype male. U. S. A.: New Mexico: Catron Co., Tularosa River just E of Aragon on N. Mex. Hwy 12, 28 July 1984 (R. W. and J. A. Garrison). Allotype female. Same data as male. Both in USNM.

Paratypes (36♂, 2♀). – NEW MEXICO: *Catron Co.*, same data as holotype and allotype, 27-28 July 1984, 22♂, 1♀ (RWG); same data, 23 August 1964 (Clifford Johnson), 3♂, 1♀ (DRP, FSCA); Gila Cliff Dwellings, 30 July 1983 (John E. Hafernik, Jr.), 4♂ (RWG); *Grant Co.*, Grapevine Campground, East Fork of Gila River at N. Mex. Hwy 15, 5600 ft., 27 July 1984 (R. W. and J. A. Garrison), 11♂ (RWG); TEXAS: *Jeff Davis Co.*, Limpia Canyon in Davis Mtns. State Park, 23 June 1958 (M. J. Westfall, Jr.), 1♂ (FSCA); Limpia Creek at Tex. Hwy 17, 3.4 mi NE of Ft. Davis, 4500 ft., 24 August 1977 (Dennis Paulson, Susan Hills), 1♂ (DRP); *Reeves Co.*, Balmorhea State Park, 13 Sept. 1983 (S. W. Dunkle), 1♂ (SWD); MEXICO: Chihuahua: 6 mi NNE of Boquilla, 16 July 1960 (Scheibner), 1♂ (RWG); Chihuahua Creek, 4 mi S of Col. Juárez, 25 Aug. 1986 (B. C. Kondratieff), 1♂ (CSUC); 'Bosuchel [probably Basuchi]', 18 Aug. 1950 (R. F. Smith), 2♂ (AMNH, RWG).

Description

Holotype male. – Entire face pale light green, slightly darker on postclypeus and anterior of frons; labrum, base of mandibles, labium ivory; vertex and antennae black; base of antefrons with transverse furrow, tumid medially, laterally with a pair of pits; postocellar tubercles small, no postocellar ridge; occiput pale green, slightly tumid medially, hind margin fringed with long hairs, crest with black along lateral margin, slightly emarginate medially; postocciput green, transverse; rear of head dark brown, becoming pale green laterally.

Prothorax light green with dark brown on middle lobe extending laterally to pleura, two adjacent laterodorsal small green spots on medial lobe. Synthorax (fig. 23) light green with following dark brown: inverted wedge-shaped middorsal stripe, its ventral end not touching collar, its dorsal end forming a narrow stripe below antealar carina and meeting narrow humeral stripe; small isolated antehumeral stripe; vestigial second lateral stripe extending from metacoxa to metaspiracle; upper end of third lateral stripe. Coxae, trochanters ivory, femora ivory with black external surfaces spreading to lateral areas at distal 0.25 (fig. 170), tibiae black with small lateral ivory stripes along basal 0.5; tarsi and armature black.

Wings (fig. 230, paratype) hyaline, venation dark brown, basal wing venation brown; anterior margin of costa yellow; pterostigma brown, darker around margin.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 2; anx: fore wing 14/12, hind wing 9/9; pnx: fore wing 9/8, hind wing 10/10; cs under pterostigma: fore wing 4/6, hind wing 6/4; anal triangular cells: 4. Hind wing 33 mm.

Abdomen (fig. 42). Segment 1 pale orange-yellow dorsally with narrow black lateral stripe, white laterally; segment 2 similar to segment 1 but with black along anterior margin of segment laterally; segment 3 similar to segment 2 but with black along transverse carina and posterior annulus; segments 4-7 similar to segment 3 but black dorsolateral stripe incomplete anteriorly so that dorsal orange-yellow merges with lateral white and with black along transverse carina, expanding ventrally, and with a similar mark posteriorly just before black annulus; segments 8-9 predominantly yellow-orange with black denticles dorsally, incomplete black dorsolateral stripe extending from anterior margin of segment but ending just before posterior margin; segment 10 yellow-orange posteriorly, orange-brown anteriorly. Abdomen 40 mm.

Cercus (fig. 110) yellow brown, strongly angulate near middle, ventral margin with inferior carina at basal 0.30. Epiprocts curved at distal 0.75, tips darkened, bluntly pointed, slightly divergent.

Accessory genitalia (fig. 65, paratype). Anterior hamule black, divided at upper 0.30, lower branch forming a small, truncate appendage; posterior hamule white, triangular, with anterior basal shoulder, tip with small, anteriorly recurved tooth; penis with small serrated lateral lobes, cornuae (fig. 87, paratype) moderately long, widely separated tips broadly rounded.

Allotype female. – Overall colouration similar to male but with more extensive pale areas on abdomen and legs; furrow anterior to medial ocellus as in male; vertex (fig. 162) with postocellar tubercles not connected but with small remnant of ridge extending medially; occiput simple, posterior margin raised with row of hairs; postocciput green, transverse.

Venational details. Fifth antenodal thickened in all wings; number of marginal cells behind fore wing paranal cells: 3/2; anx: fore wing 13/12, hind wing 10/10; pnx: fore wing 7/8, hind wing 9/10; cs under pterostigma: fore wing 6/6, hind wing 6/6. Hind wing 36 mm.

Abdomen (fig. 43) as in male, but with black dorsolateral stripe reduced, with black extending anteriorly before transverse carina. Abdomen 37 mm.

Vulvar lamina (fig. 193) with broadly planar rectangular flaps meeting at anterior margin; juncture of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Diagnosis

This species is related to *E. crotalinus* and *E. sipedon*. *Erpetogomphus crotalinus* lacks the dark thoracic stripes present in *E. heterodon* (fig. 22); the extensor surfaces of the tibiae of *E. heterodon* are black (fig. 170) (yellow in *E. crotalinus*); and the cornuae of the penis in *E. heterodon* are broadly rounded (fig. 87) (long and acutely pointed in *E. crotalinus* [fig. 86]).

Males of *E. heterodon* are most similar to *E. sipedon*, but they differ in thoracic maculation shape of the epiprocts, and structure of the penis. In *E. sipedon*, the antehumeral stripe is long and joined with the humeral stripe (fig. 19); in *E. heterodon*, this stripe is vestigial and disjunct. In *E. sipedon*, the tips of the superior appendages are slender and acuminate (figs. 105-106), not obtusely acuminate as in *E. heterodon* (figs. 110-111). The cornua of the penis in *E. sipedon* (fig. 83) possess a mesal lobe absent in *E. heterodon* (fig. 87).

Structurally, the females of *E. crotalinus, E. heterodon*, and *E. sipedon* approach one another closely. The latter two species have a relatively narrow occiput with the width across the crest about 4 times as long as its greatest length. The occiput in *E. crotalinus* is wider, about 3 times the width. I have been unable to detect morphological differences between females of *E. heterodon* and *E. sipedon*. Body maculation must be used to separate females.

Remarks

Variation. – Slight variation occurs in males within the type series. The dark dorsolateral stripe on abdominal segment 3 may be broken in the middle. In the male from Mexico (6 mi NNE Boquilla), this stripe is reduced to an isolated spot on the basal 0.30 of the segment. Similarly, the extent of black markings on abdominal segments 8-10 may be reduced.

Venational statistics for type series. Males: Number of marginal cells behind fore wing paranal cells: 0-3; anx: fore wing 11-14/11-15, hind wing 8-11/8-11; pnx: fore wing 7-11/7-11, hind wing 8-12/8-11; cs under pterostigma: fore wing 4-7/4-6, hind wing 4-7/4-7; anal triangular cells: 3-4. Hind wing 32-34 mm. Abdomen 36-40 mm.

Females: Number of marginal cells behind fore wing paranal cells: 1-4; anx: fore wing 13/12-13, hind wing 8-10/9-10; pnx: fore wing 7-9/8-9, hind wing 8-10/8-10; cs under pterostigma: fore wing 5-6/5-6, hind wing 5-6/5-6. Hind wing 34-36 mm. Abdomen 36-37 mm.

Biology. – Adult males were taken along sandy margins of the Tularosa River in New Mexico. They often sat on the bank facing the river and were easy to approach. I collected one female as it hovered over the river ovipositing. Another teneral female was flushed from nearby vegetation. At the East Fork of the Gila River, males sat on emergent rocks in the stream or by the river's edge. They occasionally made swift sorties, usually to chase another male. At this locale, *E. heterodon* was sympatric with *E. lampropeltis natrix.* Altitudinal data show *E. heterodon* to occupy high, mostly xeric areas of the southwestern United States and northern Mexico. Collection dates are from 23 June to 13 September at elevations of 1370 m (Limpia Creek, Texas) to 1700 m (Grapevine Campground, New Mexico).

Distribution (fig. 206). – *Erpetogomphus heterodon* is known only from western Texas, New Mexico, and northern Mexico. It has been collected with *E. crotalinus* in at least one locality in Mexico (Chihuahua state, Rio Pacheco, 27 Aug. 1986, B. Kondratieff, S. Dunkle, pers. comm.), and is apparently allopatric with *E. sipedon.*

Erpetogomphus compositus **Hagen *in* Selys**

(figs. 24, 25-thx, 66, 67-hamules, 88, 89-penis, 112, 113-app, 145-ept, 139-base of postfrons, 163-vertex, 194-vl, 206-distr)

Erpetogomphus compositus Hagen *in* Selys, 1858: 660 (400 sep.) (♀, 'Rivière Peros [*sic*: Pecos] (*Texas occidental*)'). – Hagen *in* Selys 1859: 536 (10 sep.) (descr. ♀); Hagen *in* Selys 1873a: 740 (12 sep.) (descr. ♂, ♀, 'Le nord de la Californie"); Selys 1873b: 519 (75 sep.) (list); Calvert 1905: 166 (Ariz.); Calvert 1908a: 45 (Ariz.); Muttkowski 1910: 86 (cat.); Calvert 1912a: 289 (mentioned); Williamson 1914a: 226 (Ariz.); Kennedy 1917a: 544 (Calif.); Seemann 1927: 22 (Calif.); Byers 1928: 51 (larva unknown); Needham and Heywood 1929: 80 (descr.); Williamson and Williamson 1930: 12 (summary of status); Tinkham 1934: 215 (W. Tex.); Ahrens 1938: 11 (Ariz., Utah); Fraser 1940: pl. 5 (penis); Ferguson 1940: 5 (Tex.); Needham and Westfall 1955: 144 (descr.); Pritchard and Smith 1956: 116 (key); Gloyd 1958: 8 (W. Tex.); Musser 1961: 54 (larva, Utah); Musser 1962: 14 (larva, Utah); Borror 1963: 104 (common name); Cruden 1964: 81 (Calif.); Montgomery 1968: 133 (distr.); Paulson and Garrison 1977: 151 (Washington); Molnar and Lavigne 1979: 130 (Wyo.); Paulson 1982: 255 (distr.); Paulson 1983: 67 (Wash.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat., attributes authorship to Selys); Bick 1990: 3 (Idaho); Bridges 1991: VII: 49 (cat.); Tsuda 1991: 5 (cat.).

Gomphus compositus. – Hagen 1861: 99 (desc. ♀, Tex.).

Gomphus (Herpetogomphus)? viperinus. – Hagen, 1873 (misidentification, Yellowstone).

Herpetogomphus compositus. – Hagen 1874: 597 (Yellowstone, Tex.); Hagen 1875a: 42 (Tex.); Hagen 1875b: 918 (N. Mex.); Selys 1879: 64 (2 sep.) (characters of genus); Kirby 1890: 60 (cat., attributes authorship to Selys); Calvert 1899: 386 (characters of genus); Currie 1903: 303 (Ariz.); Osburn 1905: 186 (mentioned); Byers 1928: 5 (larva unknown); La Rivers 1938: 85 (Nev.); La Rivers 1940a: 112 (Nev.); La Rivers 1941: 177 (Nev.).

Erpetogomphus coluber Williamson and Williamson, 1930: 17 (♂, San José de Comandu, Baja Calif. Sur). – Needham and Westfall 1955: 143 (desc.); Borror 1963: 104 (common name); Montgomery 1968: 133 (distr.); Montgomery 1973: 239 (comment on name); Paulson 1982: 255 (distr.), 266 (synonymy with *E. compositus*); Bridges 1991: VII: 49 (cat.).

Description

Male. – Entire face pale grey green with dark markings as follows: along basal margin of labium and median extension ending before distal margin (almost absent in some specimens), frontoclypeal suture, base of antefrons; vertex all dark brown or with pale median area extending posteriorly from median ocellus to anterior margin of occiput; antennae dark brown; anterior margin of vertex forming a trough at junction of postfrons, this trough with a pair of deeper pits anterolateral to median ocellus (fig. 139); occiput white green, wide, planar with slight tumid median area, crest barely convex, slightly to broadly emarginate medially, its hind margin covered with pale brown hairs; postocciput white green, transverse, not visible dorsally, rear of head dark brown.

Prothorax pale green with brown dorsolaterally on middle lobe; synthorax (fig. 24) predominantly pale green with following dark brown: well defined middorsal stripe widening to collar, its upper end extending along antealar sinus connecting with well defined humeral stripe; antehumeral stripe widened dorsally and connected basally at mesinfraepisternum; lower part of humeral stripe extending posteroventrally but not connecting with well defined sinuate second lateral stripe; lower 0.50 of this stripe encompassing metaspiracle, constricted along posterior margin at 0.50 and abruptly widening dorsally before turning anterodorsally toward subalar carina; complete third lateral stripe ending behind posterior margin of metacoxa. Pale colour of thorax light green with lighter tone almost becoming white in areas between antehumeral and humeral stripes, and between second and third lateral stripes. Coxae, trochanters white grey with slight wash of brown, tibiae pale grey green with defined superior surfaces black, basal 0.40 of metafemora with streaks of grey green or with basal 0.60 of this area largely pale, tibiae black with narrow stripe of pale grey green along basal 0.30 of lateral margin in some specimens; tarsi and armature black.

Wings hyaline with slight wash of yellow at extreme base (more so on teneral specimens), basal wing venation brown, especially anteriorly, anterior margin of costa yellow white except for anterior margin of pterostigma, costa beyond pterostigma white or darkened, but contrasting with black of pterostigma; pterostigma black.

Venational statistics. Fifth antenodal thickened in all wings; marginal cells behind fore wing paranal cells: 0-4; ; anx: fore wing 10-15/10-15, hind wing 7-11/7-11; pnx: fore wing 6-11/6-10, hind wing 7-11/7-11; cs under pterostigma: fore wing 3-6/3-6, hind wing 3-6/3-6; anal triangular cells: 2-5. Hind wing 25-32 mm.

Abdomen. Segment 1 pale grey green with broad basal semicircle of brown laterally, its posterior end touching lateral articulated area; segment 2 white with dorsolateral brown stripe sending a ventral stem posterior to auricle, and connecting with black annulus, a small brown spot at anteroventral margin of segment; segment 3 with isolated black dorsolateral spot surrounding lateral carina, distal 0.25 of segment with dorsolateral black increasing in width posteriorly and touching dorsally near black annulus; segment 4 similar to segment 3, but isolated black of transverse carina longer and touching or connecting with distal black, thus forming an incomplete midlateral stripe occupying distal 0.75 of segment and isolating ventral longitudinal wedge of white; segments 5 and 6 like segment 4, but with middorsal white becoming fuscous; segment 7 with anterior 0.5 white, except for tawny transverse carina, becoming entirely tawny posteriorly, some specimens with varying degrees of lateral black on posterior 0.25 of segment or in specimens from Baja California (*E. coluber*) with tawny areas becoming black; segments 8-10 yellow brown with darker red brown dorsally, in Baja California specimens this dark red brown replaced with well defined black on segments 8 and 9, and dark brown on segment 10. Abdomen 32-39 mm.

Cercus (figs. 112-113) ocher, in lateral view slightly concave dorsally near base and with tips slightly recumbent, cercus enlarged ventrally at basal 0.45 with inferior carina along this same area, remainder slightly concave with tip forming a blunt point. Epiprocts yellow brown, gently curved dorsally at 90°, tips (fig. 134) dorsoventrally flattened and truncate or obliquely truncate.

Accessory genitalia (figs. 66-67). Anterior hamule dark brown, divided at basal 0.5; lower branch forming a small, posteriorly directed truncate appendage; posterior hamule grey white, triangular; with anterior basal shoulder, tip bluntly rounded and armed with a small anteriorly directed tooth on posterior border; penis with lateral lobe small, roughly semicircular, serrate; cornuae (figs. 88-89) moderately long, widely separated, tips broadly rounded.

Female. – Head as in male but pale areas more extensive, especially on vertex, where dark brown may be reduced to areas around ocelli and postocellar protuberances; occiput narrower than in male, with erect curvilinear occipital crest separating easily visible postocciput (fig. 163), posterior margin of postocciput slightly concave; prothorax and thorax as in male, but with pale areas more extensive; wings with yellow at base more extensive, often with markings within second series of antenodals to level of arculus and cubitoanal area in both wings.

Abdomen in well preserved specimens with pale colours primarily white with pale orange dorsally, black dorsolateral stripes reduced and separated in their middle on segments 3-6; segment 7 similar to male but with posterior 0.25-0.30 darker laterodorsally; segments 8-10 tawny, with varying amounts of dark brown, especially dorsally, on segments 8-9; cerci ocher. Abdomen 31-37 mm.

Vulvar lamina (fig. 194) with prominent basal plates, quadrangular laminar plates acuminate posteriorly, meeting at anteromedial margin; cleft between plates forming a 90° angle; stem of Y-shaped postlamellar ridge at level of posterior margin of lamina.

Venational statistics: number of marginal cells behind fore wing paranal cells: 1-6/0-5; anx: fore wing 12-15/12-14, hind wing 8-11/9-11; pnx: fore wing 7-11/8-10, hind wing 9-11/8-11; cs under pterostigma: fore wing 3-5/4-6, hind wing. Hind wing 30-32 mm.

Diagnosis

This common, distinctive species is easily separated from its nearest ally, *E. lampropeltis*, by several structural and maculation characters. Males of *E. compositus* differ from *E. lampropeltis* in lacking the characteristic middorsal angulation of the cercus. The tip of the epiproct in *E. compositus* is truncate (fig. 134), but this structure in *E. lampropeltis* is obliquely and bluntly pointed (fig. 132). Depressions in male and female anterolateral to median ocellus will also separate the species: in *E. compositus*, an arcuate trough has more pronounced pits anterolateral to the median ocellus (fig. 139). In *E. lampropeltis*, the anterolateral pits are deeper and the intervening area directly anterior to the median ocellus is not as depressed (fig. 138). This structure in *E. lampropeltis* more closely approaches the condition found in *E. viperinus* (fig. 137).

Erpetogomphus compositus, though a boldly marked species, is lighter than *E. lampropeltis*. The occipital crest in *E. compositus* is largely pale, though there may be some darkening along the lateral 0.30 of margins in specimens from Baja California. In *E. lampropeltis*, the occipital crest is entirely dark brown and provides a striking contrast to the pale occiput. The thoracic patterns of the two species are different (figs. 20-21, 24-25), and the dorsolateral black stripes of abdominal segments 4-6 of *E. lampropeltis* are more extensive.

In the field, pale thoracic colouration will easily separate both species. *Erpetogomphus compositus* is unique in having a pale green thorax with intervening grey white areas between the antehumeral and humeral stripes and second and third lateral stripes. In *E. lampropeltis*, the thoracic colouration is grey green (*E. lampropeltis lampropeltis*) or dark green (*E. lampropeltis natrix*).

Females of *E. compositus* differ from *E. lampropeltis* in the shape of the occiput. In *E. compositus*, the occiput is narrow and the postocciput is clearly visible in dorsal view (fig. 163). In *E. lampropeltis*, the occiput is broad and the postocciput is not visible dorsally (fig. 160). Secondly, the area in front of the median ocellus mirrors the condition stated for males above. The vulvar laminae of the two species appear indistinguishable.

Remarks

Williamson and Williamson (1930) described in detail *Erpetogomphus coluber*, comprising 31 males from San José de Comandu, Baja California. In comparing *E. coluber* with other species, they stated that *E. coluber* would, in Calvert's (1905) key to the genus '...run to AA, page 160, and if the individual be one with the facial dark markings reduced, it will run to *H. compositus*. Drs. Calvert and Kennedy regard *coluber* as distinct from any described species.' The Williamsons sent two males to Calvert, who commented, 'No special reason for thinking it *diadophis* [= *E. eutainia*]; like a small *compositus*; differs in size; has broader metepisternal dark stripe; brown on [abdominal segments] 3-7 more extended; brown on 8-10 much darker; darker lines or stripes on the frontoclypeal and clypeo-labral sutures'. Finally, the Williamsons commented on the affinities of *E. coluber* to *E. compositus* as follows: '*Compositus* is certainly its closest relative and the derivation of *coluber* from *compositus*, through geographical isolation in Baja California, is almost certain and is a case exactly parallel, so far as speciation goes, to that of certain species, of several genera, endemic in Florida. *Coluber* is separated from *compositus* by its darker color, especially of the last four abdominal segments and by venational characters, especially the two-celled anal triangle and the single row of cells posterior to A in the front wing.'

I have seen the holotype and 15 paratypes of *E. coluber* and believe, as did Paulson (1982), that they represent diminutive, melanic examples of *E. compositus*. The specific differences ascribed to *E. coluber* are those of venation only, and I believe these to be correlated to their smaller size. I have found no differences in body morphology, including the accessory genitalia.

Variation. – Two specimens from San Diego County appear intermediate to *E. coluber* and *E. compositus* s.s. These males have more pronounced dark thoracic stripes, but the dorsum of abdominal segments 8-10 lacks dark brown markings typical of *E. coluber*. However, other *E. compositus* have varying amounts of dark brown on these segments. The hind wing anal triangle in 3 of 16 specimens of *E. coluber* has 3 anal triangular cells instead of 2, and a 2-celled anal triangle, though rare, does exist in *E. compositus* (s.s.). For example, of 21 males I measured from California, Arizona, and another from northern Baja California, one of the San Diego males and another from Riverside, California, had one wing each with two cells. These two specimens had shorter hind wings (26 mm and 28 mm, respectively) than is typical for *E. compositus* (s.s.). Statistics for the number of anal triangular cells show it to be variable within *E. compositus* (s.s.). The number of wings with range of stated conditions is (number of wings follows in parentheses): 3 (19), 4 (19), 5 (2). Hind wing lengths from the San Diego males are 25-26 mm, well within the range for *E. coluber*. The next smallest specimen is a male from Riverside (28 mm), the same male with two anal triangular cells in one hind wing.

Most wings of *E. coluber* which I have examined have no marginal cells behind the fore wing paranal cells, but 6 of 32 (19%) did. Eight of 42 (19%) wings of *E. compositus* (s.s.) had no marginal cells.

Williamson and Williamson (1930) warned of fallibility of some of their characters among the paratypes they examined: 'The face markings are very pronounced in some and scarcely discernible in others; there is considerable variation in the extent of the dark thoracic markings [fig. 25] and this variation occurs independently on the mesepisternum and metepisternum, so an individual may have the dark humeral and antehumeral relatively extensive and the two dark lateral stripes relatively reduced and *vice versa*.'

With the exception of specimens from Baja California and the two specimens from San Diego, body colouration appears remarkably constant throughout its range. The male from Baja California Norte (Guadalupe Hot Springs) is more like typical *E. compositus*, but it has no marginal cells behind the fore wing paranal cells. The hind wing length (29 mm) and other venational characters indicate a closer relationship to more northerly populations.

The female holotype was collected with the type series of *E. designatus* and was probably collected in the vicinity of Roswell, New Mexico in 1854-1855. See remarks under *E. designatus* for further details.

Venational details. Holotype female of *E. compositus*: number of marginal cells behind fore wing paranal cells: 2/4; anx: fore wing 13/13, hind wing 9/10; pnx: fore wing 8/9, hind wing 9/8; cs under pterostigma: fore wing 5/6, hind wing 5/6. Holotype male of *E. coluber*: number of marginal cells behind fore wing paranal cells: 0/0; anx: fore wing 12/12, hind wing 9/9; pnx: fore wing 7/7, hind wing 9/9; cs under pterostigma: fore wing 2/2, hind wing 4/4.

Biology. – This species and *Progomphus borealis* McLachlan *in* Selys are the two most conspicuous gomphid elements along most desert streams and irrigation ditches in the southwestern United States. In Arizona, this species occurs commonly in the Lower Sonoran Zone, and in ecotonal fingers into the Upper Sonoran Zone. Kennedy (1917a), who collected *E. compositus* at certain sites in the northern Central Valley of California, writes: 'One female, a teneral, was taken on the irrigating ditch across the river from Oroville.' Collecting along the lower Truckee River south of Pyramid Lake, Nevada, Kennedy (1917a) mentions that 'This widely spread species occurred sparingly on the riffles of the lower Truckee. The males appeared to be more nervous and more touchy, flying farther for conflict with passing males than the males of *Ophiogomphus morrisoni nevadensis*.'

The two males collected at the Boyce Thompson Southwestern Arboretum in Pinal County, Arizona, had the following annotation by H. K. Gloyd: '[in] Creek, arboretum. Canyon, after rain and run-off almost over. between 5 & 7: 00 p.m., water low, few dragonflies seen'. Williamson and Williamson (1930) provided a lengthy account of the type locality and assemblage of Odonata present with *Erpetogomphus coluber*. In August, 1972, I collected several *E. compositus* with *Stylurus plagiatus* (Selys) at Riverside Park, Yuma, Arizona. Adults were taken in the late afternoon on grassy areas shaded by trees. Adults of this species and *Progomphus borealis* were abundant along Big Chico Creek in Chico, Butte County, California in June and July of 1974, 1976, and 1978. They sat on exposed sand bars near the edge of the creek, and both were difficult to approach. *Progomphus borealis* was the more wary. In the late afternoon, I have collected *E. compositus* away from water, resting on dry desert scrub. Collection dates range from 24 May (Nevada: Clark Co.) to 13 Dec. (Calif.: San Bernardino Co.).

Distribution (fig. 206). – *Erpetogomphus compositus* is a desert species found commonly in the southwestern United States. It has been taken as far east as Dallas (Hagen, 1875a), but most records from Texas are from the western portion of the state. It occurs in eastern New Mexico and is common in low desert regions of Arizona, especially southwest of the Mogollon Rim. It is common in the arid regions of southern California and penetrates north through the Central Valley to Chico. Paulson and Garrison (1977) list it from south central Washington. The species was listed from Oregon by Hagen (1875a, 1875b) with no specific locality); but specimens were recently collected from the John Day River, Deschutes Co., Oregon (Valley 1993). *Erpetogomphus compositus* occupies river systems in the Great Basin of Nevada, but its most easterly distribution is unknown. Bick (1990) lists a specimen from Owyhee Co., Idaho. Hagen (1874) records it from the Yellowstone, but it was probably taken in a more arid environment around what is present-day Yellowstone National Park. Molnar and Lavigne (1979) also cite it without specific locality from Wyoming, based on previous records given by Needham and Heywood (1929), Needham and Westfall (1955), and Pritchard and Smith (1956). All of these records probably originated from the original Hagen (1874) citation. In Utah, the species apparently penetrates only the southwesternmost part of the state. The most southerly distribution for *E. compositus* is also unknown. Except for *E. coluber*, the only records I have observed from mainland Mexico are two males collected by J. H. Williamson in Hermosillo, Sonora. The distribution of *E. compositus* in Texas, New Mexico, and Arizona indicates that it must be further widespread in northern Mexico.

Material

Type data. – Of *E. compositus*: Holotype female with following label data: 'Aug/ 16' [handwritten], 'Hagen' printed [two of these labels attached], '*compositus*' written in an unknown hand; red label 'HOLOTYPE [printed] / *Erpetogomphus compositus* / Hagen 1857 [*sic*, should be 1858] '♀' handwritten by RWG. In MCZC. Of *E. coluber*: Holotype male dry in envelope with following data: '*E. coluber*' written in pencil by E. B. Williamson, 'Mexico/ State of Baja California/ San Jose de Comandu/ J. H. Williamson/ Oct 10 1923' [all stamped]/ ♂214.' handwritten by EBW, 'Type' handwritten in pencil by EBW on side of label. In UMMZ.

Type locality of *E. compositus* herein restricted to vicinity of Roswell, Chaves Co., New Mexico (see remarks under *E. designatus*).

Other material (151♂, 46♀, including holotype ♀ *E. compositus* and holotype ♂ *E. coluber*). – U. S. A.: ARIZONA: *Cochise Co.*, Miller Cyn., Huachuca Mtns., (CC); pond at Slaughter Ranch, San Bernardino Valley, 15 mi E of Douglas, 1169 m, (RWG); 5 mi E of Hereford (CC); San Pedro River, 9 mi SW of Tombstone, (BYUC); San Pedro River, at Hereford Rd., (RWG); *Coconino Co.*, Havasu Canyon, 3 mi N of Supai, 923m, (RWG); Supai, (CDFA); *Graham Co.*, 3 mi SE of Bylas, valley of the Gila, 2000 ft., (UMMZ); Roper Lake, 5 mi S of Safford (RWG); *Maricopa*

Co., Granite Reef Dam, (UMMZ); Mesa, (UMMZ); Phoenix, (RWG); slough ponds by Verde River, by Ariz. Hwy 87, Ft. McDowell Indian Reservation (RWG); Tempe (UMMZ); *Mohave Co.,* spring, Hwy 15 bridge, Littlefield, (BYUC, RWG); Virgin River, Big Bend, (BYUC); *Pima Co.,* Organ Pipe Cactus Nat'l. Mon., Quitobaquito, (Long Beach State Univ.); Quitobaquito Springs, 15 mi S of Lukeville, Organ Pipe Cactus Nat'l. Mon., (RWG); *Pinal Co.,* Boyce Thompson Southwestern Arboretum, 4 1/2 mi SW of Superior, (UMMZ); 8 mi NW of Florence, (UMMZ); *Santa Cruz Co.,* Santa Cruz River, Sonoita Creek Ranch (on way to Salero Cyn.), *ca.* 2 mi W of Patagonia, by Ariz. Hwy 82, (RWG); *Yavapai Co.,* Oak Creek at Cornville, 1077 m, (CSUC); *Yuma Co.* Ave 3E at Co. 14 St., SE of Yuma, (RWG); Riverside Park, nr. Colorado River, Yuma, (RWG); N. R. Adair Park, McPhaul Bridge, by Gila River, *ca.* 15 mi ENE of Yuma, (RWG); California: *Butte Co.,* Bidwell City Park, by Big Chico Creek, Chico, 61 m, (RWG); Oroville, (UMMZ); *Fresno Co.,* Friant, San Joaquin River, (UMMZ); *Imperial Co.* Calexico, (BYUC); canal 8 mi E of Holtville, sea level, (DRP); ditch 4.7 mi E of Bond's Corner, (DRP); Hot Mineral, (LACM); irrigation canal 7.3 mi E of Holtville, (DRP); irrigation canal at Winterhaven, (DRP); *Inyo Co.,* Hunter Cyn., Salino Valley, (LACM); Laws, Owens River, (UMMZ); Lone Pine, Owens River, (UMMZ); *Los Angeles Co.,* Tanbark Flat, (CDFA); *Mono Co.,* 5 mi N of Benton Station, 5300 ft., (UMMZ, LACM); *Riverside Co.* Blythe, (CC); Coachella Valley Preserve, NE of Thousand Palms, (J. Cole); Palm Springs, (LACM); Whitewater River nr. Salton Sea, (DRP); *San Bernardino Co.,* Colorado River at Moabi Rd., S of Needles, (RWG); Lost Palm Cyn., Joshua Tree N. Mon., (Long Beach State Univ.); Parker Dam, (RWG); *San Diego Co.*: T14S, R5E, (CASC); San Felipe Creek, 13.8 mi E of Julian, 615 m, (DRP); San Felipe Creek at Scissors Crossing, 11.9 mi E of Julian, 738 m, (DRP, RWG); Sentenac Cyn., (LACM); Vallecito, (LACM); *Yolo Co.,* Cache Creek at William H. 'Bill' Davis Memorial Picnic Area, by Calif. Hwy 16, 6 mi N of Rumsey, 132 m, (RWG); Nevada: *Clark Co.,* Logandale, (BYUC); *Elko Co.,* Carlin, Humboldt River, (UMMZ); 8.5 mi NW of Currie, (UMMZ); *Humboldt Co.,* Can Spring, 3 mi S of Pahuhe Meadows, (UMMZ); *Lincoln Co.,* 6 mi S of Alamo, (UMMZ); *Nye Co.,* Amargosa R., 2 mi below Beatty, (UMMZ); *Pershing Co.,* Lovelock, Humboldt River, (UMMZ); *Washoe Co.,* Pyramid Lake, Truckee River, (UMMZ); *White Pine Co.,* 2 mi NW of Preston, (UMMZ); Texas: *Brewster Co.,* Big Bend Nat'l Park, 1 mi N of Rio Grande Village, (RWG); Boquillas Cyn., Big Bend Nat'l. Park, (CSUC); Rio Grande Village, Big Bend Nat'l. Park, (CSUC); *Maverick Co.,* Quemado, (LACM); Utah: *Washington Co.,* St. George, (CC); Beaver Dam Wash, Terry Ranch, (BYUC); Beaver Dam Wash, Lytle Ranch, (BYUC); Gunlock, W of Veyo, (BYUC); Virgin River, Virgin, (BYUC); Mexico: *Baja Calif. Norte*: Guadalupe Hot Spgs., Guadalupe Cyn., Sierra Juarez, (CSUC); *Baja Calif. Sur.* San José de Comandu, 10 Oct. 1923 (J. H. Williamson), 15♂ (all paratypes of *E. coluber*) (UMMZ, RWG, FSCA, USNM); *Sonora*: Hermosillo, (UMMZ).

Erpetogomphus boa Selys

(figs. 26-thx, 44, 45-abd, 68-hamules, 90-penis, 114, 115-app, 135-ept, 164-vertex, 167-postocciput, 195, 196-vl, 207-distr)

Erpetogomphus boa Selys, 1859: 37 (11, sep.) (descr. ♂ 'Vera Cruz, Mexique. Par M. Salle. (Collect. Selys.)'). – Walsh 1863: 253 (mentioned); Selys 1873b: 519 (75, sep.) (list); Calvert 1905: 165 (notes); Calvert 1907: 399 (possible identity with *E. elaps*); Muttkowski 1910: 86 (cat.); Ris 1917: 153 (notes and descr. of 2nd known ♂); Williamson and Williamson 1930: 11 (summary of status); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27 (cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.31 (cat.); Tsuda 1991: 95 (cat.).

Erpetogomphus crotalinus, nec Hagen *in* Selys, 1854. – Selys 1859: 537 (11, sep.) (♀ descr. 'Vera Cruz, Mexique. Par M. Salle. (Collect. Selys.)' = *E. crotalinus* Hagen *in* Selys, 1858.

Gomphus boa. – Hagen 1861: 100 (descr. from Selys).

Herpetogomphus boa. – Walsh 1862: 389 (mentioned); Hagen 1875a: 42 (cat.); Selys 1879: 64 (2, sep.); Calvert 1899: 386 (list, English translation of Selys, 1879); Calvert 1908b: 693 (mentioned).

Description

Male. – Labrum, clypeus, and frons light blue green, paler along sides of labrum and lateral lobes of postclypeus; base of mandibles pale green, tips black; base of antefrons anterior to median ocellus with narrow, arcuate, V-shaped sulcus, shallower medially; vertex dark brown with usual postocellar tubercles, occiput tumid medially, pale green brown, its posterior margin ciliated, transverse to slightly concave, slightly emarginate in the middle, or more rarely smoothly curved, postocciput green, tumid; rear of head red brown.

Prothorax red brown, synthorax (fig. 26) predominantly green, area around middorsal carina washed with brown, often appearing as a faded middorsal stripe; antehumeral and humeral stripes dark brown, united into one large stripe; most of this stripe occupying posterior 0.30 of mesepisternum, metastigma black, a wash of brown between metepisternum and metepimeron often forming an obscure, narrow thoracic stripe, subalar carina darkened with brown, mesinfraepisternum and metinfraepisternum brown; metasternum green-brown. Coxae pale grey- brown with some green on exterior surfaces, trochanters grey brown, femora tawny at base, becoming dark brown distally, tibiae and tarsi black.

Venational statistics (n = 13, including lectotype ♂). Fifth antenodal (occasionally fourth, sixth, or seventh) thickened in all wings; marginal cells behind fore wing paranal cells: 0- 4/0-4; anx: fore wing 13-15/13-16, hind wing 9-11/10-12; pnx: fore wing 9-12/9-11, hind wing 10-13/10-13; cs under pterostigma: fore wing 5-7/5-7, hind wing 5-7/5-7; anal triangular cells: 4-5. Hind wing 33-34 mm.

Abdomen (fig. 44). Segment 1 brown dorsally, becoming green laterally; segment 2 with blue green middorsal stripe, with dorsolateral stripe of brown surrounding green auricle, lateral margin near hamules pale greenish white; segment 3 with green middorsal stripe bounded on sides by dorsolateral stripes of brown, lateral areas of tergites pale green becoming white posteriorly, anterior transverse carina edged with black expanding laterally interrupting white lateral areas of segment, thus forming two pale spots, posterior transverse carina also black, expanding laterally so that posterior 0.2 of segment is black; segments 4-6 similar to segment 3, but with middorsal brown stripe narrowed anteriorly so that whitish green side almost touches middorsal green; segment 7 with anterior 0.5 dull white, conspicuously traversed by black anterior transverse carina, posterior 0.5 of segment red brown; segments 8-10 red brown with ventral and posterior borders of each segment black. Appendages red brown with apices becoming black. Abdomen 37-40 mm.

Cercus (fig. 115) nearly straight, swollen anteriorly, apical 0.5 abruptly concave dorsally and covered with thick series of strong black bristles. Epiprocts about 0.5 the length of superiors, strongly curved dorsally; tips slightly divergent, each a thick, blunt point (fig. 135).

Accessory genitalia (fig. 68). Anterior hamule black, glabrous, deeply forked with posterior branch slightly longer than anterior, the whole structure resembling a talon; anterior branch of hamule with a small semi-oval planar surface on outer side, this area covered with small hairs. Posterior hamule pale green or white, becoming brown near tip; in lateral view, tip obtusely pointed with posterior margin gently convex. Penis (fig. 90) with lateral lobes poorly developed posteriorly, almost circular, its margin serrated.

Female. – Overall colouration as in male, but with pale areas on abdomen and legs more extensive. On abdomen (fig. 45), brown on terminal segments extending anteriorly so that green middorsal and dorsolateral brown stripes become ill-defined. Lateral margins of abdominal segments mostly white and similar to male except that white extends posteriorly to segment 8. abdomen 37-40 mm.

Vertex with slightly tumid, oval areas posterior to lateral ocelli; posterior margin of occiput (fig. 164) elevated and nearly straight; postocciput green, tumid medially (fig. 167).

Venational statistics. Fifth antenodal (occasionally fourth, sixth, or seventh) thickened in all wings; anx: fore wing 13-16/13-16, hind wing 10-12/10-11; pnx: fore wing 9-13/9-12, hind wing 10-13/10-14; cs under pt: fore wing 5-7/5-8, hind wing 5-8/5-8. Hind wing 34-37 mm.

Vulvar lamina (fig. 195) membranous, diagonally corrugated, outer margin of plate with strong costate ridge, area immediately mesal to ridge furrow-like, with a smaller tumid area occupying the center, medial area tumid, posterior margin of each plate a thin, membranous ridge, postlamellar ridge long, greatly surpassing hind margin of lamina, its Y-shaped juncture at distal 0.30 of sternum. Abdomen 37-40 mm.

Diagnosis

Erpetogomphus boa is most similar to *E. cophias*, but is easily distinguished by the thoracic pattern and the male caudal appendages. A well-defined combined antehumeral and humeral stripe is present in *E. boa*, but no such stripe is present in *E. cophias*. The superior appendages of *E. cophias* possess a large ventral ridge which ends in a prominent tooth 0.30 the length of the appendage (fig. 116). This structure is lacking in *E. boa* (fig. 115). Dorsally, the apical 0.30 of the superior appendages of *E. cophias* contains a few strong bristles, not as many or as stout as in *E. boa*.

The females of these two species are similar morphologically, but may be distinguished by the thoracic pattern. The postocciput of *E. boa* (fig. 164) does not have the posterior depressions on each side found in *E. cophias* (fig. 165).

Females of *E. boa* superficially resemble females of *E. viperinus*, but the latter have a pair of circular depressions on abdominal sternite 9 posterior to the juncture of the postlamellar ridge which are absent in *E. boa*. The vulvar lamina of *E. viperinus* (fig. 184) is totally unlike that of *E. boa* (figs. 195-196).

Remarks

This species has been known from only two specimens: Selys' type and an incomplete male described by Ris (1917). The lectotype is a teneral male with the apical 0.5 of the cerci missing (fig. 114), but it was apparently complete at the time of the original description. The original description of the male is as follows (translated from the French): 'Pterostigma light yellow brown. Head and thorax yellow, femora yellow, with an external brown stripe, short, the anterior four tarsi brownish black.

'[male]. Superior appendages swollen at their base, with an obtuse tooth above at the end of the swelling; their points rounded, slightly bent inwards, hairy. Inferior appendage divided, branching a little distance, attaining 1/2 length of the superior. Occiput nearly straight. Tibiae brown.'

Selys' (1859) description of the female led Calvert (1905) to believe that it was really a specimen of *E. crotalinus*; and my examination of this female confirms Calvert's assertion. *Erpetogomphus crotalinus* appears to be restricted to the Pacific side of Mexico, and I doubt that the locality ('Vera Cruz') is correct for this specimen. In the supplement to the Biologia (Calvert, 1907), Calvert received drawings of the incomplete abdominal appendages of the type which led him to remark that *E. boa* seemed hardly different from *E. elaps*. Ris (1917) provided a history of the type male of *E. boa* and remarked (translated from the German): 'I examined a long time ago in the Hamburg Museum an old male that was different from *elaps* and corresponds with the description of *boa*, that its identity [with *boa*] seemed likely. The locality is, unfortunately, uncertain, the label reads 'Agua Caliente' without further information. Its preservation is fair, the tip of the inferior appendages are missing about the distal fourth as shown in the figure...'

Examination of the hamules of the lectotype verifies the identity of a series of *E. boa* all collected in southern Veracruz; and the Agua Caliente specimen of Ris is also *E. boa*.

Calvert (1905) postulated that *E. sipedon* might be the female of *E. boa*. Although I have not seen a pair of *E. boa* in copula or in tandem, I am confident in ascribing these females to *E. boa*. The similarity of the vulvar laminae in *E. boa* and *E. cophias* (whose males are closely related) further strengthens my conviction that *E. sipedon* does not represent the female of *E. boa*. López (*in litt.*) has observed tandem pairs, confirming the female sex of this restricted species.

The male epiprocts, which are robust and form a sharp point, are apparently responsible for structural damage to the vertex of many females during mating. Of the 26 females I examined, 14 (54%) had two holes medially to the postoccipital tubercles. Some of these specimens had encrusted haemolymph surrounding the wounds. Dunkle (1984, 1991) reviews cases of traumatic mating among other anisopteran Odonata, but their negative effect, if any, is unknown. Of the remaining 12 females, which were uninjured, 5 were teneral and had not yet mated.

Venational details of lectotype male: fifth antenodal thickened in fore wings, fourth in hind wings; marginal cells behind fore wing paranal cells: 1?/2; anx: fore wing 14/14, hind wing 10/10; pnx: fore wing 10/10, hind wing 10/11; cs under pterostigma: fore wing 5/6, hind wing 5/5; anal triangular cells: 4. Hind wing 34 mm.

Biology. – Most specimens were obtained at a city park near Jalapa. Individuals were found by flushing them from low vegetation about 50 m from a small stream. Adults spent most of their time resting and were difficult to detect among the green foliage. Its habits are similar to those reported for *E. viperinus*. Adults prefer parts of small, low volume sandy-bottomed streams where banks are often covered by trees. Reproductive maturation continues through July. Copulation apparently occurs primarily in open areas near streams. Ensuing pairs fly some distance from these sites. Some males settle at the edge of the stream, but passing females are unreceptive there. Females, like other members of this genus, oviposit unattended, flying over the water, stopping briefly to drop eggs from a height of about 40 cm. López has observed *E. boa* captured by spiders (Araneidae) and robber flies (Asilidae).

Collection dates are July and August. Altitudes of capture range from 1150 m (Orizaba) to 1300 m (Jalapa).

Distribution (fig. 207). – *Erpetogomphus boa* has been taken only in central Veracruz between 18°50'N and 19°30'N along the eastern foothills of the Sierra Madre Oriental.

Material

Type data. – Lectotype male by present designation with following data: small green label 'Vera Cruz/Salle', yellow rectangular label: 'ERPET. BOA / ♂' [this last label probably added by Selys during or after 1879], all in Selys' hand; two pencilled labels on red tags: 'No. 100'; and two pencilled white labels: '28', all in an unknown hand. The caudal appendages and accessory genitalia are shown in fig. 114. The female specimen originally described as the female of *E. boa* is actually *E. crotalinus* and possesses the following labels: small green label: 'Vera Cruz/Salle'; and white label: '*Herp. boa* S. / ♀', both in Selys' hand. Both specimens in IRSN.

Other material (13♂, including lectotype ♂; 26♀). – MEXICO: *Veracruz*: Parque Javier Clavijero, Jalapa, 1300 m, 21 June 1980 (Raul López), 1♂ (RWG); (same data), 11 Aug. 1980 (A. Garcés), 1♂ (UNAM); (same data), 13 Aug. 1980 (R. López), 1♂ (UNAM); (same data), 16 Aug. 1980 (A. Garcés), 1♂ (UNAM); (same data), 20 Aug. 1980, 1♀ (UNAM); (same data), 5 Aug. 1981, (R. López), 2♂, 6♀ (RWG); (same data), 6 Aug. 1981, 1♂ (UNAM); (same data), 1 Aug. 1982, 3♂, 1♀ (RWG); (same data), 9 Aug. 1982, 1♀ (UNAM); (same data), 19 Aug. 1982, 3♀ (UNAM); (same data), Bosque Mesofilo de Montaña, 12 June 1981 (R. López), 1♀ (UNAM); Barranca de Cayoapa, Teocelo, (no collector), 1♀ (RWG); 4.8 mi N of Coscomatopec, (M. A. Ortiz, O. S. Flint), 1♂, 2♀ USNM); 2.5 mi S of Huatusco, 23 July 1966 (M. A. Ortiz, O. S. Flint), 1♀ (USNM); 4.7 mi N of Huatusco, Puente Ruiz Cortines, 31 July 1966 (M. A. Ortiz, O. S. Flint), 3♀ (USNM); Orizaba, Ojo de Agua, 3800 ft. (D. R. Paulson), 1♂, 5♀ (DRP, FSCA).

Erpetogomphus cophias Selys

(figs. 27-thx, 46-abd, 69-hamules, 91-penis, 116-app, 165-vertex, 197-vl, 207-distr)

Erpetogomphus cophias Selys, 1858: 332 (72 sep.) (descr. ♂ 'Le Mexique, d'après un mâle du Museum de Paris'). – Selys 1859: 537 (11 sep.) (descr. ♂); Selys 1869: 175 (12 sep.) (descr. ♀); Selys 1873b: 519 (75 sep.) (list); Calvert 1899: 386 (mentioned); Calvert 1905: 164 (descr. ♂, ♀); Calvert 1907: 398 (mention of new figure); Calvert 1909: 481 (seasonal distr.); Muttkowski 1910: 86 (cat.); Williamson and Williamson 1930: 12 (summary of status); Montgomery 1973: 239 (comment on name); Paulson 1982: 255 (Mex.); Davies and Tobin 1985: 27

(cat.); Tsuda 1986: 87 (cat.); Bridges 1991: VII.52 (cat.); Tsuda 1991: 95 (cat.).
Gomphus cophias. – Hagen 1861: 100 (descr. ♂).
Herpetogomphus cophias. – Walsh 1862: 389 (mentioned); Hagen 1875a: 42 (cat.); Selys 1879: 64 (2 sep.) (characters of genus); Kirby 1890: 60 (cat).

Description

Neotype male. – Entire face pale green; base of mandibles pale green, tips black; antefrons pale green with wash of brown at base; vertex brown, with some green on tubercle behind each lateral ocellus; two prominent cone-shaped pits anterolateral to median ocellus; scape and pedicel dark brown, flagella missing; occiput broad, its dorsal surface evenly convex, especially medially, its posterior margin slightly arcuate; crest with long brown hairs; postocciput light green, evenly concave, rear of head red brown.

Prothorax primarily brown, with light green medially on anterior, median, and posterior lobes; synthorax entirely pale green with wash of brown ventrally above coxae. Coxae and trochanters pale grey green, femora pale grey green becoming tawny distally, a dark brown streak on lateroextensor surfaces of femora occupying almost all of profemora, about 0.60 of mesofemora, and distal 0.30 of metafemora; tibiae, tarsi, and armature black. Wings hyaline, venation dark brown basally, black distally; anterior margin of costa pale yellow to proximal end of pterostigma; pterostigma brown, veins bordering it black.

Venational details. Fifth antenodal thickened in all wings; no marginal cells behind fore wing paranal cells; anx: fore wing 13/13, hind wing 9/9; pnx: fore wing 7/7, hind wing 7/9; cs under pterostigma: fore wing 5/5, hind wing 5/4; anal triangular cells: 4 . Hind wing 29 mm.

Abdomen predominantly pale with following dark brown markings: vestige of midlateral stripe on segment 1; this stripe more defined on segment 2, especially behind auricle; annulus; midlateral stripe on segment 3, transverse carina and darker annulus; segments 4-6 similar to segment 3 but stripes darker, each beginning at a little beyond beginning of segment, enlarging at transverse carina, narrowing and then widening, especially posteriorly, but not touching dorsally; segment 7 with transverse carina and posterior 0.40 of segment laterally; segment 8 pale yellow brown with ill-defined dorsolateral dark stripe; segment 9 similar to segment 8, but with a longitudinal lateral middorsal spot on posterior 0.75 of segment; segment 10 pale ocher with dark red brown along anterior 0.20 of segment. Pale areas of segments 1-7 primarily pale olive dorsally and ventrally; pale areas of segments 8-10 red brown dorsally and ventrally. Abdomen 35 mm.

Cercus yellow brown, linear, slightly concave dorsally beyond basal 0.30, tip smoothly rounded, ventral margin with inferior carina at basal 0.30, terminating in a distinct ventral tooth; dorsal concave area of cerci with scattered thick bristles. Epiprocts yellow brown, distal 0.50 curved dorsally at 90°, as is typical of genus, tips slightly divergent, each with a thick, blunt point.

Accessory genitalia. Anterior hamule black, glabrous, deeply forked, with posterior branch slightly longer than anterior, the whole structure resembling a talon; distal 0.20 of anterior branch with a longitudinal, obtuse V-shaped area. Posterior hamule spatulate, pale green, becoming brown near tip; in lateral view, tip obtusely pointed with a small, blunt cephalad directed tooth on rear margin. Peduncle of penis with prominent rounded foliate erect lateral lobes, its posterior margin not prominent, forming a gentle bilobed area; penis with lateral lobes poorly developed posteriorly, forming a serrated semicircle; membranous hood not overlapping; cornuae well developed, parallel sided, their tips evenly rounded.

Female. – Overall colouration as in male, head with prominent conical pits anterolateral to median ocellus as in male; vertex with tumid oval area posterior to lateral ocelli; occiput narrow, crest prominent, straight to slightly sinuate along medial 0.30, lateral arms bent posteriorly; prominent transverse postoccipital pit (fig. 165) immediately behind lateral arms of crest, medial area of postocciput tumid.

Pro- and synthorax as in male, femora with brown areas reduced with little brown on extensor surface of metafemora.

Venational statistics (n = 2): number of marginal cells behind fore wing paranal cells: 2-4/1-3; anx: fore wing 13/13, hind wing 9-11/9-10; pnx: fore wing 9/8-9, hind wing 9-10/10; cs under pterostigma: fore wing 5/4-5, hind wing 4-6/4-5. Hind wing 32-34 mm.

Abdomen with brown dorsolateral stripe more reduced than male, more prominent and expanded around lateral carinae; segments 8-9 tawny, cercus pale ocher. Vulvar lamina (fig. 197) membranous, diagonally corrugated; posterior margin of each plate gently curved, a prominent ridge along its border, a prominent long diagonal depression immediately anterior to posterior margin; plates meeting medially at tumid area; cleft between plates a small notch; juncture of Y-shaped postlamellar ridge well posterior to vulvar laminar plates; area on each side of central stem of postlamellar ridge darkened, with a slight depression. Abdomen 35-37 mm.

Diagnosis

Erpetogomphus cophias is most similar to *E. boa* and is diagnosed under that species. The characteristic ventral tooth of the cercus in the male and the postoccipital depressions in the female are autapomorphic characters.

Remarks

This is apparently a rare species. Williamson and Williamson (1930) stated that there were only 10 known specimens. Only one other specimen from Michoacan, collected in 1941, has come to my attention. I have examined only 3 males and 4 females, of which one male and one female are teneral and in poor condition. I can see no noticeable differences among the few specimens examined.

Variation. – Venational details of one additional male: number of marginal cells behind fore wing paranal cells: 3/2; anx: fore wing 11/12, hind wing 9/8; pnx: fore wing 9/8, hind wing 9/10; cs under pterostigma: fore wing 5/5, hind wing 5/5; number of anal triangular cells 3/3. Hind wing 30 mm.

Biology. – Nothing is known of the biology of this species.

Distribution (fig. 207). – Like *E. boa, E. cophias* has a restricted distribution and apparently replaces *E. boa* in the highlands of west-central Mexico south of 20°N and west of 100°W. Records indicate an elevational gradient of 1525 m (Cuernavaca) to 2438 m (Omilteme) and flight during June and July.

Material

Type data. According to Dr. J. Legrand (*in litt.* 11 May 1984), the holotype male from 'Le Mexique, d'après un mâle du Museum de Paris', is missing, there remaining only a large rectangular green label with [handwritten] '*E. cophias*, Selys' which was originally attached to the specimen. Dr. Legrand was kind enough to send a male of which he states, '...we have from ex Martin's collection a specimen called *O. cophias* Selys (determined by Selys himself, according to Martin...),' which he suggested I designate as neotype. This I now do. The neotype male contains the following data: white label in R. Martin's hand: '*Ophiogomphus* / *cophias* Selys/ Det. De Selys/ Mexique', small green label printed: 'MUSEUM PARIS / Coll. R. MARTIN 1920', and red rectangular label handwritten: '*Erpetogomphus* / *cophias* Selys ♂ / NEOTYPE / des./ R. W. Garrison 1986'. The abdomen is detached and is in a triangular envelope pinned beneath the specimen.

Other material (3♂, 4♀, including neotype ♂). – MEXICO: *Guerrero*: Omilteme, 8000 ft., July 1888 (H. H. Smith), 1♀, (BMNH); *Michoacan*: Tancítaro, 6000 ft. (1846 m), 4th Hoogstraal Mexican Biological Expedition, 28 July 1941 (H. Hoogstraal), 1♂ (UMMZ); *Morelos*: Cuernavaca, June 1897 (O. W. Barrett), 1♂, 1♀ (ANSP); June 1888 (H. H. Smith), 1♂ (BMNH); 8 July 1900 (C.C. Deam), 2♀ (UMMZ).

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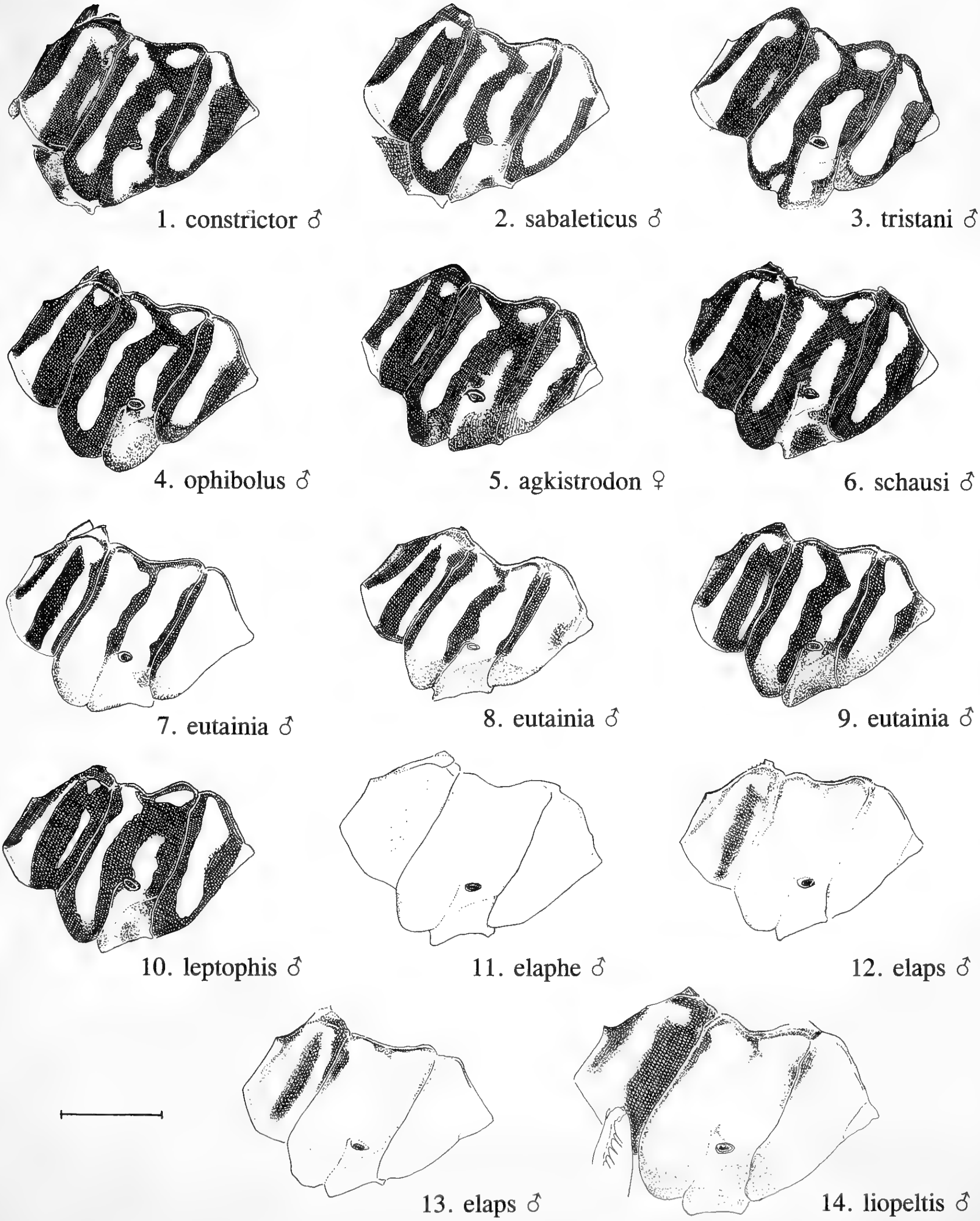
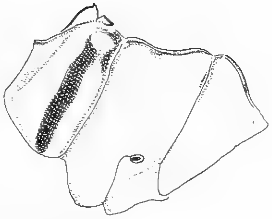
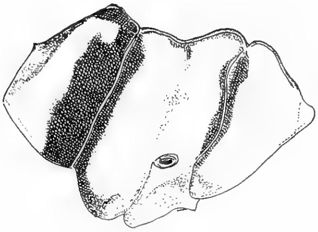


1. constrictor ♂
2. sabaleticus ♂
3. tristani ♂
4. ophibolus ♂
5. agkistrodon ♀
6. schausi ♂
7. eutainia ♂
8. eutainia ♂
9. eutainia ♂
10. leptophis ♂
11. elaphe ♂
12. elaps ♂
13. elaps ♂
14. liopeltis ♂

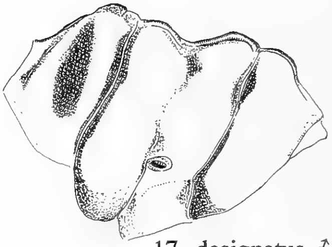
Figs. 1-14. Synthorax of *Erpetogomphus* species, lateral view (males, except given otherwise). – 1, *constrictor* (Honduras); 2, *sabaleticus* (holotype); 3, *tristani* (Costa Rica); 4, *ophibolus* (Mexico: Veracruz State); 5, *agkistrodon* (female holotype); 6, *schausi* (holotype); 7, *eutainia* (Texas: Gonzales Co.); 8, *eutainia* (Mexico: Veracruz State); 9, *eutainia* (Costa Rica); 10, *leptophis* (holotype); 11, *elaphe* (holotype); 12, *elaps* (Mexico: Sinaloa State); 13, *elaps* (Mexico: Morelos State); 14, *liopeltis* (holotype). Scale line: 3 mm.



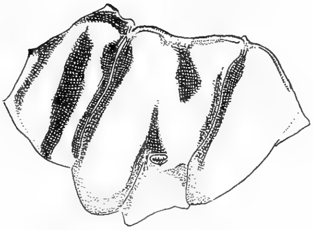
15. bothrops ♂



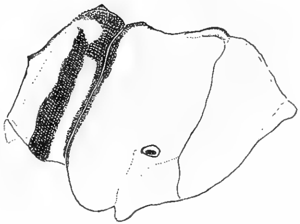
16. viperinus ♂



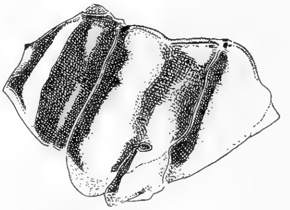
17. designatus ♂



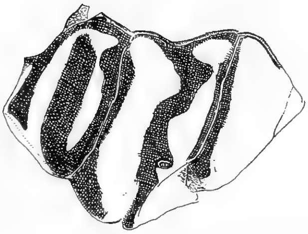
18. designatus ♂



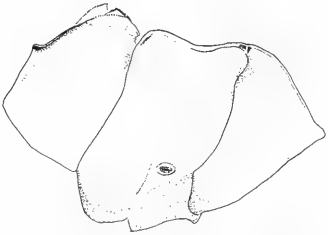
19. sipedon ♀



20. lampropeltis lampropeltis ♂

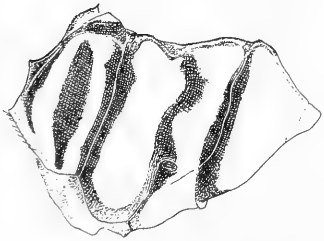


21. lampropeltis natrix ♂

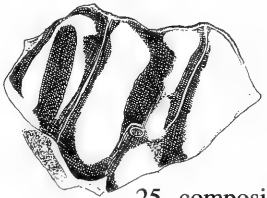


22. crotalinus ♂

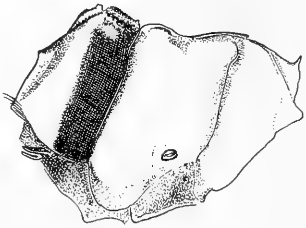
23. heterodon ♂



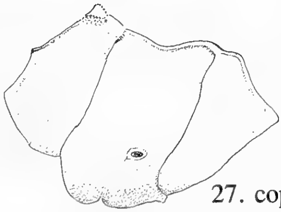
24. compositus ♂



25. compositus ♂

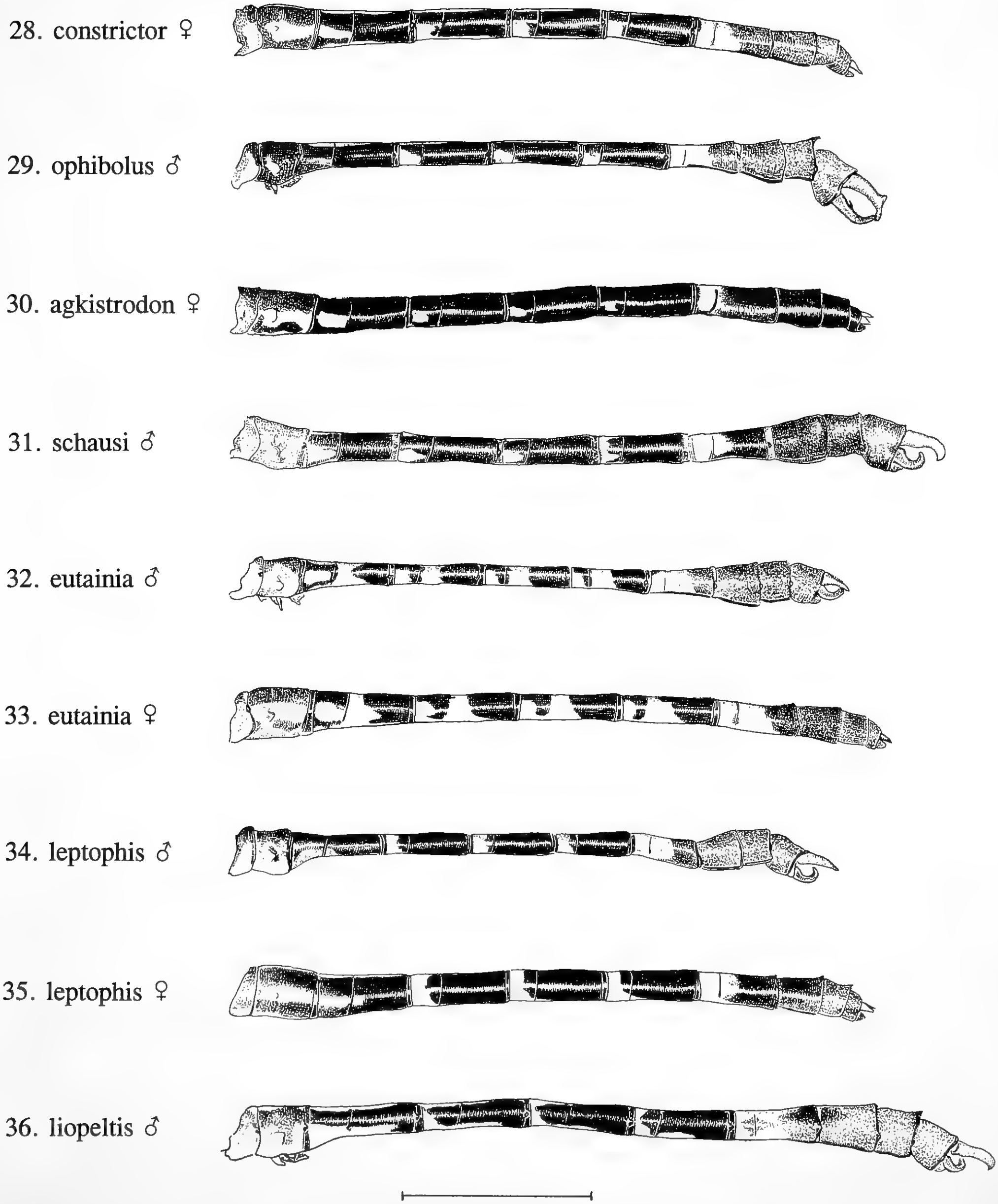


26. boa ♂

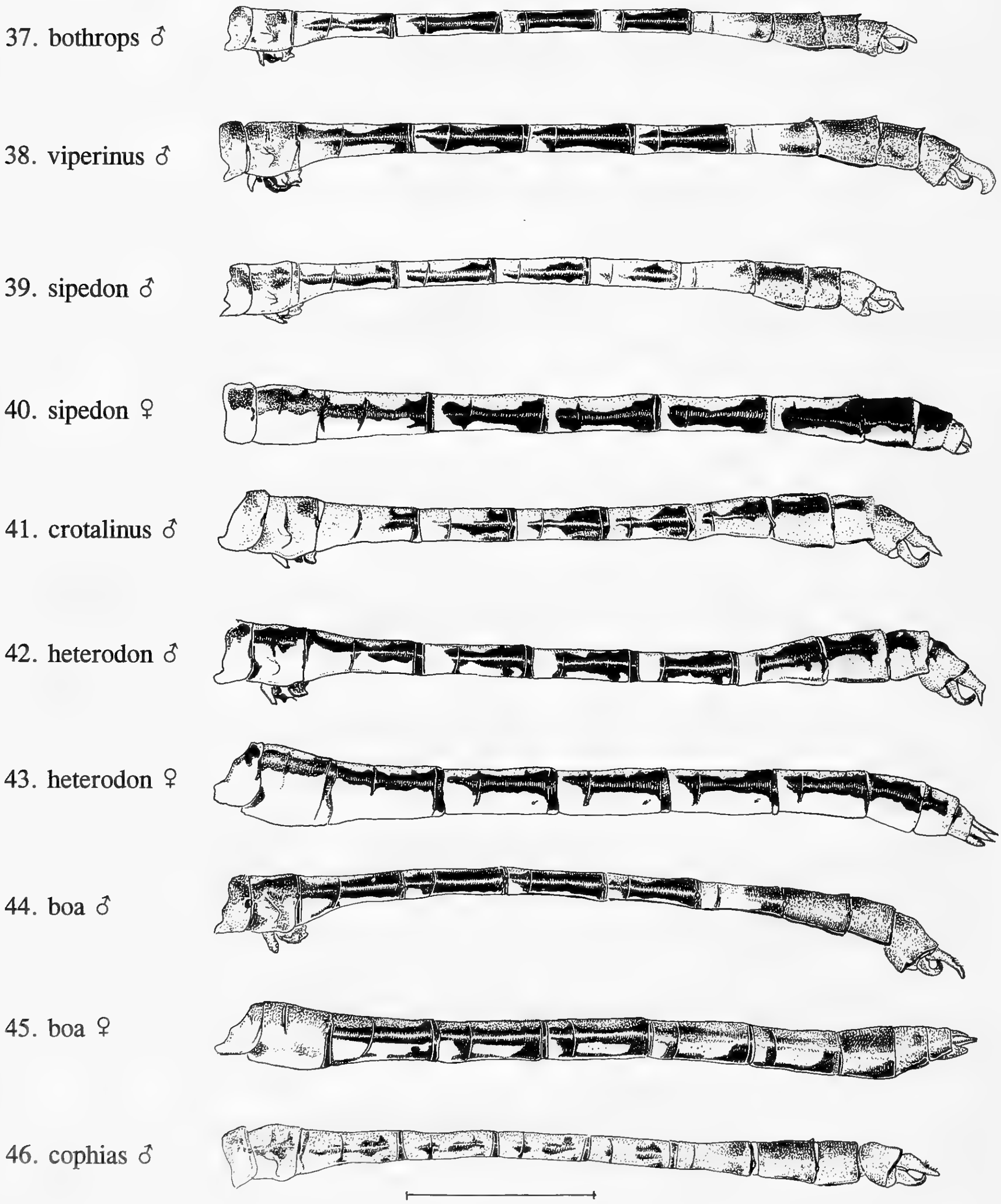


27. cophias

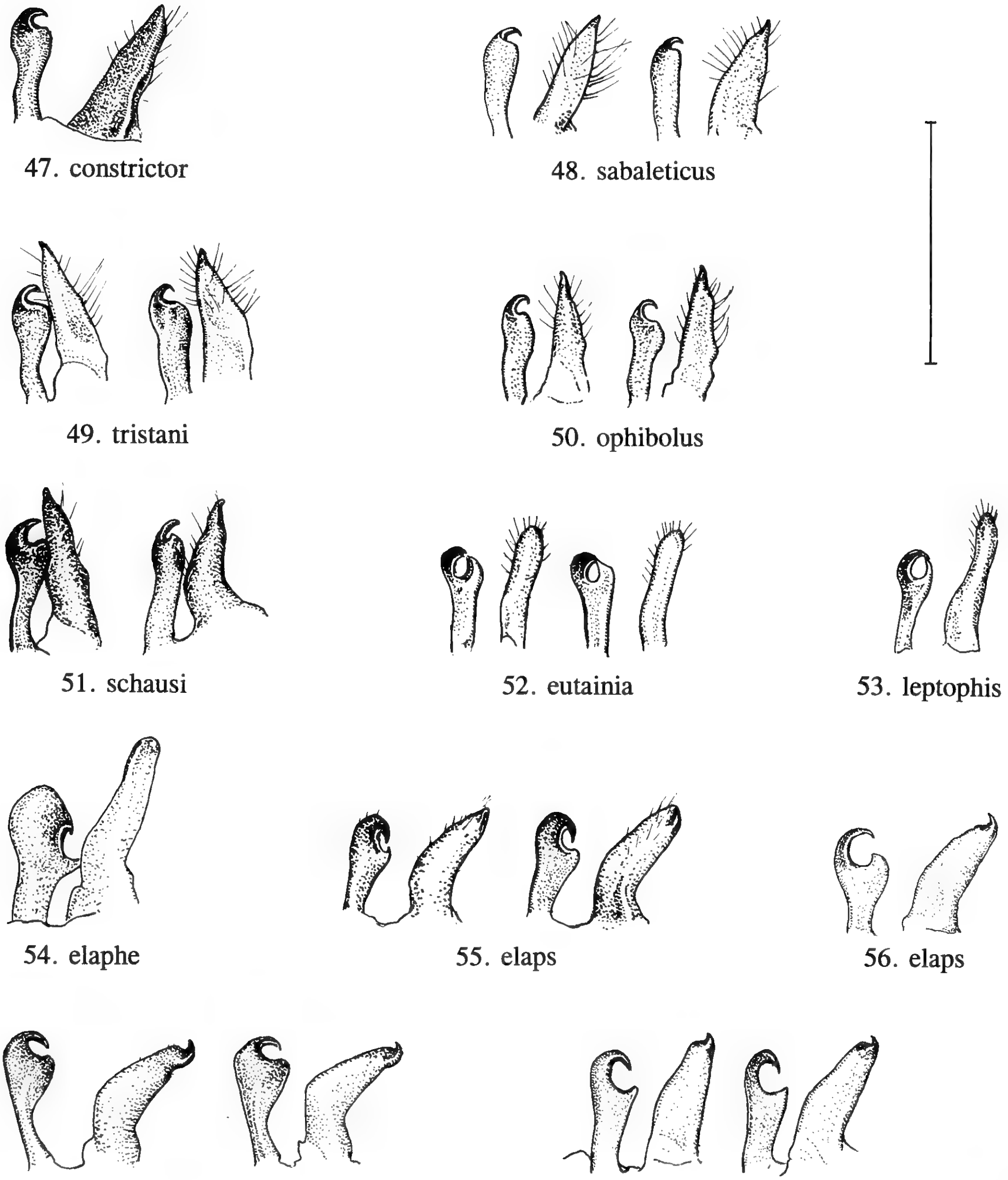
Figs. 15-27. Synthorax of *Erpetogomphus* species, lateral view (males, except given otherwise). – 15, *bothrops* (holotype); 16, *viperinus* (Mexico, Veracruz State); 17, *designatus* (lectotype); 18, *designatus* (Mexico, Durango State); 19, *sipedon* (female holotype); 20, *l. lampropeltis* (holotype); 21, *lampropeltis natrix* (holotype); 22, *crotalinus* (lectotype); 23, *heterodon* (holotype); 24, *compositus* (California, Yolo Co.); 25, *compositus* (paratype of *coluber*); 26, *boa* (Mexico: Veracruz State); 27, *cophias* (Mexico: Morelos State). Scale line 3 mm.



Figs. 28-36. Abdomen, lateral view. – 28, *constrictor* ♀ (Honduras); 29, *ophibolus* ♂ (Mexico: Veracruz State); 30, *agkistrodon* ♀ (holotype); 31, *schausi* ♂ (holotype); 32, *eutainia* ♂ (Texas: Gonzales Co.); 33, *eutainia* ♀ (idem); 34, *leptophis* ♂ (holotype); 35, *leptophis* ♀ (allotype); 36, *liopeltis* ♂ (holotype). Scale line 10 mm.



Figs. 37-46. Abdomen, lateral view. – 37, *bothrops* ♂ (holotype); 38, *viperinus* ♂ (Mexico: Veracruz State); 39, *sipedon* ♂ (Mexico: Morelos State); 40, *sipedon* ♀ (holotype); 41, *crotalinus* ♂ (Mexico: Jalisco State); 42, *heterodon* ♂ (holotype); 43, *heterodon* ♀ (allotype); 44, *boa* ♂ (Mexico: Veracruz State); 45, *boa* ♀ (idem); 46, *cophias* ♂ (Mexico: Morelos State). Scale line 10 mm.



47. constrictor

48. sabaleticus

49. tristani

50. ophibolus

51. schausi

52. eutainia

53. leptophis

54. elaphe

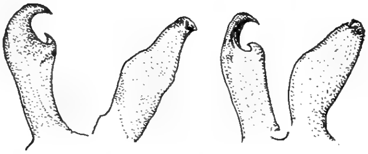
55. elaps

56. elaps

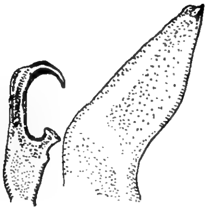
57. liopeltis

58. bothrops

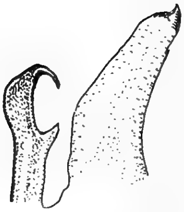
Figs. 47-58. Anterior and posterior hamules. First view is anterolateral view showing profile of anterior hamule; second view (when shown) is lateral view showing profile of posterior hamule. – 47, *constrictor* (Mexico: San Luis Potosi State); 48, *sabaleticus* (holotype); 49, *tristani* (Costa Rica); 50, *ophibolus* (Mexico: Veracruz State); 51, *schausi* (holotype); 52, *eutainia* (Texas: Gonzales Co.); 53, *leptophis* (holotype); 54, *elaphe* (Costa Rica); 55, *elaps* (holotype); 56, *elaps* (variant) (Mexico: Chiapas State); 57, *liopeltis* (paratype); 58, *bothrops* (paratype). Scale line 2 mm.



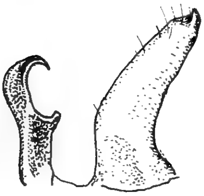
59. viperinus



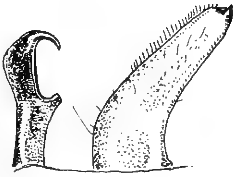
60. designatus



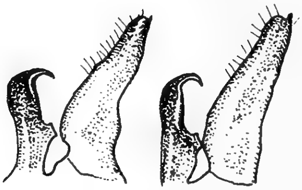
61. sipedon



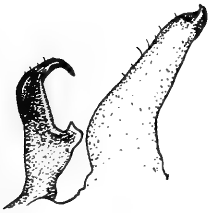
62. lampropeltis
lampropeltis



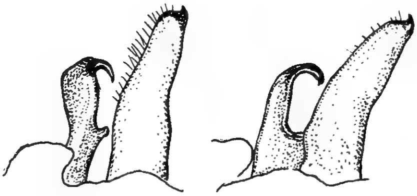
63. lampropeltis natrix



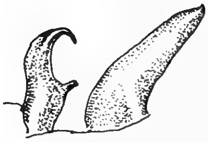
64. crotalinus



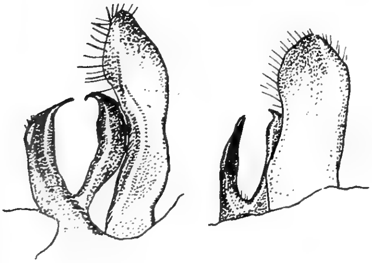
65. heterodon



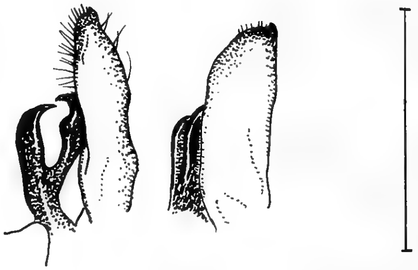
66. compositus



67. compositus

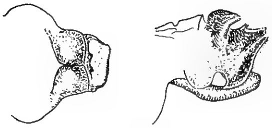


68. boa

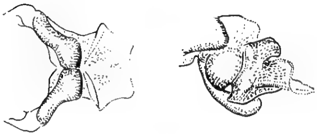


69. cophias

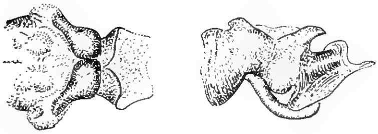
Figs. 59-69. Anterior and posterior hamules. First view is anterolateral view showing profile of anterior hamule; second view (when shown) is lateral view showing profile of posterior hamule. – 59, *viperinus* (Mexico: Veracruz State); 60, *designatus* (lectotype); 61, *sipedon* (Mexico: Morelos State); 62, *l. lampropeltis* (California: Ventura Co.); 63, *l. natrix* (holotype); 64, *crotalinus* (Mexico: Michoacan State); 65, *heterodon* (New Mexico: Catron Co.); 66, *compositus* (Arizona: Pima Co.); 67, *compositus* (paratype of *coluber*); 68, *boa* (lectotype); 69, *cophias* (Mexico: Morelos State). Scale line 2 mm.



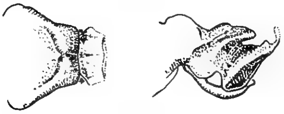
70. constrictor



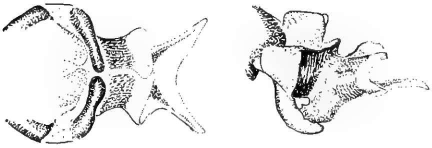
71. sabaleticus



72. tristani



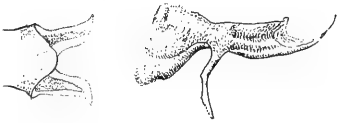
73. ophibolus



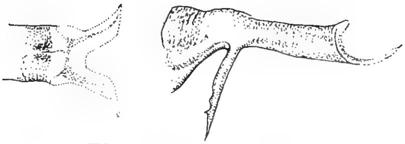
74. schausi

75. eutainia

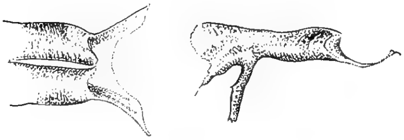
76. leptophis



77. elaphe



78. elaps



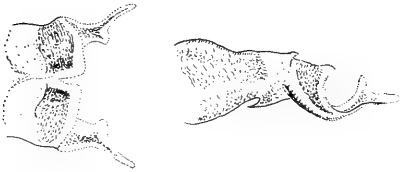
79. liopeltis

80. bothrops

Figs. 70-80. Penis segment 4, left: dorsal view, right: lateral view. – 70, *constrictor* (Mexico: San Luis Potosi State); 71, *sabaleticus* (holotype); 72, *tristani* (Costa Rica); 73, *ophibolus* (Mexico: Veracruz State); 74, *schausi* (holotype); 75, *eutainia* (Texas: Gonzales Co.); 76, *leptophis* (holotype); 77, *elaphe* (Costa Rica); 78, *elaps* (holotype); 79, *liopeltis* (paratype); 80, *bothrops* (Mexico: Tamaulipas State). Scale line 1 mm.

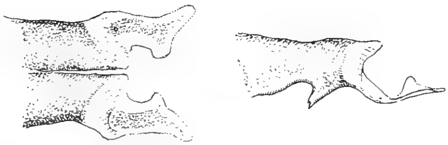
81. viperinus

82. designatus

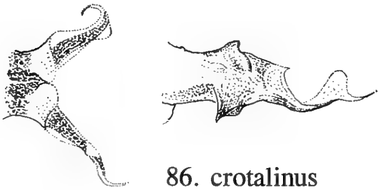


83. sipedon

84. lampropeltis lampropeltis



85. lampropeltis natrix



86. crotalinus

87. heterodon

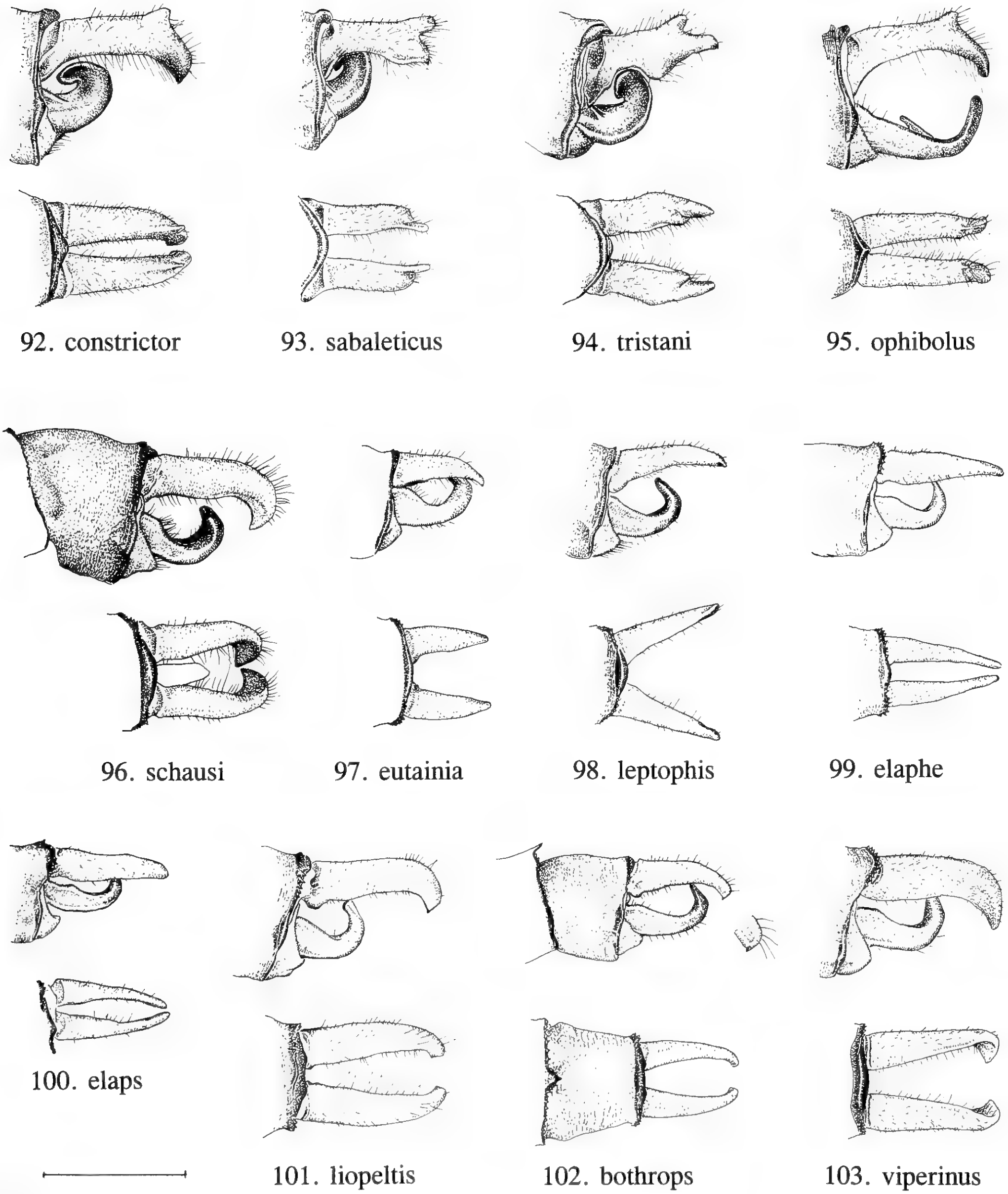
88. compositus

89. compositus

90. boa

91. cophias

Figs. 81-91. Penis segment 4, left: dorsal view, right: lateral view. – 81, *viperinus* (Mexico: Veracruz State); 82, *designatus* (Texas: Gonzales Co.); 83, *sipedon* (Mexico: Morelos State); 84, *l. lampropeltis* (California: Ventura Co.); 85, *l. natrix* (Arizona: Cochise Co.); 86, *crotalinus* (Mexico: Michoacan State); 87, *heterodon* (New Mexico: Catron Co.); 88, *compositus* (CA: Yolo Co.); 89, *compositus* (paratype of *coluber*); 90, *boa* (lectotype); 91, *cophias* (Mexico: Morelos State). Scale line 1 mm.



92. constrictor

93. sabaleticus

94. tristani

95. ophibolus

96. schausi

97. eutainia

98. leptophis

99. elaphe

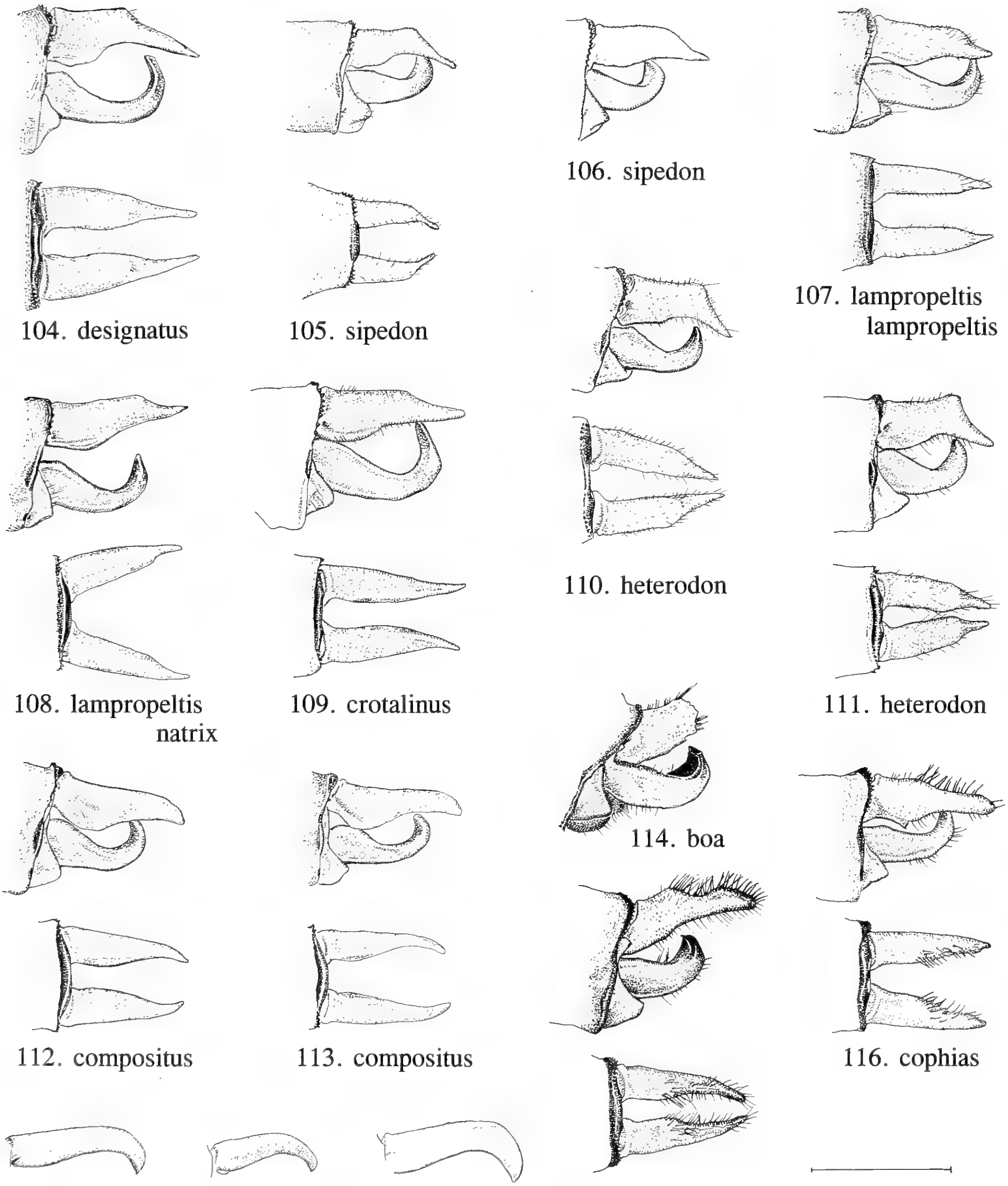
100. elaps

101. liopeltis

102. bothrops

103. viperinus

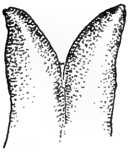
Figs. 92-103. Caudal appendages of male, above = lateral view, below = dorsal view of cerci. – 92, *constrictor* (Mexico: Tamaulipas State); 93, *sabaleticus* (holotype); 94, *tristani* (holotype); 95, *ophibolus* (Mexico: Veracruz State); 96, *schausi* (holotype); 97, *eutainia* (Texas: Gonzales Co.); 98, *leptophis* (holotype); 99, *elaphe* (Costa Rica); 100, *elaps* (holotype); 101, *liopeltis* (holotype); 102, *bothrops* (holotype); 103, *viperinus* (lectotype). Scale line 5 mm.



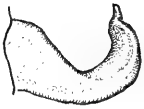
104. designatus
105. sipedon
106. sipedon
107. lampropeltis lampropeltis
108. lampropeltis natrix
109. crotalinus
110. heterodon
111. heterodon
112. compositus
113. compositus
114. boa
115. boa
116. cophias
117. liopeltis
118. bothrops
119. viperinus

Fig. 104-116. Caudal appendages of male, above = lateral view, below = dorsal view of cerci. – 104, *designatus* (lectotype); 105, *sipedon* (Mexico: Morelos State); 106, *sipedon* (only lateral view) (Mexico: Durango State); 107, *l. lampropeltis* (California: Ventura Co.); 108, *l. natrix* (holotype); 109, *crotalinus* (lectotype); 110, *heterodon* (holotype); 111, *heterodon* (Mexico: Durango State); 112, *compositus* (California: Yolo Co.); 113, *compositus* (paratype of *coluber*); 114, *boa* (only lateral view) (lectotype); 115, *boa* (Mexico: Veracruz State); 116, *cophias* (Mexico: Morelos State). Figs. 117-119. Right cercus, mediolateral view. – 117, *liopeltis* (Mexico: Nuevo Leon State); 118, *bothrops* (Mexico: Nayarit State); 119, *viperinus* (Mexico: Veracruz State). Scale line 5 mm.

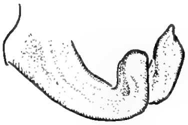
120. tristani



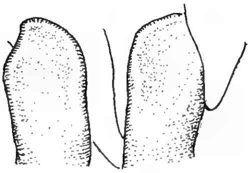
121. ophibolus



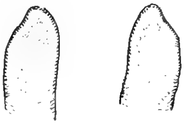
122. eutainia



123. eutainia

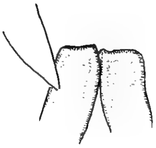


124. eutainia

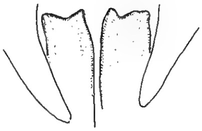


125. eutainia

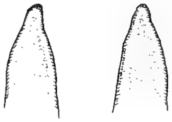
126. liopeltis



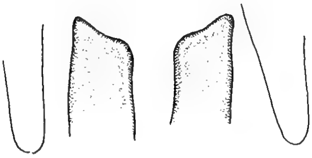
127. bothrops



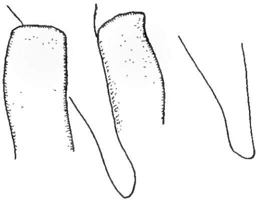
128. bothrops



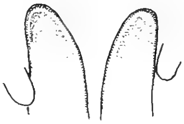
129. viperinus



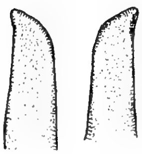
130. designatus



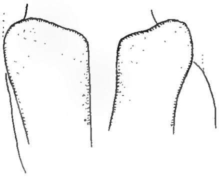
131. designatus



132. lampropeltis
lampropeltis



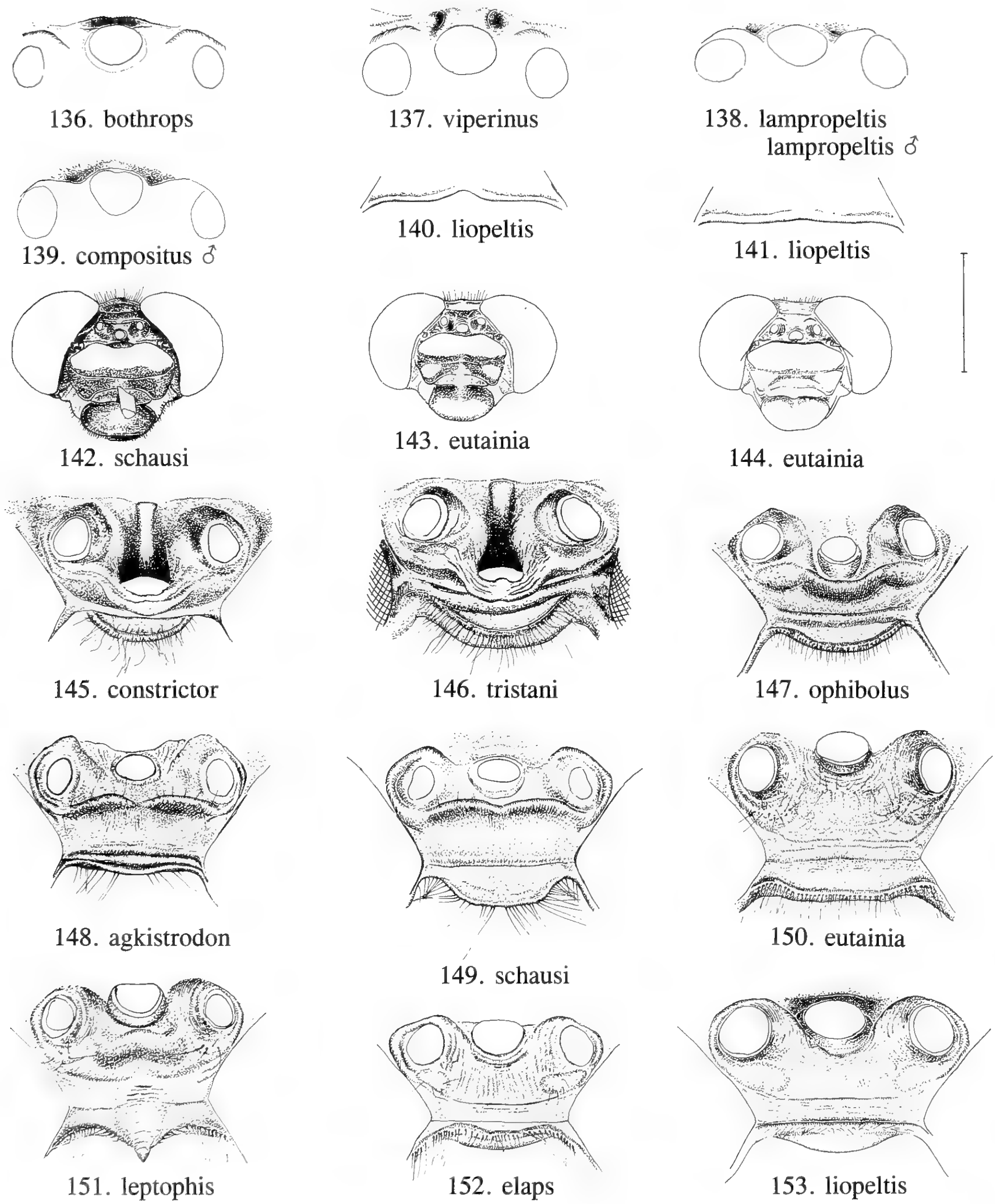
133. crotalinus



134. compositus

135. boa

Figs. 120-135. *Erpetogomphus*. – 120, tip of epiproct of male, posterior view, *tristani* (Costa Rica); 121, idem, *ophibolus* (Mexico: Veracruz State); 122, epiproct, lateral view, *eutainia* (Texas: Gonzales Co.); 123, idem, dorsolateral view; 124-135, tip of epiprocts of male, posterior view, 124, *eutainia* (Texas: Gonzales Co.); 125, *eutainia* (Guatemala); 126, *liopeltis* (Mexico: Nuevo Leon State); 127, *bothrops* (Mexico: Nayarit State); 128, *bothrops* (holotype); 129, *viperinus* (Mexico: Veracruz State); 130, *designatus* (Texas: Gonzales Co.); 131, *designatus* (Mexico: Durango State); 132, *l. lampropeltis* (California: Ventura Co.); 133, *crotalinus* (Mexico: Jalisco State); 134, *compositus* (Arizona: Coconino Co.); 135, *boa* (Mexico: Veracruz State). Scale line 2 mm (figs. 122-123), 1 mm (figs. 120-121, 124-135).



136. bothrops

137. viperinus

138. lampropeltis lampropeltis ♂

139. compositus ♂

140. liopeltis

141. liopeltis

142. schausi

143. eutainia

144. eutainia

145. constrictor

146. tristani

147. ophibolus

148. agkistrodon

149. schausi

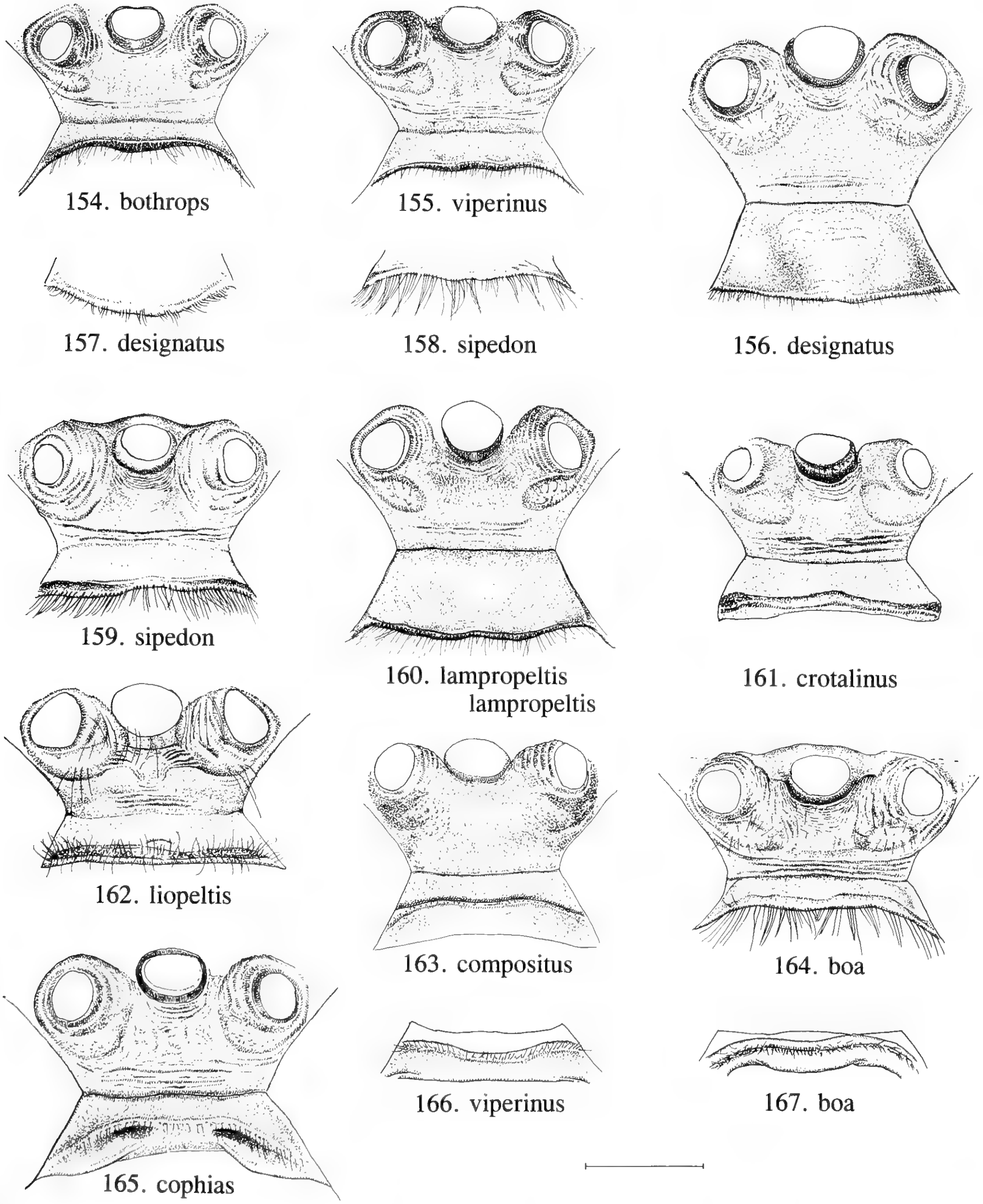
150. eutainia

151. leptophis

152. elaps

153. liopeltis

Figs. 136-153. *Erpetogomphus*. – 136-139. Anterior part of frons, dorsal view. 136, *bothrops* ♀ (Mexico: San Luis Potosi State); 137, *viperinus* ♀ (Mexico: Veracruz State); 138, *l. lampropeltis* ♂ (California: Ventura Co.); 139, *compositus* ♂ (AZ: Maricopa Co.). – Figs. 140-141. Crest outline of occiput, dorsal view. 140, *liopeltis* (holotype), 141, *liopeltis* (Mexico: Nuevo Leon State). – Figs. 142-144. Head, anterior view. 142, *schausi* (holotype); 143, *eutainia* (Costa Rica); 144, *eutainia* (Texas: Gonzales Co.). – Figs. 145-153. Vertex, occiput of female, dorsal view. 145, *constrictor* (Honduras); 146, *tristani* (Costa Rica); 147, *ophibolus* (Mexico: Veracruz State); 148, *agkistrodon* (holotype); 149, *schausi* (Costa Rica); 150, *eutainia* (Texas: Gonzales Co.); 151, *leptophis* (allotype); 152, *elaps* (Mexico: Morelos State); 153, *liopeltis* (allotype). Scale line 4 mm (figs. 142-144); 1 mm (136-141, 145-153).



154. bothrops

155. viperinus

157. designatus

158. sipedon

156. designatus

159. sipedon

160. lampropeltis lampropeltis

161. crotalinus

162. liopeltis

163. compositus

164. boa

166. viperinus

167. boa

165. cophias

Figs. 154-165. Vertex, occiput of female, dorsal view. 154, *bothrops* (allotype); 155, *viperinus* (Mexico: Veracruz State); 156, *designatus* (paralectotype); 157, *designatus* (Mexico: Durango State); 158, *sipedon* (form 'b') (Mexico: Puebla State); 159, *sipedon* (holotype); 160, *l. lampropeltis* (California: Ventura Co.); 161, *crotalinus* (paralectotype); 162, *heterodon* (allotype); 163, *compositus* (holotype); 164, *boa* (Mexico: Veracruz State); 165, *cophias* (Mexico: Guerrero State). – Figs. 166-167. Crest and part of rear of head (postocciput) of female, dorsal view. 166, *viperinus* (Mexico: Veracruz State); 167, *boa* (Mexico: Veracruz State). Scale line 1 mm.

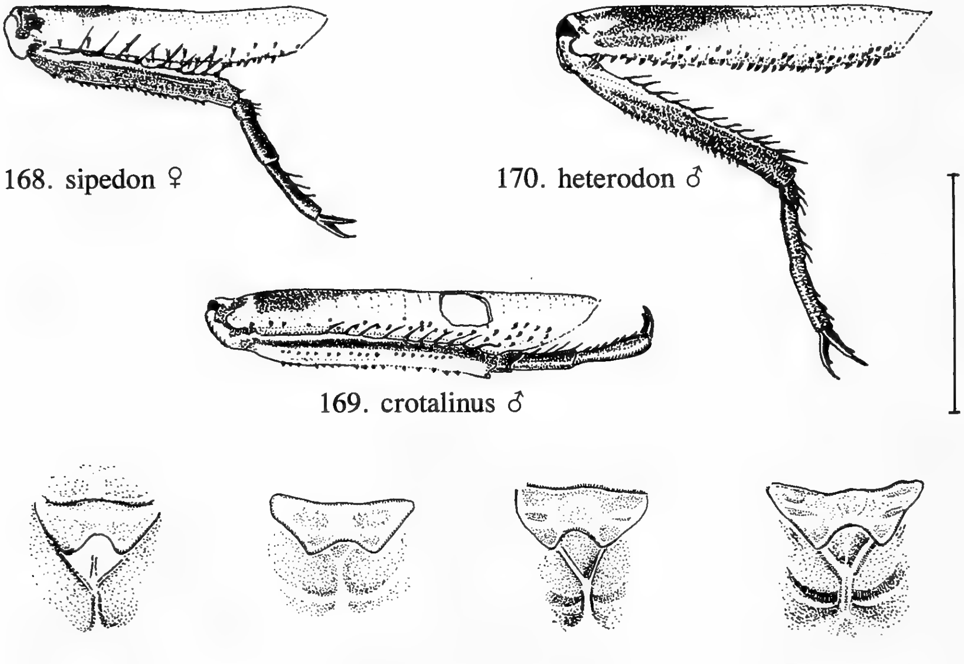
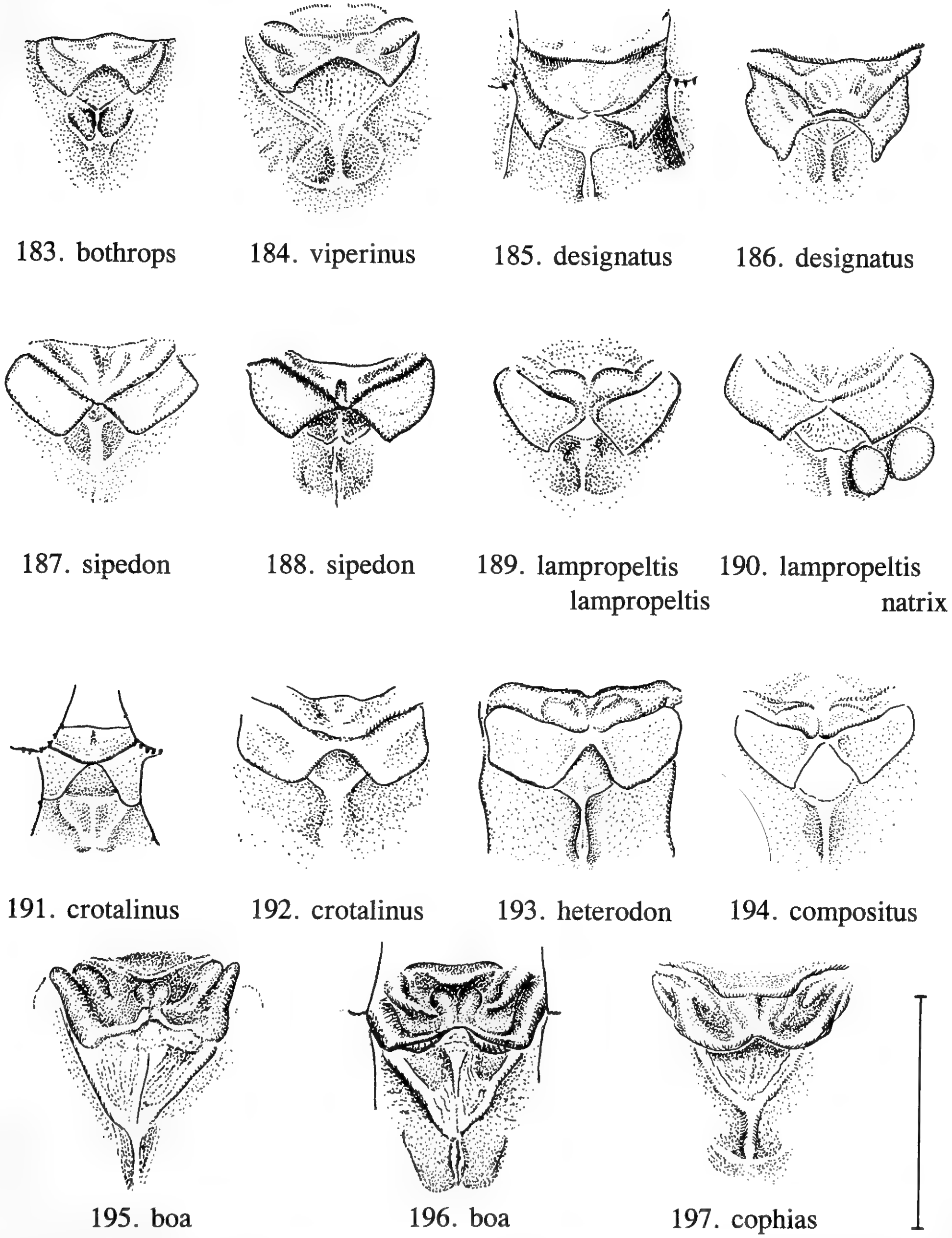
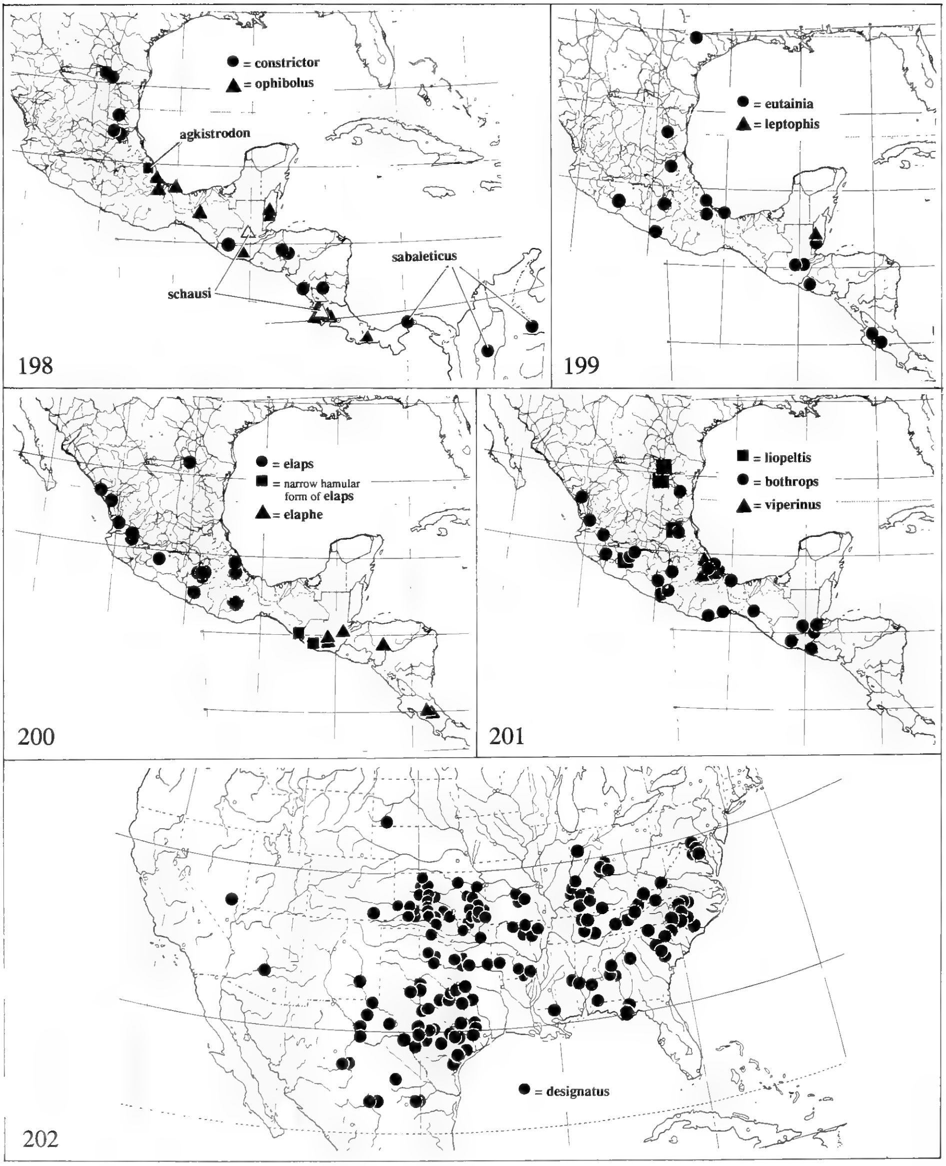


Fig. 168-170. Metathoracic leg, lateral view. – 168, *sipedon* ♀ (holotype); 169, *crotalinus* ♂ (lectotype); 170, *heterodon* ♂ (holotype). – Figs. 171-182. Vulvar lamina, dorsal view. – 171, *constrictor* (Honduras); 172, *sabaleticus* (allotype); 173, *tristani* (allotype); 174, *tristani* (Costa Rica); 175, *ophibolus* (Mexico: Veracruz State); 176, *agkistrodon* (holotype); 177, *schausi* (Costa Rica) (distorted on right side); 178, *eutainia* (Mexico: Veracruz State); 179, *leptophis* (allotype); 180, *elaphe* (Costa Rica); 181, *elaps* (Mexico: Morelos State); 182, *liopeltis* (Mexico: Nuevo Leon State). Scale line 4 mm (figs. 168-170), 2 mm (figs. 171-182).

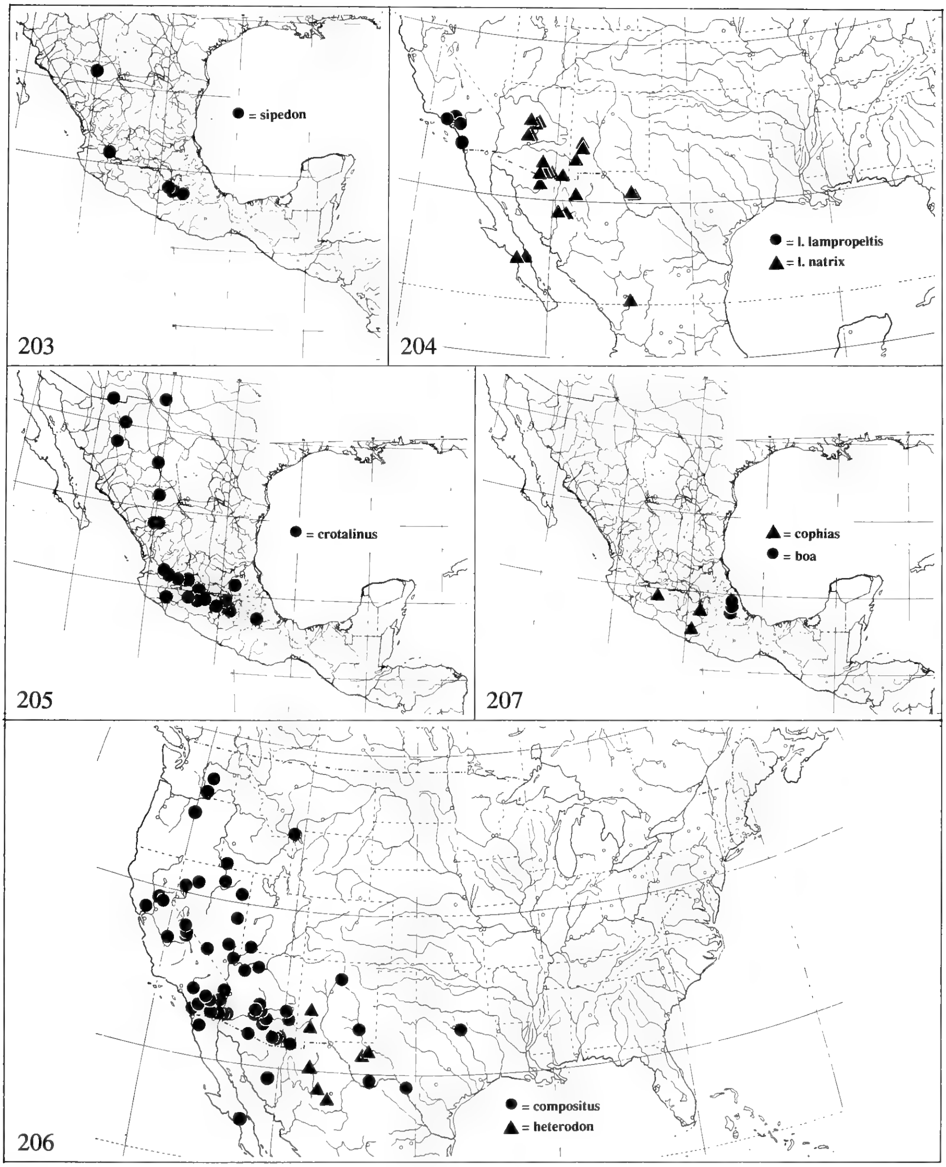


183. bothrops
184. viperinus
185. designatus
186. designatus
187. sipedon
188. sipedon
189. lampropeltis lampropeltis
190. lampropeltis natrix
191. crotalinus
192. crotalinus
193. heterodon
194. compositus
195. boa
196. boa
197. cophias

Figs. 183-197. Vulvar lamina, dorsal view. – 183, *bothrops* (allotype); 184, *viperinus* (Mexico: Veracruz State); 185, *designatus* (paralectotype); 186, *designatus* (Texas: Gonzales Co.); 187, *sipedon* (holotype); 188, *sipedon* (paratype); 189, *l. lampropeltis* (California: Ventura Co.); 190, *l. natrix* (allotype); 191, *crotalinus* (paralectotype); 192, *crotalinus* (Mexico: Jalisco State); 193, *heterodon* (allotype); 194, *compositus* (Arizona: Maricopa Co.); 195, *boa* (Mexico: Veracruz State); 196, *boa* (Veracruz State); 197, *cophias* (Mexico: Guerrero State). Scale line 2 mm.

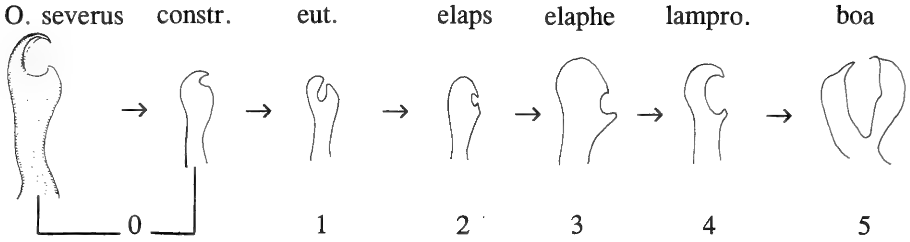


Figs. 198-202. Distribution patterns. – 198, *E. ophibolus* group; 199, *E. eutainia* group; 200, *E. elaps* group (in part); 201, *E. elaps* group (in part); 202, *E. designatus.*

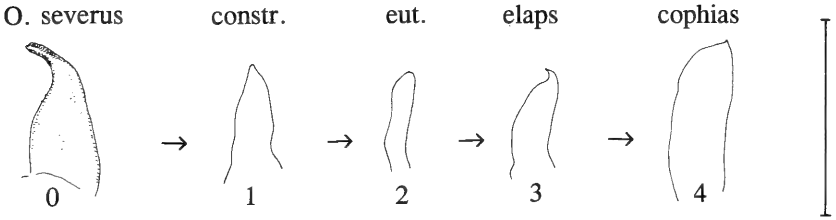


Figs. 203-207. Distribution patterns. 203, *E. sipedon*; 204, *E. lampropeltis*; 205, *E. crotalinus*; 206, *E. heterodon* and *E. compositus*; 207, *E. boa* and *E. cophias*.

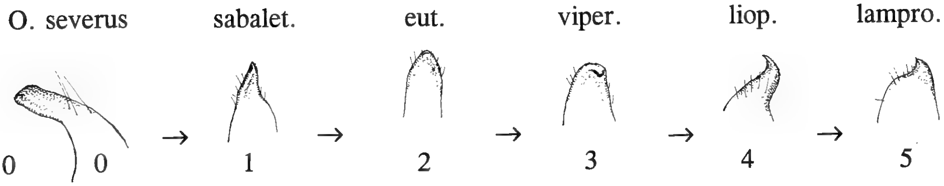
208

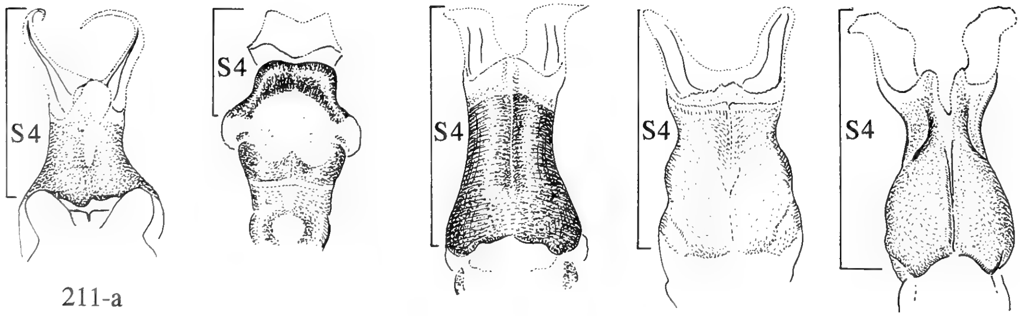


209



210





211-a Ophiogomphus severus

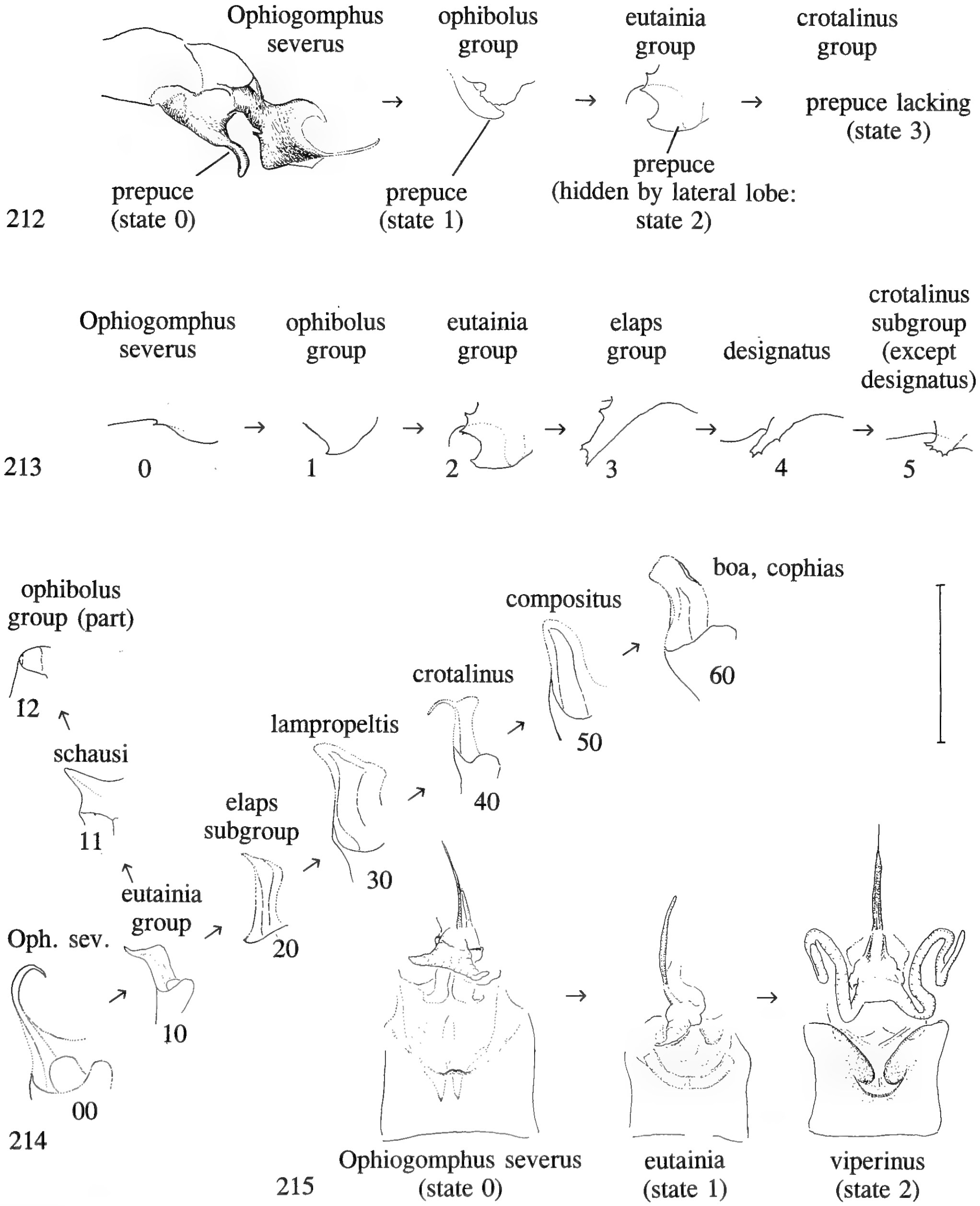
211-b tristani

211-c viperinus

211-d compositus

211-e boa

Figs. 208-211. – 208, morphocline of anterior hamule, character states 0-5; 209, morphocline of posterior hamule, character states 0-4; 210, morphocline of tip of posterior hamule, character states 0-5; 211, dorsal view of fourth segment of penis (S4); figs. 211a and 211b have 4th segment about as long as wide, figs. 211c-e about twice as long as wide. Scale line 2 mm (figs. 208-209); 1 mm (figs. 210-212).



Figs. 212-215. – 212, morphocline of prepuce of penis, character states 0-3; 213, morphocline of shape of lateral lobe, character states 0-5; 214, morphocline of cornua: character states 0-6 for character 19 and character states 0-2 for character 20; 215, morphocline of spermatheca in dorsal (internal) view character states 0-2 (figures show dorsal (internal) view of sternum 9 (including postlamellar ridge). Spematheca is dorsad of vulvar lamina). Scale line 1 mm (figs. 212, 215); 0.5 mm (figs. 213-214).

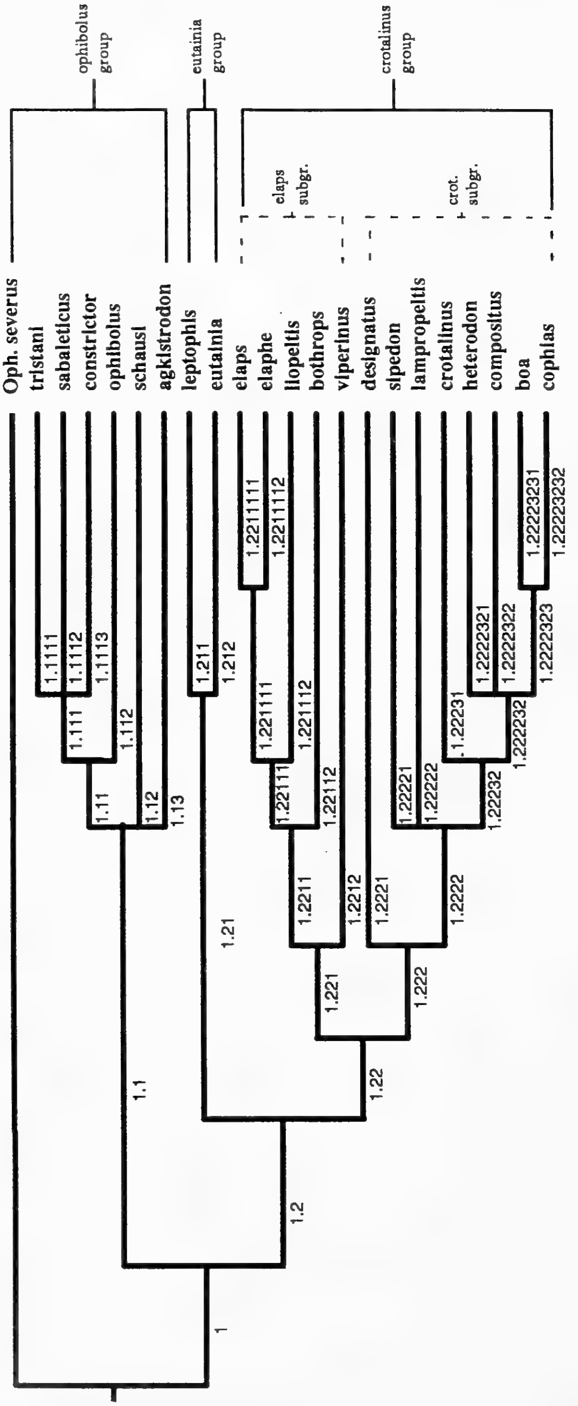


Fig. 216. cladogram.

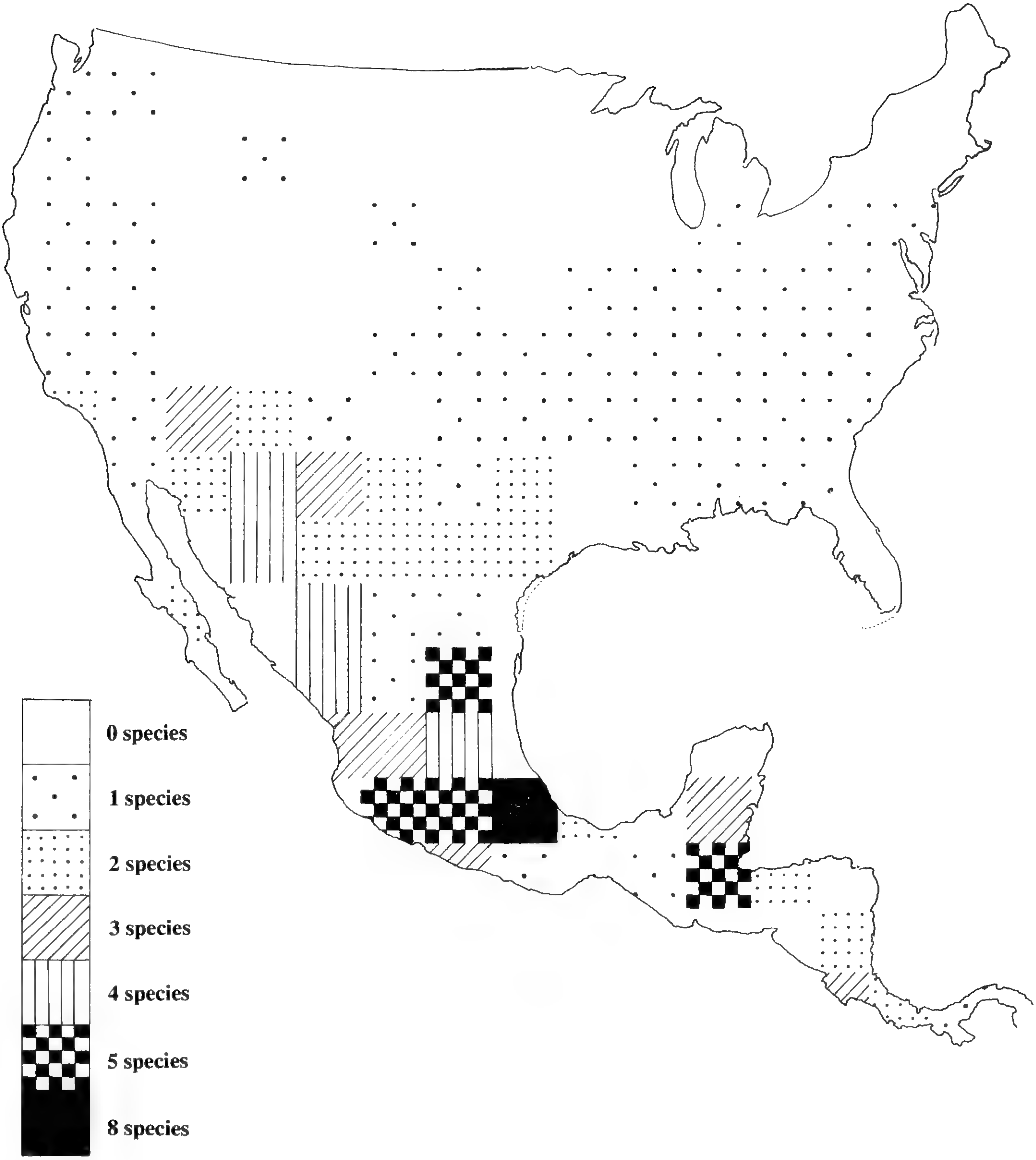
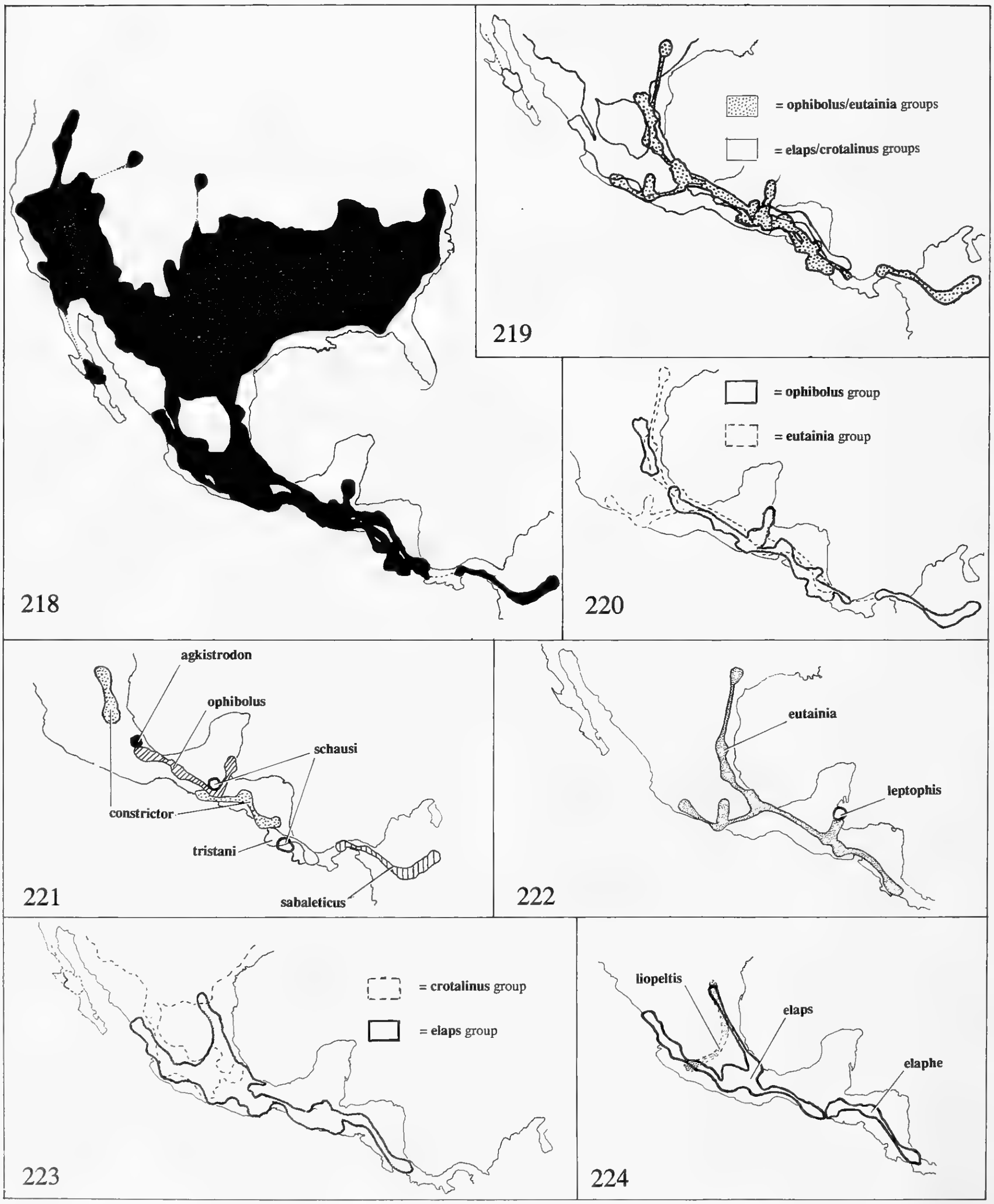
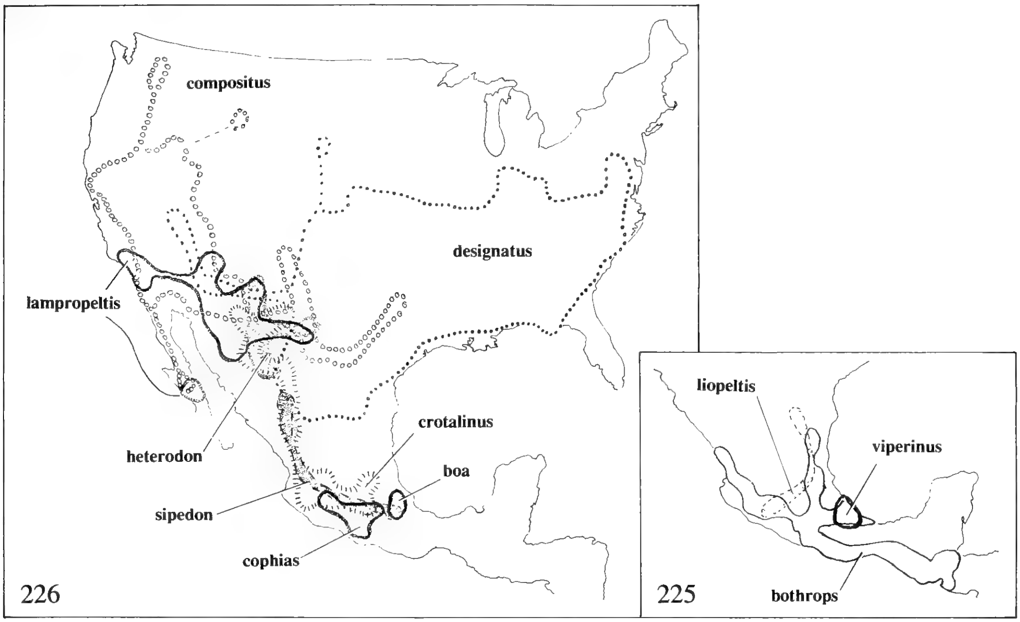
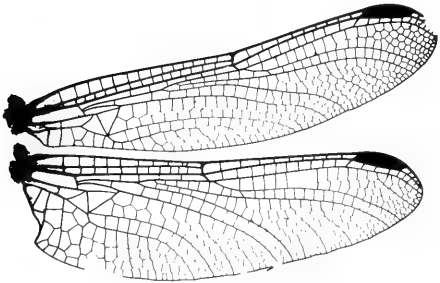


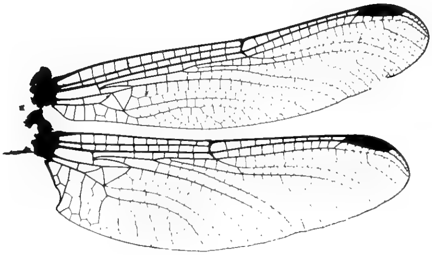
Fig. 217. geographic distribution of *Erpetogomphus* collected in the U. S. A., Mexico, and Central America. Each square is approximately 150 kilometers square.

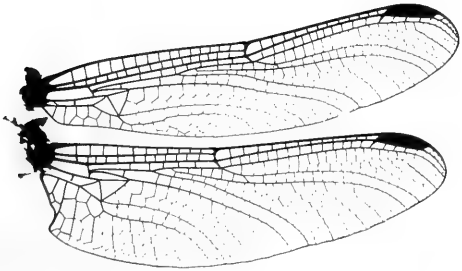


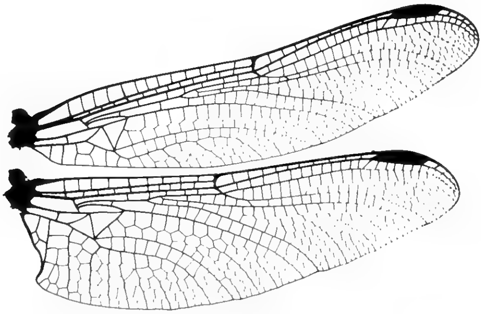
Figs. 218-224. – 218, Generalized track for genus *Erpetogomphus*; 219, generalized tracks for *Erpetogomphus ophibolus* / *eutainia* and *E. elaps* / *crotalinus* groups; 220, generalized tracks for *Erpetogomphus ophibolus* and *E. eutainia* groups; 221, tracks of species within the *Erpetogomphus ophibolus* group; 222, tracks of species within the *Erpetogomphus eutainia* group; 223, generalized tracks for *Erpetogomphus crotalinus* and *E. elaps* groups; 224, tracks of species within the *Erpetogomphus elaps* group (in part).




227. liopeltis


228. bothrops


229. viperinus


230. heterodon

Figs. 225-230. – 225, tracks of species within the *Erpetogomphus elaps* group (in part); 226, tracks of species within the *Erpetogomphus crotalinus* group; 227, pair of wings of *liopeltis* ♂ (Mexico: Nuevo Leon State); 228, idem, *bothrops* ♂ (Mexico: Nayarit State); 229, idem, *viperinus* ♂ (Mexico: Veracruz State); 230, idem, *heterodon* ♂ (N. Mexico: Grant Co.)

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THE PHYLOGENY OF THE SUBGENUS *TIPULA* (*SAVTSHENKIA*) (DIPTERA: TIPULIDAE), WITH SPECIAL REFERENCE TO THE WESTERN MEDITERRANEAN FAUNA

In memory of E. N. Savchenko (12.VII.1909 - 8.I.1994)

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, figs. 1-202, tabs. 1-5, appendices A-C. [ISSN 0040-7496]. Published 15 December 1994.

The phylogeny of the currently recognized 87 species and subspecies of the subgenus *Tipula* (*Savtshenkia* Alexander) (Diptera, Tipulidae) is discussed in reference to 87 morphological characters of the adults. The distribution of the species and subspecies of *Savtshenkia* is briefly outlined. Taxonomic novelties include the description of three new western Palaearctic species, viz. *alpha*, *omega*, and *trinacria*; the establishment of the synonymy of *broweri* Alexander under *fragilina* Alexander, *insignifica* Alexander under *invenusta* Riedel, *nebulipennis* Alexander under *alpium* Bergroth, *packardi* Alexander under *invenusta* Riedel, and *perparvula* Alexander under *ignobilis* Loew; the elevation of the subspecies *subsignata haennii* Dufour to species rank; and the removal of the species *convexifrons* Holmgren from *Savtshenkia*.

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Key words. – Diptera, Tipulidae, *Savtshenkia*, phylogeny, western Mediterranean.

As part of a research project on the historical biogeography of the western Mediterranean region, the phylogeny of the subgenus *Tipula* (*Savtshenkia* Alexander) is discussed. *Savtshenkia* as defined here, contains 87 described species and subspecies, of which 22 have a restricted distribution in the western Mediterranean. Special emphasis is laid on the establishment of the phylogenetic position of these western Mediterranean endemics, as they offer potential clues to a better understanding of the historical biogeography of the area.

The species constituting the subgenus *Savtshenkia* were formerly grouped in the *marmorata* species group of the genus *Tipula* Linnaeus (Alexander 1919a, 1919b et seqq.). The same assemblage of species has also been known as the *fragilis* group (Alexander 1934 et seqq.) and *obsoleta* group (Lackschewitz 1936). Usually, these species groups were referred to the subgenus *Oreomyza* Pokorny (Alexander 1934, Edwards 1931). Savchenko (1961), misinterpreting Riedel (1913) regarding the type species of *Pterelachisus* Rondani, synonymized *Oreomyza* under the latter taxon. Savchenko's lapsus resulted in the improper use of the name *Pterelachisus* for the species at present placed in *Savtshenkia*. Although Savchenko's reasoning was fallacious, Mannheims (1962a) showed that the synonymy of *Oreomyza* and *Pterelachisus* sensu Rondani in itself was valid and introduced the name *Savtshenkia* to replace *Pterelachisus* sensu Savchenko. As Mannheims omitted to denote the type species of this new taxon, *Savtshenkia* remained a nomen nudum until Alexander (1965a) designated *rufina* Meigen as the type species. (In the literature, a paper by Alexander published in the 1965 volume of the Philippine Journal of Science is usually cited as the relevant reference for the authorship of the name *Savtshenkia*. As the pertaining publication was actually issued August 9, 1966, Alexander's paper that appeared in Pacific Insects of June 20, 1965, should be accepted as the correct reference for the type designation.)

Savtshenkia has an essentially Holarctic distribution (fig. 1), with 65 species and subspecies occurring in the Palaearctic Region and eight in the Nearctic Region. Both regions have two species in common. In addition to the Holarctic members of the subgenus, five Oriental and 12 Afrotropical species and subspecies are known. The Oriental fauna of *Savtshenkia* has a single species in common with the Palaearctic fauna, the Afrotropical fauna shows no species overlap

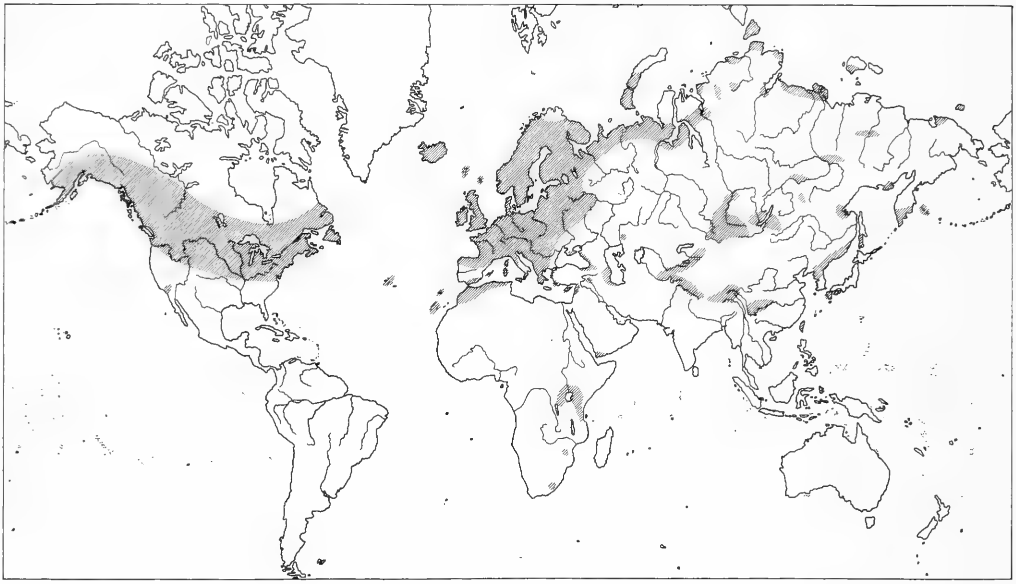


Fig. 1. Global distribution of the subgenus *Tipula* (*Savtshenkia*).

with that of any other biogeographical region. At the end of this paper a brief account of the distribution of the species of *Savtshenkia* is provided. I will present more detailed information on the distribution of the western Mediterranean species and their closest relatives in a forthcoming paper on the historical biogeography of the western Mediterranean. In Appendix A, three western Palaearctic species of *Savtshenkia* are described as new, five synonymies are established, while one subspecies is raised to species rank and one species is removed from the subgenus. The resulting list of species and subspecies of *Savtshenkia* as recognized in this paper is given in table 1.

Savchenko (1961, under *Pterelachisus*) and Theowald (1957, under *Oreomyza*, 1967, 1973, 1978) arranged the (western) Palaearctic members of *Savtshenkia* in a number of species groups. Theowald's 1957 and 1967 arrangements were based on characters of the preadult stages of western Palaearctic species and contained four species groups (table 2). Savchenko (1961) recognized five species groups plus a miscellaneous group within the fauna of the former USSR (table 3). Theowald's 1973/1978 classification of the adults of *Savtshenkia* in 14 species groups basically is a refinement of Savchenko's 1961 concept (table 3). The arrangements of both authors will be compared with the results of the present study in the 'Discussion of adopted phylogeny', below.

Material, methods and terminology

During the course of this investigation material representing 78 species and subspecies of *Savtshenkia* was examined (table 1). Most specimens used for the present study originated from the Institute for Systematics and Population Biology (Zoological Museum), Amsterdam. Supplementary material was studied during a short stay at the United States National Museum of Natural History, Smithsonian Institution, Washington D.C. In addition to this, material was borrowed from the following institutions: Academy of Natural Sciences, Philadelphia; Musée d'Histoire Naturelle, Neuchâtel; Natural History Museum, London; Staatliches Museum für Naturkunde, Stuttgart; United States National Museum of Natural History, Smithsonian Institution, Washington D.C.; Zoologiska Institutionen, Systematiska avdelningen, Lund.

The majority of specimens consisted of pinned material; in addition to this, material preserved in alcohol was studied from the collections in Amsterdam, Lund, and Neuchâtel.

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

Table 1. List of species and subspecies of *Tipula* (*Savtshenkia*) as recognized in this paper. Abbreviations: +: examined; -: not examined; u: unknown; Afro: Afrotropical Region; Nea: Nearctic Region; Or: Oriental Region; Pal: Palaearctic Region; Th., Duf. & Oost.: Theowald, Dufour & Oosterbroek.

	♂	♀	Region
aberdareica Alexander, 1956	+	u	Afro
a. ulugurica Alexander, 1962	u	-	Afro
akeleyi Alexander, 1956	+	u	Afro
alpha sp. n.	+	+	Pal
alpium Bergroth, 1888	+	+	Nea, Pal
asbolodes Speiser, 1909	+	-	Afro
aspromontensis Theowald, 1973	+	+	Pal
aster Theischinger, 1983	+	u	Pal
atlas Pierre, 1924	+	+	Pal
baltistanica Alexander, 1936	+	+	Or, Pal
benesignata Mannheims, 1954	+	+	Pal
boreosignata Tjeder, 1969	+	u	Pal
breviantennata Lackschewitz, 1933	+	+	Pal
caligo Alexander, 1956	+	+	Afro
cheethami Edwards, 1924	+	+	Pal
chrysocephala Mannheims, 1958	+	u	Afro
confusa Van der Wulp, 1887	+	+	Pal
corsosignata Th., Duf. & Oost. 1982	+	+	Pal
cyrnosardensis Th., Duf. & Oost. 1982	+	+	Pal
draconis Alexander, 1964	+	u	Afro
eleonorae Theischinger, 1978	+	u	Pal
elgonensis Alexander, 1956	+	u	Afro
eugeni Theowald, 1973	+	+	Pal
fragilina Alexander, 1919	+	+	Nea
fragilis Loew, 1863	+	+	Nea
gimmerthali Lackschewitz, 1925	+	+	Pal
g. mattheyi Theowald & Dufour, 1983	-	u	Pal
g. pteromaculata Th., Duf. & Oost. 1982	+	u	Pal
glaucocinerea Lundström, 1915	+	+	Pal
goriziensis Strobl, 1893	+	+	Pal
graciae Alexander, 1947	+	u	Nea
grisescens Zetterstedt, 1851	+	+	Pal
haennii Dufour, 1991 stat.n.	+	-	Pal
hancocki Alexander, 1956	+	+	Afro
hartigiana Th., Duf. & Oost. 1982	+	+	Pal
holoptera Edwards, 1939	+	+	Pal
ignobilis Loew, 1863	+	+	Nea
imperfecta Riedel, 1914	-	-	Afro
interserta Riedel, 1913	+	+	Pal
invenusta Riedel, 1919	+	-	Nea, Pal
i. microinvenusta Dufour, 1990	+	+	Pal
i. subinvenusta Slípka, 1950	+	+	Pal
jeekeli Mannheims & Theowald, 1959	+	+	Pal
kiushiuensis Alexander, 1925	+	+	Pal
koreana Alexander, 1934	+	+	Pal
letifera Alexander, 1951	-	u	Pal
limbata Zetterstedt, 1838	+	+	Pal
lundbladi Mannheims, 1962	+	+	Pal
macaronesica Savchenko, 1961	+	u	Pal
mannheimsi Theowald, 1973	+	u	Pal
minuscula Savchenko, 1971	-	-	Pal
mohriana Alexander, 1954	+	+	Pal
multipicta Becker, 1908	+	+	Pal
nephrotomoides Alexander, 1924	+	+	Afro
n. invariegata Alexander, 1956	u	+	Afro
nielseni Mannheims, & Theowald, 1959	+	+	Pal
nivalis Savchenko, 1961	-	-	Pal
obsoleta Meigen, 1818	+	+	Pal
odontostyla Savchenko, 1961	+	-	Pal
omega sp. n.	+	u	Pal
ornata Theowald & Oosterbroek, 1987	+	+	Pal
pagana Meigen, 1818	+	+	Pal
pechlaneri Mannheims & Theowald, 1959	+	+	Pal
persignata Alexander, 1945	+	u	Pal
p. tofina Alexander, 1945	+	u	Pal
phoroctenia Alexander, 1919	+	+	Nea
postposita Riedel, 1919	+	-	Pal
productella Alexander, 1928	-	u	Nea
rufina Meigen, 1818	+	+	Pal
r. maderensis Lackschewitz, 1936	+	+	Pal
sardosignata Mannheims & Theowald, 1959	+	+	Pal
sciadoptera Alexander, 1964	+	u	Or
serrulifera Alexander, 1942	+	+	Pal
signata Staeger, 1840	+	+	Pal
simulans Savchenko, 1966	+	+	Pal
sordidipes Alexander, 1961	+	+	Or
staegeri Nielsen, 1922	+	+	Pal
subalpium Savchenko, 1961	-	u	Pal
subnodicornis Zetterstedt, 1838	+	+	Pal
subsignata Lackschewitz, 1933	+	+	Pal
s. cazorla Dufour, 1991	+	u	Pal
subvafra Lackschewitz, 1936	+	+	Pal
tetragramma Edwards, 1928	-	u	Or
trinacria sp. n.	+	+	Pal
tulipa Dufour, 1983	+	u	Pal
venerabilis Alexander, 1936	+	u	Or
villeneuvii Strobl, 1909	+	+	Pal

was carried out using a Wild stereomicroscope with a magnification of up to 100 times. 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 a drop of glycerol. The microvial was pinned with the relevant specimen.

The parsimony program HENNIG86, version 1.5 (Farris 1988) was used to analyse the phylogeny. More information on the calculation procedures followed is given in 'Discussion of adopted phylogeny'.

The terms for the structures of *Savtshenkia* as used in the character discussion are in general in accordance with the terms employed by McAlpine (1981), with a few additions for particular features of the Tipulidae of the study group. The terms are explained in figs. 3-6, 12, and 58. It should be noted that I consider the structure lateral of the gonapophysis in *Savtshenkia* homologous with the fragmentum

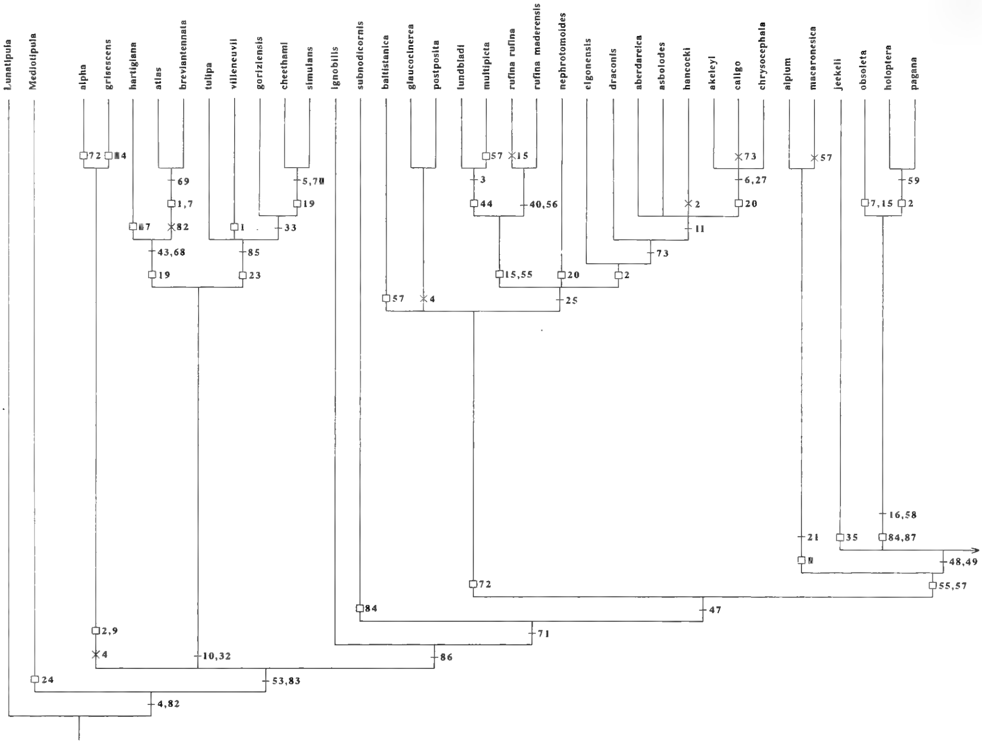


Fig. 2. Strict consensus tree of 14 equally parsimonious trees derived after successive weighting for the species and subspecies of *Tipula* (*Savtshenkia*). –: synapomorphy; □: homoplasy; ✕: reversal.

in the sense of Rees & Ferris (1939) and Frommer (1963) and name it accordingly (figs. 3, 4). Mannheims (1951) denoted the same sclerite A9s (appendage of sternite 9). Suture x is employed in the sense of Neumann (1958). A recent overview of the morphology of the terminalia of Tipulidae was given by Tangelder (1985) to which paper the reader is referred to for further details.

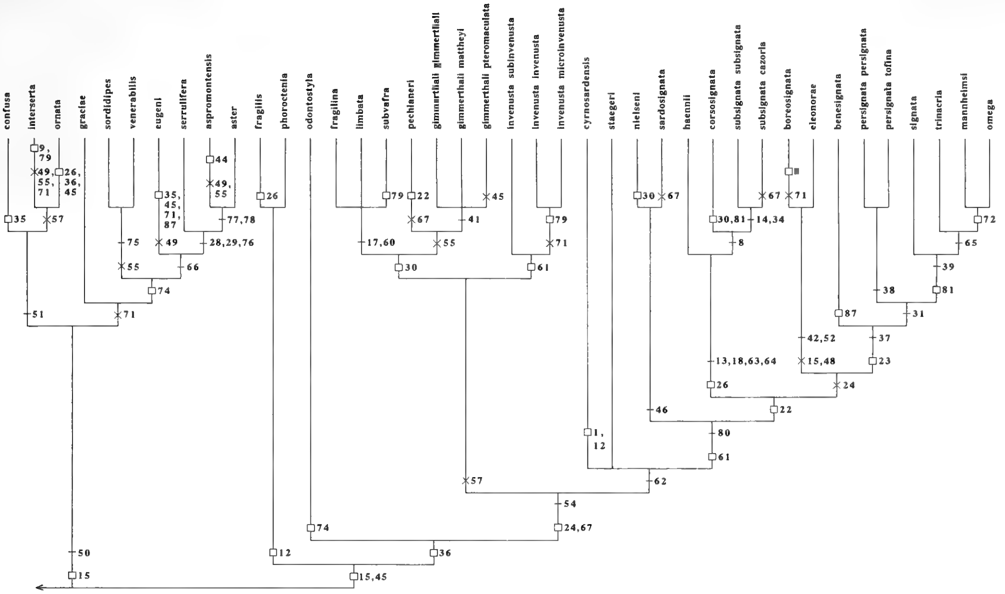
Acronyms used throughout the text are the following:

BMNH: Natural History Museum, London, England; BSNH: Boston Society of Natural History, Boston, Massachusetts, U.S.A.; CNCI: Canadian National Collection, Biosystematics Research Centre, Ottawa, Ontario, Canada; MCZC: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, U.S.A.; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MRAC: Koninklijk Museum voor Midden Afrika, Tervuren, Belgium; USNM: United States National Museum, Smithsonian Institution, Washington D.C., U.S.A.; ZIAS: Zoological Institute, Russian Academy of Sciences, St. Petersburg, Russia; ZMAN: Institute for Systematics and Population Biology, Department of Entomology, Zoological Museum, Amsterdam, the Netherlands.

BIOLOGY

In general, the members of *Savtshenkia* are adapted to either mountainous, high latitudinal, or autumnal conditions. Within these limits, adults of the respective species of *Savtshenkia* show a wide variety of preferred biotopes. They can be found in alpine *Rhododendron* assocations, the heath zone at about 3300 m, mountainous wet or dry *Pinus* forests and mixed woods, low woods, low moorlands, marshes, bogs, and gardens. The species may occur in the vegetation near the sources and on the banks of streams, on boulders in streams, on dripping rocks, and in the splash zone of cascades (Alexander 1961, Audcent 1932, Brunhes & Dufour 1992, Bryce 1956, Coulson 1959, 1962, Dufour 1983, 1986, 1990, 1991, Mannheims & Pechlaner 1963, Stubbs 1992, Theowald 1973, Theowald, Dufour & Oosterbroek 1982).

The larvae of the species of *Savtshenkia* are associated with mosses and liverworts. They are recorded



from mosses on stones and logs in and along cold streams, from wet moorland mosses and mosses of cold bogs of tundra and high mountains, as well as from relatively dry mosses on walls, stones and trees (Gelhaus 1986).

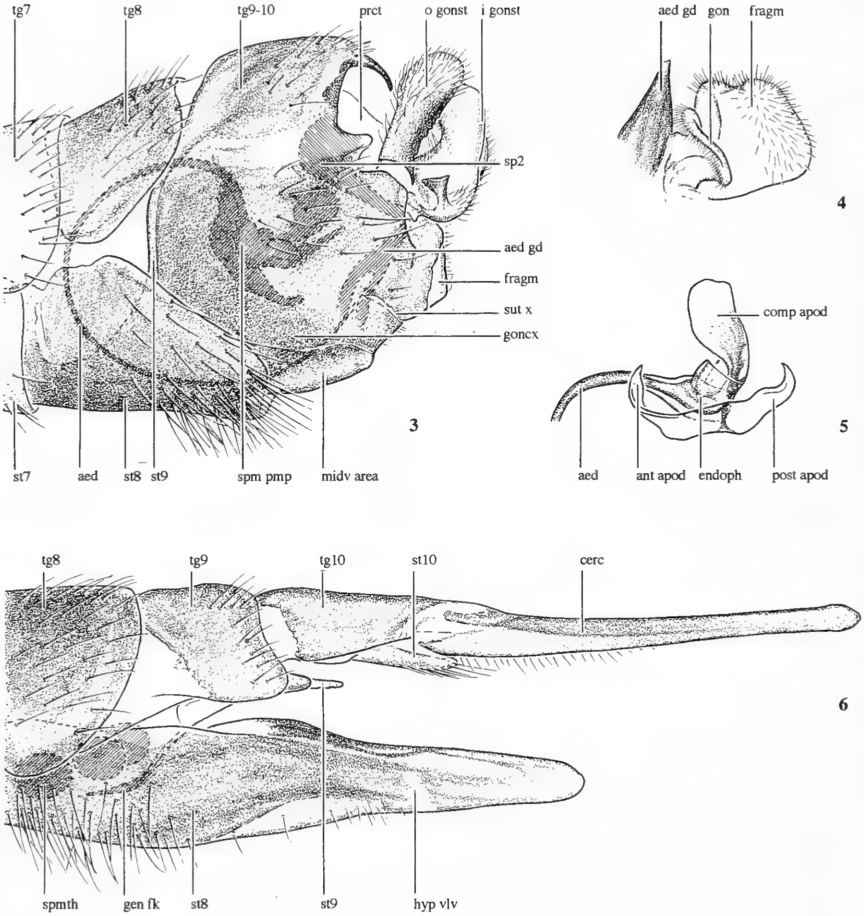
As in most Tipulidae, the majority of species of *Savtshenkia* have a one-year life cycle. A few are, or appear to be, bivoltine (viz. *alpium*, *breviantennata*, *rufina rufina*, and *rufina maderensis*; Dufour 1986, Mannheims 1951, Theowald 1973). On the other hand, Lantzov (1982) suggested a long term larval development for the arctic species *glaucocinerea* of up to six years. [Multi-annual life cycles are known of other species of Tipulidae with a northerly distribution; see Pritchard (1983) for an overview of life cycles in Tipulidae.]

Details on the copulation of a few species of *Savtshenkia* were given by Hemmingsen (1954, 1962; viz. *limbata*, *signata*, *staegeri*, and *subsignata*). Hemmingsen (1952) provided a short account on oviposition of the species *confusa* (as *marmorata*) and *rufina*.

SYSTEMATIC POSITION

The species and subspecies of *Savtshenkia* can be distinguished from other Tipulidae by the following derived character states: (1) Adult, male terminalia: sp2 medially blackish sclerotized (character 53, below); (2) Adult, female terminalia: dorsal margin of hypogynial valve blackish sclerotized (character 83, below); (3) Larva: eight anal papillae arranged in four pairs. The number of anal papillae in other groups of Tipulidae is either six, four, two, or zero (Gelhaus 1986, Theowald 1957, 1967). As both adult characters occur also in other genera and subgenera of Tipulidae, the larval character seems to offer the best criterion to distinguish *Savtshenkia* from the remainder of Tipulidae.

The systematic position of *Savtshenkia* within the Tipulidae is not yet fully established. Savchenko (1966, 1979, 1983) placed *Savtshenkia* next to the subgenus *Tipula* (*Mediotipula* Pierre), a relationship substantiated by the presence in the female pupa of a laterally placed small tubercle at the apex of the sheath of the hypogynial valve (see Theowald 1957, 1967). In species of the genus *Dolichopeza* Curtis, the sheath of the hypogynial valve is also provided with an extension, but here the extension is much bigger than in *Mediotipula* and *Savtshenkia*, and is placed near midlength of the sheath (Byers 1961, Theowald 1957, 1967, Wood 1952). *Dolichopeza* probably is not closely related to *Mediotipula* and *Savtshenkia*, and the extension of the sheath of the hypogynial



Figs. 3-6. *Tipula* (*Savtshenkia*) *rufina rufina*. – 3, male terminalia, lateral view; 4, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 5, sperm pump, lateral view; 6, female terminalia, lateral view.
Abbreviations: aed: aedeagus; aed gd: aedeagal guide; ant apod: anterior apodeme; cerc: cercus; comp apod: compressor apodeme; endoph: endophallus; fragm: fragmentum; gen fk: genital fork; gon: gonapophysis; goncx: gonocoxite; hyp vlv: hypogynial valve; i gonst: inner gonostylus; midv area: midventral area: o gonst: outer gonostylus; post apod: posterior apodeme; prct: proctiger; sp2: lateral part of genital bridge; spm pmp: sperm pump; spmth: spermatheca; st7 etc.: sternite 7 etc.; sut x: suture x; tg7 etc.: tergite 7 etc.

valve in *Dolichopeza* supposedly is not homologous to that of *Mediotipula* and *Savtshenkia*. Theowald (1978) accepted Savchenko's views regarding a sister group relationship of *Mediotipula* and *Savtshenkia*. Another character state which could be indicative of a close phylogenetic relationship of *Mediotipula* and *Savtshenkia* is the shape of wing cell m1. In both subgenera this cell is 'bell-shaped', narrowing towards the wing margin, whereas it usually widens towards the wing margin in other Tipulidae (character 4, below). The genital fork in both *Mediotipula* and *Savtshenkia* is broadest at its anterior part, a presumed apomorphy within Tipulidae (character 82, below). *Mediotipula* at present contains 12 recognized species with a primarily Mediterranean distribution (Oosterbroek & Theowald 1992).

Conflicting with a presumed sister group relationship of *Mediotipula* and *Savtshenkia* is the presence of a separate sclerite lateral of the gonapophysis in *Savtshenkia*. As stated above (section 'Material, methods and terminology'), I consider this sclerite homologous with the so-called fragmentum as found in other Tipulidae. The presence of a fragmentum is a derived character state within the Tipulidae and could substantiate a phylogenetic relationship of *Savtshenkia* with the complex of *Lunatipula* and allies (here after referred to as the *Lunatipula* group). The fragmentum is absent in *Mediotipula.* The *Lunatipula* group contains about 1200 species of Tipulidae, that is circa one fourth of the total number of species of the family. Besides the subgenus *Lunatipula* Edwards, the *Lunatipula* group includes the following subgenera of *Tipula*: *Beringotipula* Savchenko, *Eremotipula* Alexander, *Eumicrotipula* Alexander, *Hesperotipula* Alexander, *Labiotipula* Alexander, *Lindnerina* Mannheims, *Odonatisca* Savchenko, *Pectinotipula* Alexander, *Pterelachisus* Rondani, *Ramatipula* Alexander, *Serratipula* Alexander, *Setitipula* Alexander, *Triplicitipula* Alexander, and *Vestiplex* Bezzi. The phylogenetic relationships of the species of the *Lunatipula* complex are still largely unresolved, but it is nevertheless clear that not all of the subgenera in their present delimitation represent monophyletic taxa (e.g., *Lunatipula* and *Pterelachisus*).

In the discussion of the characters, I will refer to the species of the *Lunatipula* group and *Mediotipula* as outgroups of *Savtshenkia.*

CHARACTER DISCUSSION

In this section I will discuss the characters used in the phylogenetic analysis of *Savtshenkia.* Preceding a more detailed discussion of each character, a couplet shortly defines the alternative character states and gives their codes. The character state matrix is presented in table 4. Although I did not examine the male of *gimmerthali mattheyi*, this subspecies is, according to its authors, very similar to the nominotypical form, differing only in minute discriminating characters. Therefore, I feel safe to copy the score of the male characters of *gimmerthali gimmerthali* for this subspecies. In the discussion of the characters below, the resulting strict consensus tree (fig. 2) will often be mentioned to point out the species which show a particular character state. I have done this in order to save space and for convenience, rather than presenting a list of species for each of the distinguished states. The results of the phylogenetic analysis are discussed in the next section. Species and subspecies of *Savtshenkia* which for various reasons are not included in the character discussion below, are dealt with in Appendix B. A list of autapomorphies of the species and subspecies of *Savtshenkia* is presented in Appendix C.

Antenna

1. – Flagellum: (0) well developed in male; (1) short, about the length of head or shorter.

The male antenna of most species of *Savtshenkia* is well developed and relatively long, with the flagellomeres being about 2.5 times as long as their diameter at the greatest width, or longer (figs. 7, 11, 171). A similar state represents the presumed groundplan condition of the *Lunatipula* group and *Mediotipula.* A few members of *Savtshenkia* are characterized by a conspicuously short flagellum in the male. The flagellomeres of the pertaining species are about two times as long as their diameter or shorter (fig. 8). The species with exceptionally short male antennae are *atlas*, *breviantennata*, *cyrnosardensis*, and *villeneuvii.*

2. – Flagellum: (0) male flagellomeres well developed; (1) male flagellomeres longer than standard length.

As noticed under the previous character, the flagellomeres of the males of *Savtshenkia* are usually about 2.5 times as long as their diameter at greatest width or slightly longer. Flagellomeres distinctly longer than this are found in *alpha*, *grisescens*, *holoptera*, *pagana*, and most Afrotropical species (the clade *elgonensis* to *chrysocephala*; figs. 9, 10, 152). In the pertaining species, the male flagellomeres are about 5 to 6.5 times as long as wide. The only Afrotropical species of *Savtshenkia* of which the male antennae are not conspicuously long are *hancocki* and *nephrotomoides* (and the unexamined *imperfecta* which doubtfully belongs to *Savtshenkia*; see Appendix B).

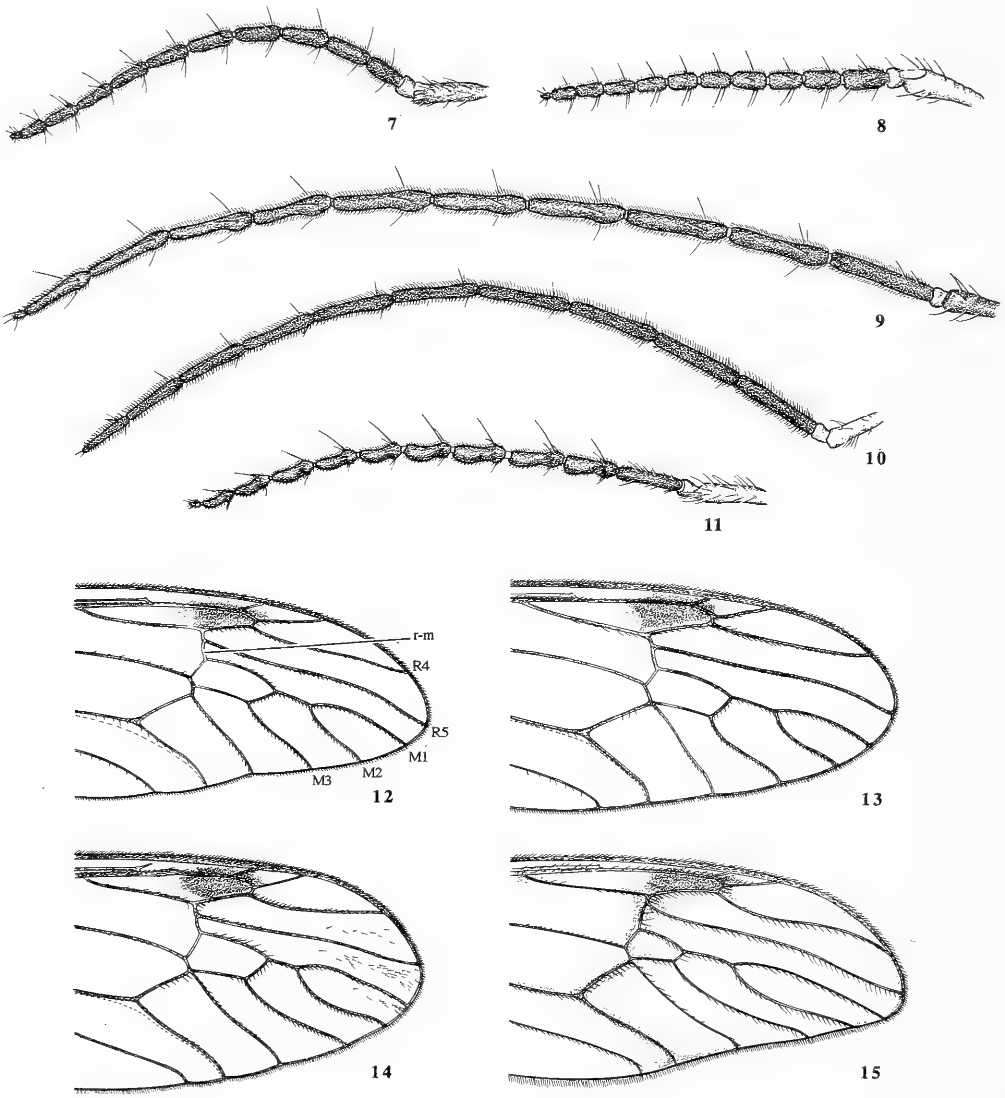
3. – Flagellum: (0) male flagellomeres with slightly enlarged base, remainder cylindrical; (1) flagellomeres more or less reniform.

In the genus *Tipula* sensu lato, the flagellum is usually composed of eleven segments of which the intermediate ones have a slightly bulbous base and a cylindrical apical part (figs. 7-10, 152, 171). This character state probably represents the groundplan condition of the *Lunatipula* group and *Mediotipula.* The same state is also found in most species of *Savtshenkia.* The species *lundbladi* and *multipicta* differ from the other species of *Savtshenkia* by having the intermediate flagellomeres more or less reniform (fig. 11). In the *Lunatipula* group, a similar form of the flagellomeres is present in most species of the subgenus *Vestiplex.* These species appear, however, to represent a more derived group within *Vestiplex.*

Wing

4. – Cell m1 shape: (0) widening towards wing margin; (1) constricted before wing margin.

In the Tipulidae veins M1 and M2, enclosing cell m1, usually diverge towards the wing margin (fig. 12). This situation probably represents the groundplan condition of the *Lunatipula* group, which contains only a few species that have cell m1 constricted near the margin of the wing. In most species of *Mediotipula*, cell m1 is bell-shaped or paunchy ('bauchig', Mannheims & Pechlaner 1963; Theowald 1973) with veins M1 and M2 approaching towards

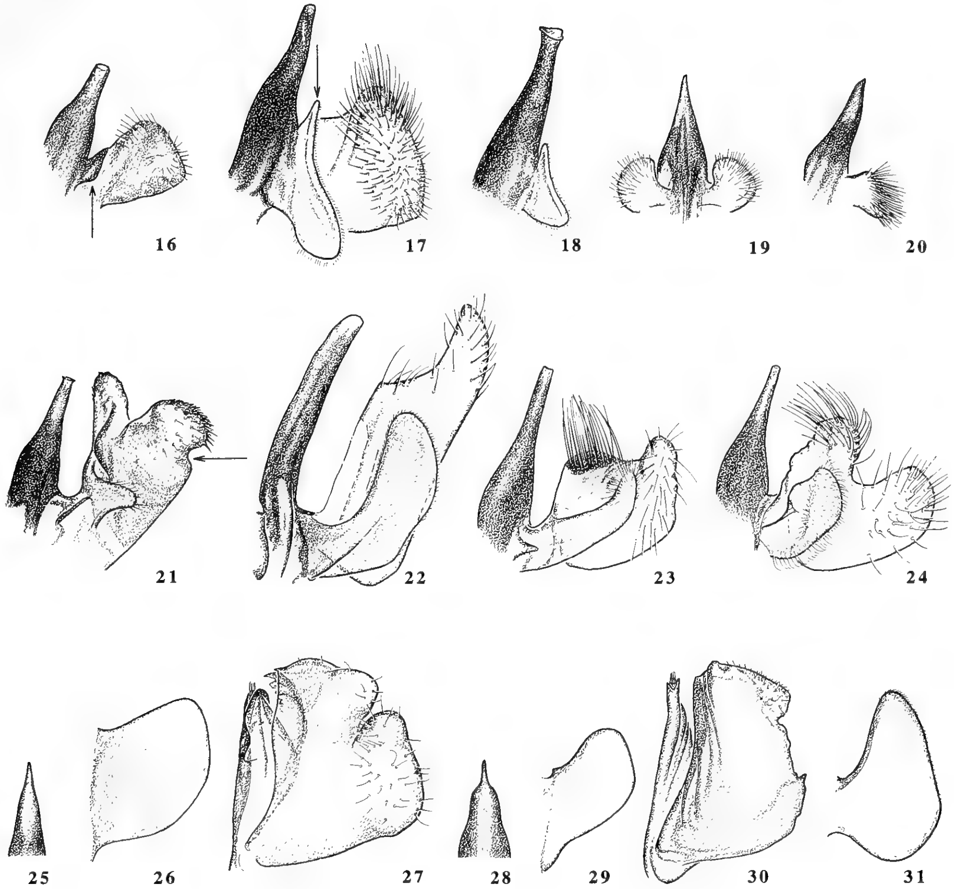


Figs. 7-15. – 7-11, male antenna; 7, *Tipula* (*Savtshenkia*) *hartigiana*; 8, *T.* (*S.*) *atlas*; 9, *T.* (*S.*) *grisescens*; 10, *T.* (*S.*) *elgonensis*; 11, *T.* (*S.*) *lundbladi*; 12-15, tip of wing; 12, *T.* (*S.*) *grisescens*; 13, *T.* (*S.*) *goriziensis*; 14, *T.* (*S.*) *cheethami*; 15, *T.* (*S.*) *akeleyi*. Abbreviations: M1 etc.: medial vein 1 etc.; R4 etc.: radial vein 4 etc.; r-m: radial-medial crossvein.

the margin of the wing, a state which probably represents the groundplan condition of *Mediotipula*. The majority of species of *Savtshenkia* also show this latter character state (figs. 13-15). Only a few species of *Savtshenkia* have veins M1 and M2 diverging towards the wing tip, viz. *alpha*, *glaucocinerea*, *grisescens*, and *postposita*. The species *subnodicornis* usually has cell m1 narrowing, but specimens of this species are known which show a widening cell m1.

5. – Cells of wing tip: (0) membrane covered with microtrichia only; (1) membrane partly covered with macrotrichia.

Most species of Tipulidae have the membrane of the wing tip covered with microtrichia only, appearing bare under low magnification (figs. 12, 13, 15). This situation is found in the species of the *Lunatipula* group, *Mediotipula*, and in most species of *Savtshenkia*. The species *cheethami* and *simulans* are



Figs. 16-31. – 16, *Tipula* (*Savtshenkia*) *grisescens*, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 17, *T.* (*S.*) *hartigiana*, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 18, *T.* (*S.*) *atlas*, aedeagal guide with right gonapophysis, posteromedial view; 19, *T.* (*S.*) *draconis*, aedeagal guide with gonapophyses, ventral view after microscopic slide holotype; 20, *T.* (*S.*) *aberdareica*, aedeagal guide with right gonapophysis, posteromedial view; 21, *T.* (*S.*) *obsoleta*, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 22, *T.* (*S.*) *fragilis*, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 23, *T.* (*S.*) *limbata*, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 24, *T.* (*S.*) *pechlaneri*, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 25-27, *T.* (*S.*) *haennii*, 25, aedeagal guide, tip, posterior view; 26, right gonapophysis, medial view; 27, right fragmentum, posteromedial view; 28-30, *T.* (*S.*) *corsosignata*, 28, aedeagal guide, tip, posterior view; 29, right gonapophysis, medial view; 30, right fragmentum, posteromedial view; 31, *T.* (*S.*) *subsignata subsignata*, right gonapophysis, medial view.

unique within *Savtshenkia* by having macrotrichia on the membrane of the wing tip. The macrotrichia cover the wing to a larger extent in *simulans* than in *cheethami*. The density of the macrotrichia is also higher in the former species. Macrotrichia are usually restricted to cells r4, r5, and m1 in *cheethami* (fig. 14), while in *simulans* cell m2 and the tip of cell m3 are also provided with macrotrichia.

6. – Crossvein r-m: (0) apical section directed towards wingtip, or at most transverse to longitudinal axis of wing; (1) apical section directed towards base of wing.

In Tipulidae crossvein r-m usually lies in an oblique position relative to the longitudinal axis of the wing, with its apical part directed towards the wing tip. This situation is found in the species of the *Lunatipula* group, *Mediotipula*, and in the majority of species of *Savtshenkia* (figs. 12-14). Three species of *Savtshenkia* have the apical end of r-m directed towards the base of the wing, viz. *akeleyi*, *caligo*, and *chrysocephala* (fig. 15).

Male terminalia

7. – Aedeagal guide, apex: (0) tapering towards tip; (1) at tip with flaring rim.

As is usual in the Tipulidae, the apex of the aedeagal guide is the narrowest part of this structure in the species of the *Lunatipula* group, *Mediotipula*, and the majority of species of *Savtshenkia* (figs. 4, 16, 17, 19, 20, 22-25, 28, 162, 182, 194). The species *atlas*, *breviantennata*, and *obsoleta* have the apex of the aedeagal guide bent outwards as a flaring rim (figs. 18, 21).

8. – Aedeagal guide, apex: (0) gradually tapering towards tip; (1) subapically abruptly narrowed, terminating in a slender point.

The aedeagal guide in Tipulidae normally gradually narrows towards its apex, as it does in almost all species of *Savtshenkia* (caudal view, fig. 25). The apex of the aedeagal guide of *corsosignata*, *subsignata subsignata*, and *subsignata cazorla* differs from that of the other species of *Savtshenkia* by the abruptly constricted apex which terminates in a slender tip (fig. 28).

9. – Aedeagal guide, gonapophysis: (0) well developed; (1) very short or almost completely absent.

Gonapophyses are usually well developed in the Tipulidae, a state which probably represents the groundplan condition of the *Lunatipula* group and *Mediotipula*. The majority of species of *Savtshenkia* also have well developed gonapophyses which occur in a wide range of sizes and shapes (figs. 4, 17-24, 26, 29, 31, 182, 194). The gonapophyses are very short or almost completely absent in the species *alpha*, *alpium*, *boreosignata*, *grisescens*, *interserta*, and *macaronesica* (figs. 16, arrow, 162).

10. – Aedeagal guide, gonapophysis: (0) dorsal margin evenly fused with base of aedeagal guide; (1) anterodorsally slightly extended, thus with free-lying dorsal tip.

In general, the dorsal margin of the gonapophysis in the Tipulidae gradually merges with the base of the aedeagal guide. This situation probably represents the groundplan condition of the *Lunatipula* group and *Mediotipula*. The gonapophyses of most species of *Savtshenkia* also show this character state (figs. 16, 21-24, 162, 182, 194). The species of the clade *hartigiana* to *simulans* are characterized by their typically shaped gonapophyses, which differ from the gonapophyses of the other species of *Savtshenkia* by the presence of a free anterodorsal extension (figs. 17, arrow, 18).

11. – Aedeagal guide, gonapophysis: (0) pubescent or short haired; (1) long haired.

The covering of the gonapophyses in the Tipulidae usually consists of pubescence or short hairs, as is the presumed groundplan state of the *Lunatipula* group and *Mediotipula*. A similar condition is found in the majority of species of *Savtshenkia* (figs. 4, 17-19, 21-24). A number of Afrotropical species of *Savtshenkia* are distinguished from the remainder of the subgenus by the dense and elongate hairing of the gonapophyses, viz. *aberdareica*, *akeleyi*, *asbolodes*, *caligo*, *chrysocephala*, and *hancocki* (fig. 20).

12. – Aedeagal guide, gonapophysis: (0) present, variously shaped; (1) a large and elongate structure.

The gonapophyses of the Tipulidae show a wide range of shapes. When present, they are usually well developed and rather slender. This is the state that occurs in most of the species of *Savtshenkia* and is the presumed groundplan condition of its outgroups (-figs. 4, 17-21, 23, 24, 182, 194). The Nearctic species *fragilis* and *phoroctenia* differ from the majority of species of *Savtshenkia* by their extremely large and elongate gonapophyses (fig. 22). The only other species of *Savtshenkia* with similarly enlarged gonapophyses is the western Mediterranean *cyrnosardensis*.

13. – Aedeagal guide, gonapophysis: (0) a relatively slender structure; (1) a large blade.

As noted under the previous character, the plesiomorphous condition of the gonapophyses in *Savtshenkia* is probably represented by a well developed, rather slender structure (figs. 4, 17-21, 23, 24, 182, 194). Large mediolaterally flattened gonapophyses are found in *corsosignata*, *haennii*, *subsignata subsignata*, and *subsignata cazorla* (figs. 26, 29, 31; see also next character).

14. – Aedeagal guide, gonapophysis: (0) at apex at most moderately enlarged; (1) dorsally and ventrally extended and thus widening towards broad apex.

The two subspecies *subsignata subsignata* and *subsignata cazorla* are characterized by their expanded gonapophyses (fig. 31). This character state corresponds with character 6 of Dufour (1991).

15. – Aedeagus: (0) short, directly curving from sperm pump to aedeagal guide, anteriorly reaching as far as abdominal segment 8; (1) elongate, anteriorly running to segment 7 or beyond.

A relatively short aedeagus which loops in the median sagittal plane from the sperm pump through abdominal segment 8 and from there to the aedeagal guide, is the presumed groundplan state of this feature in the *Lunatipula* group. The species of *Mediotipula* also show this character state, as do a number of species of *Savtshenkia* (figs. 3, 155). Other species of *Savtshenkia* have a longer aedeagus. The aedeagus in these species reaches anteriorly at least to segment 7 and often lies coiled inside the abdomen (figs. 173, 185). The species involved constitute the clades *confusa* to *aster* and *fragilis* to *omega*. Extremely long aedeagi were found in *corsosignata*, *ornata*, and *staegeri*, species in which the aedeagus reaches abdominal segment 1. The species pair *boreosignata* and *eleonorae* is characterized by a peculiarly modified aedeagal complex (character 52). Although belonging to the clade *fragilis* to *omega*, they have a short aedeagus.

16. – Fragmentum: (0) either absent, or posterior margin convex or slightly concave; (1) posterior margin subapically with sharp emargination.

The fragmenta of the species of the *Lunatipula* group and *Savtshenkia* occur in a diversity of forms. Usually, the posterior margin near the dorsal tip of the structure is convex. This is the presumed groundplan condition of the *Lunatipula* group and the common character state in *Savtshenkia* (figs. 4, 16, 17, 22-24, 27, 30, 162, 182, 194). (The fragmentum is absent in the species of *Mediotipula*.) The fragmenta of the species *holoptera*, *obsoleta*, and *pagana* differ from the standard situation of *Savtshenkia* by the presence of a distinct emargination just below the dorsal apex (fig. 21, arrow).

17. – Fragmentum: (0) either absent, or anterior part sclerotized as the remainder of the structure; (1) anterior part dorsally blackish sclerotized.

In general, the fragmentum is yellowish-brown in colour and uniformly sclerotized in the species of the *Lunatipula* group and *Savtshenkia* (figs. 4, 16, 17, 21, 22, 24, 162, 182, 194). A unique state is found in the species *fragilina*, *limbata*, and *subvafra*, where the dorsal margin of the anterior part of the fragmentum is blackish sclerotized (fig. 23).

18. – Fragmentum: (0) either absent, or anterior part a rounded lobe; (1) anterior part a separate anterocaudally flattened extension with slender tip.

The fragmentum consists of a single undivided sclerite in the species of the *Lunatipula* group and most species of *Savtshenkia* (figs. 4, 16, 17, 21-24, 162, 182, 194). In *corsosignata*, *haennii*, *subsignata subsignata*, and *subsignata cazorla*, the anterior part of the fragmentum is characteristically modified in a slender tipped structure which stands apart from the posterior part (figs. 27, 30). The few hairs of the brush on top of the anterior part of the fragmentum are very short in these four taxa.

19. – Gonocoxite, midventral area: (0) variously shaped, usually tumescent; (1) with cone-shaped membranous extension.

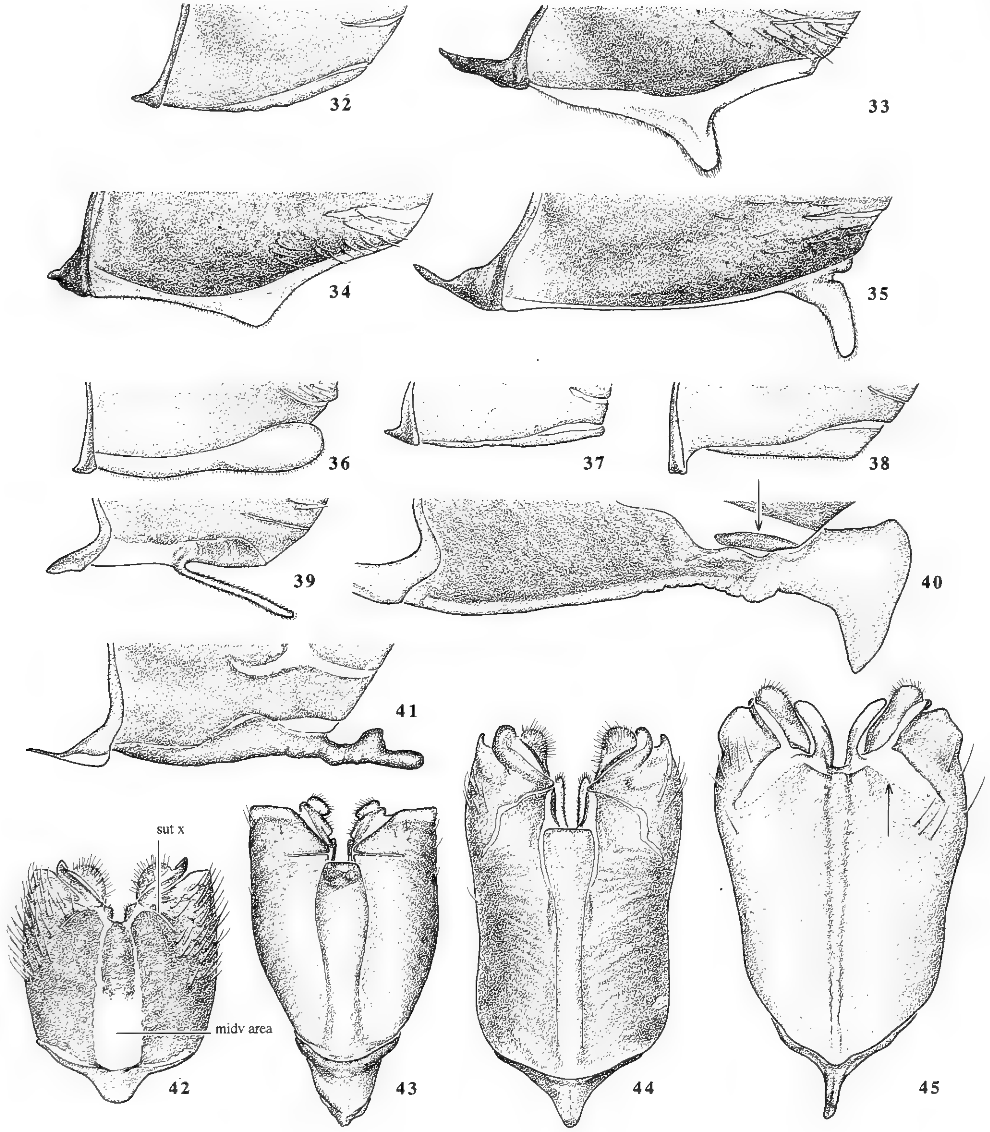
The midventral area in between the gonocoxites is represented by a tumescent structure in the presumed groundplan state of the *Lunatipula* group and *Mediotipula*. The majority of species of *Savtshenkia* also have a tumescent midventral area (fig. 32), but a number of species show a modification of this part of the terminalia. The species *atlas*, *breviantennata*, *cheethami*, *hartigiana* and *simulans* have the midventral area provided with a ventrally directed cone-shaped membranous projection. The projection is relatively low in *atlas* and *breviantennata* (fig. 34), in the other species listed it is longer and more slender (figs. 33, 35). The structure is placed near the posteroventral margin of the gonocoxites in *cheethami* (fig. 35), in the four other species it has a more anterior position (figs. 33, 34).

Other species of *Savtshenkia* with a projection to the area in between the gonocoxites are *alpium*, *aspromontensis*, *macaronesica*, *ornata*, *phoroctenia*, and a few Afrotropical species. As the actual shapes of the projections differ notably among these species, a number of different character states are distinguished. In the species *alpium* and *macaronesica*, the appendage is membranous, dorsoventrally flattened and midventrally placed (character 21; fig. 39), in *ornata* it is swollen, sclerotized and posteriorly projecting (fig. 40), in *phoroctenia* it is slender, sclerotized and posteriorly projecting (fig. 41). The modifications of the midventral area in *ornata* and *phoroctenia* are characteristic of the respective species and represent autapomorphies (see Appendix C). Males of the species *aspromontensis* originating from Greece (Peloponnisos, Crete) have the midventral area posteriorly terminating in a small and low extension. A similar extension is absent in specimens of *aspromontensis* from the type locality in southern Italy. I could not find other distinguishing characters between male specimens of the populations from Greece and from Italy and consider them conspecific. The Afrotropical species of *Savtshenkia* with a modified midventral area include *akeleyi*, *caligo*, *chrysocephala*, and *nephrotomoides*. These species are characterized by a relatively large and bulbous extension to the midventral area (next character).

20. – Gonocoxite, midventral area: (0) posterior part not bulbous; (1) bulbous.

As noted under the previous character, the midventral area in *Savtshenkia* usually is tumescent. The Afrotropical species *caligo*, *chrysocephala*, *nephrotomoides*, and, to a lesser extent, *akeleyi*, are distinguished by a posteroventrally projecting lobe near the posterior margin of the midventral plate. The lobe is large in the first three species listed (fig. 36), in *akeleyi* it is relatively low (fig. 38).

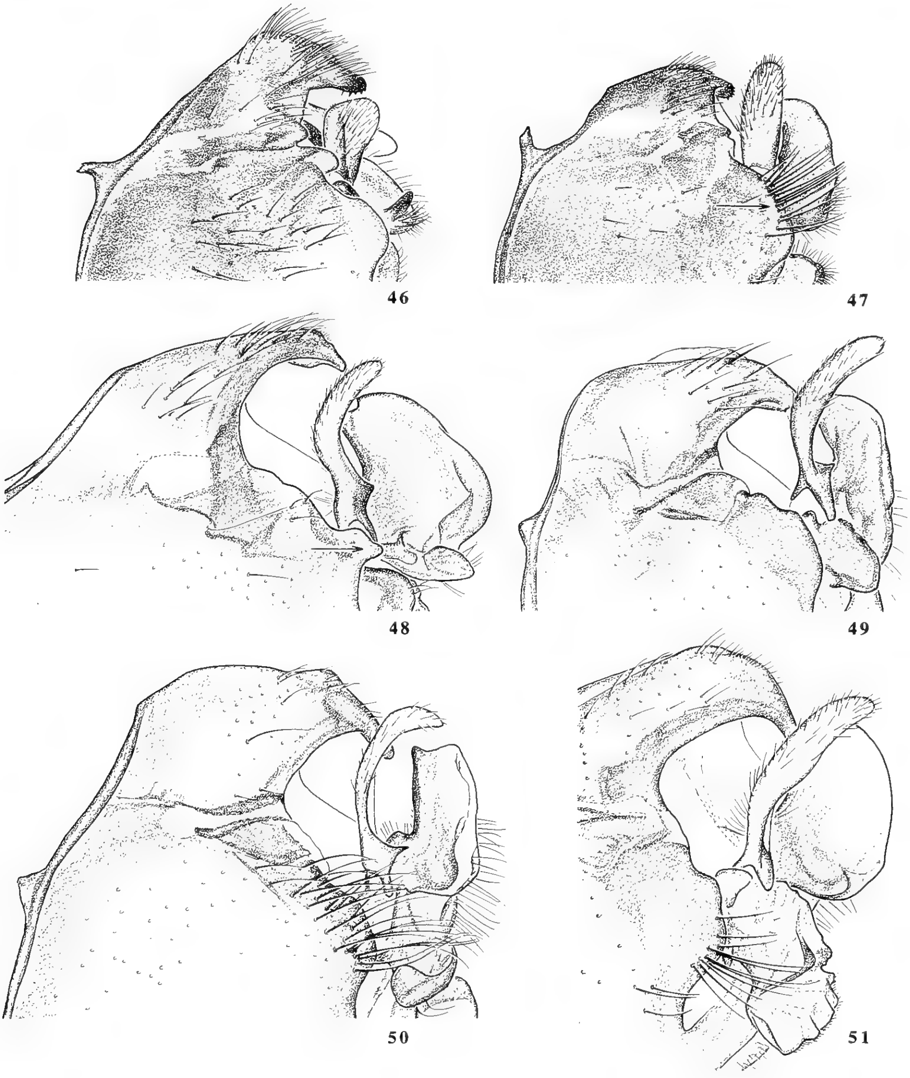
21. – Gonocoxite, midventral area: (0) without



Figs. 32-45. – 32-41, male sternite 9, left gonocoxite and midventral area, lateral view; 32, *Tipula* (*Savtshenkia*) *grisescens*; 33, *T.* (*S.*) *hartigiana*; 34, *T.* (*S.*) *atlas*; 35, *T.* (*S.*) *cheethami*; 36, *T.* (*S.*) *nephrotomoides*; 37, *T.* (*S.*) *aberdareica*; 38, *T.* (*S.*) *akeleyi*; 39, *T.* (*S.*) *alpium*; 40, *T.* (*S.*) *ornata*; 41, *T.* (*S.*) *phoroctenia*; 42-45, male sternite 9, gonocoxites and midventral area, ventral view; 42, *T.* (*S.*) *baltistanica*; 43, *T.* (*S.*) *lundbladi*; 44, *T.* (*S.*) *nielseni*; 45, *T.* (*S.*) *haennii*.
Abbreviations: midv area: midventral area; sut x: suture x.

flattened appendage; (1) at about midlength with dorsoventrally flattened appendage.

As stated above, the midventral area in between the gonocoxites is tumescent in most species of *Savtshenkia*. The species *alpium* and *macaronesica* are distinguished from the other species of *Savtshenkia* by the presence of a dorsoventrally flattened membranous appendage at about midlength of the midventral area. The appendage is long in *alpium* (fig. 39), in *macaronesica* it is considerably shorter. (The unexamined *subalpium* has a small tongue-shaped appendage to the midventral area and is probably closely related to *alpium* and *macaronesica*; see Appendix B).



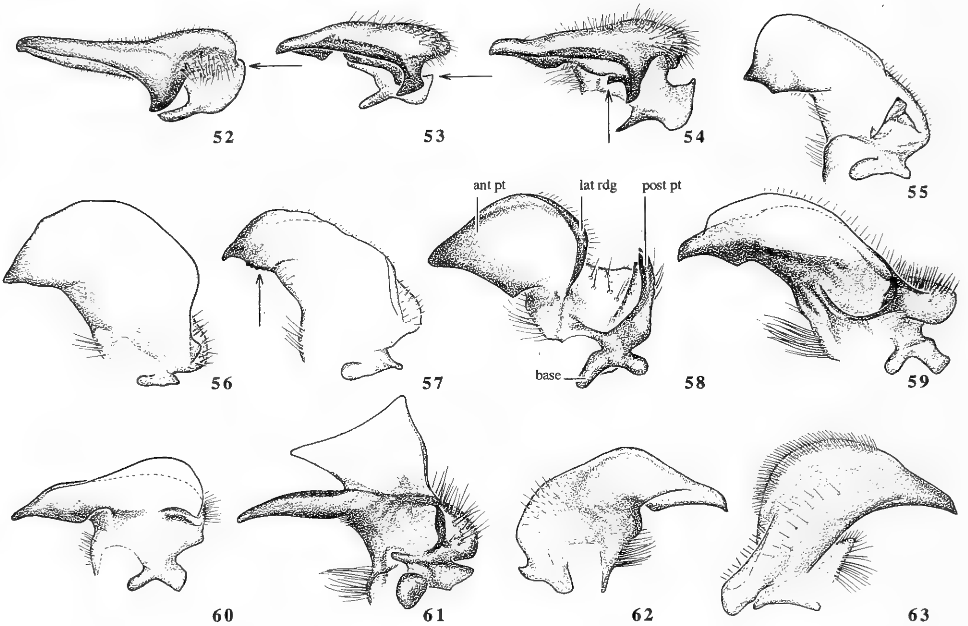
Figs. 46-51. Male tergite 9-10 and dorsal part of left gonocoxite plus appendages, lateral view. – 46, *Tipula* (*Savtshenkia*) *hartigiana*; 47, *T.* (*S.*) *tulipa*; 48, *T.* (*S.*) *haennii*; 49, *T.* (*S.*) *boreosignata*; 50, *T.* (*S.*) *benesignata*; 51, *T.* (*S.*) *persignata tofina*.

22. – Gonocoxite, midventral area: (0) broad and usually separated from gonocoxites by membranous zone; (1) narrow and fused with gonocoxites.

The midventral area is probably broad in the groundplan states of the *Lunatipula* group and *Mediotipula*. The majority of species of *Savtshenkia* also have a broad midventral area in between the gonocoxites (figs. 42-44). It either is membranous, or partly or entirely sclerotized. In most *Savtshenkia* species with a sclerotized midventral area, a membranous zone (partly) separates the plate from the gonocoxites. The species *pechlaneri* and the members of the clade *haennii* to *omega* have a slender parallel sided and sclerotized midventral area which is largely fused with the ventromedial margins of the gonocoxites (fig. 45).

23. – Gonocoxite, posterodorsal margin: (0) with scattered short setae; (1) with concentration of long and strong setae.

The gonocoxites of most species of Tipulidae are covered with scattered setae, a situation which probably represents the groundplan condition of this char-



Figs. 52-63. Left inner gonostylus. – 52, *Tipula* (*Savtshenkia*) *grisescens*, dorsal view; 53, *T.* (*S.*) *villeneuvii*, dorsal view; 54, *T.* (*S.*) *goriziensis*, dorsal view; 55, *T.* (*S.*) *rufina rufina*, lateral view; 56, *T.* (*S.*) *aberdareica*, lateral view; 57, *T.* (*S.*) *akeleyi*, lateral view; 58, *T.* (*S.*) *confusa*, lateral view; 59, *T.* (*S.*) *ornata*, lateral view; 60, *T.* (*S.*) *serrulifera*, lateral view; 61, *T.* (*S.*) *aspromontensis*, lateral view; 62, *T.* (*S.*) *fragilis*, medial view; 63, *T.* (*S.*) *odontostyla*, medial view.
Abbreviations: ant pt: anterior part; lat rdg: lateral ridge; post pt: posterior part.

acter for the *Lunatipula* group and *Mediotipula*. It is also found in most species of *Savtshenkia* (figs. 3, 46, 48, 49, 155). Within *Savtshenkia*, the species of the clades *tulipa* to *simulans* and *benesignata* to *omega* are distinguished by a concentration of strong setae along the posterodorsal margin of the gonocoxites (figs. 47, arrow, 50, 51, 173, 185). The setae are placed in two or three irregular rows. They extend dorsally towards the membranous suture separating the gonocoxite from tergite 9-10 in the species of the clade *tulipa* to *simulans* and in *benesignata* (figs. 47, 50). In the species of the clade *persignata* to *omega*, the setae are confined to a more ventral position (fig. 51, 173, 185).

24. – Gonocoxite, posterodorsal margin: (0) posterodorsal corner rounded off; (1) with posterior projection.

The posterodorsal corner of the gonocoxites is presumably rounded off in the groundplan condition of the *Lunatipula* group, as it is in the majority of species of *Savtshenkia*. In the species of *Mediotipula* and a number of species of *Savtshenkia*, the posterodorsal margin of the gonocoxite is extended into a more or less well developed projection (fig. 48, arrow). The species of *Savtshenkia* which show this character state are those of the range *fragilina* to *subsignata cazorla*.

25. – Gonocoxite, suture x: (0) angle between suture x and the median line about 45° or less; (1) angle between suture and median line much wider, up to 90°.

Suture x usually stands oblique to the median line of the body under an angle of about 45° or less in the Tipulidae. This probably is the groundplan condition of the character for the *Lunatipula* group and *Mediotipula*, and is the general state in *Savtshenkia* (figs. 42, 44, 45). In the species *lundbladi*, *multipicta*, *rufina*, and the Afrotropical members of the subgenus, the angle is much wider, often reaching a magnitude of about 90° (fig. 43). (The direction of suture x could not be adequately studied in the celluloid preparation of the holotype of *elgonensis*, the only known specimen of this species.)

26. – Gonocoxite, suture x: (0) narrow; (1) broad.

Suture x usually is rather narrow in the Tipulidae, a condition considered the groundplan state of the *Lunatipula* group and *Mediotipula*. A narrow suture x is also found in the majority of species of *Savtshenkia* (figs. 3, 32-39, 41-44). The species and subspecies *corsosignata, haennii, subsignata subsignata,* and *subsignata cazorla* differ from the other members of *Savtshenkia* by their broad suture x (fig. 45, arrow). The suture is straight in these four taxa. Other species of *Savtshenkia* with a broad suture x are *fragilis* and *ornata.* In *fragilis,* suture x is sigma-shaped, in *ornata* it is, as many other genital features in this species, very different from that of the remainder of species of *Savtshenkia.* In *ornata,* suture x encompasses an isolated sclerite (fig. 40, arrow; see Appendix C).

27. – Inner gonostylus, anterior part: (0) ventral surface smooth, or at most rugged; (1) serrate.

The ventral surface of the anterior part of the inner gonostylus usually is smooth in Tipulidae. It is considered the groundplan state of the *Lunatipula* group and *Mediotipula,* and is found in the majority of species of *Savtshenkia* (all figures that depict the inner gonostylus in side view, except 57). Three Afrotropical members of *Savtshenkia* are characterized by a partly serrate lower margin of the anterior part of the inner gonostylus, viz. *akeleyi, caligo,* and *chrysocephala* (fig. 57, arrow).

28. – Inner gonostylus, anterior part: (0) crest absent on posterodorsal margin of anterior part; (1) crest present.

The anterior part of the inner gonostylus probably lacks a crest in the groundplan state of the *Lunatipula* group. All species of *Mediotipula* are devoid of a crest on this part, as are most species of *Savtshenkia* (the majority of figures depicting the inner gonostylus). Three species of *Savtshenkia* have a well developed membranous crest on the posterodorsal margin of the anterior part of the inner gonostylus, viz. *aspromontensis, aster,* and *serrulifera.* The crest is dorsally rounded in *aster* and *serrulifera* (fig. 60), but it is grotesquely widening towards its slightly concave dorsal margin in *aspromontensis* (fig. 61).

29. – Inner gonostylus, anterior part: (0) anteriorly terminating in various ways; (1) anteriorly terminating in a prolonged nipple.

The anterior part of the inner gonostylus shows a wide range of forms in the *Lunatipula* group, *Mediotipula,* and *Savtshenkia.* In *Savtshenkia* it is often short and terminates anteroventrally in a more or less acute tip (the majority of figures showing the inner gonostylus). The species *aspromontensis, aster,* and *serrulifera* have a uniquely shaped anterior part which gradually tapers towards an anteriorly extended slender nipple-like projection (figs. 60, 61). The extension is longest in *aspromontensis* (fig. 61) and *aster.*

30. – Inner gonostylus, anterior part: (0) tip single; (1) tip bifid.

The anterior part of the inner gonostylus terminates in a single tip in the majority of Tipulidae, a situation representing the presumed groundplan condition of the *Lunatipula* group and *Mediotipula.* The majority of species of *Savtshenkia* also have the tip of the anterior part of the inner gonostylus undivided (-figs. 55-63, 68, 70-75, 161, 181, 193). The species *corsosignata, nielseni,* and the representatives of the clade *fragilina* to *gimmerthali* differ from the other species of *Savtshenkia* in having a bifid anterior tip of the inner gonostylus. The tip in most of these species shows a relatively broad dorsal and finer lateroventral point (figs. 64-67). In *corsosignata* (fig. 69), the smaller tip lies in a more lateral position compared with that of the other species with a bifid tip.

31. – Inner gonostylus, anterior part: (0) narrowing towards pointed tip; (1) abruptly bent, almost truncate at tip.

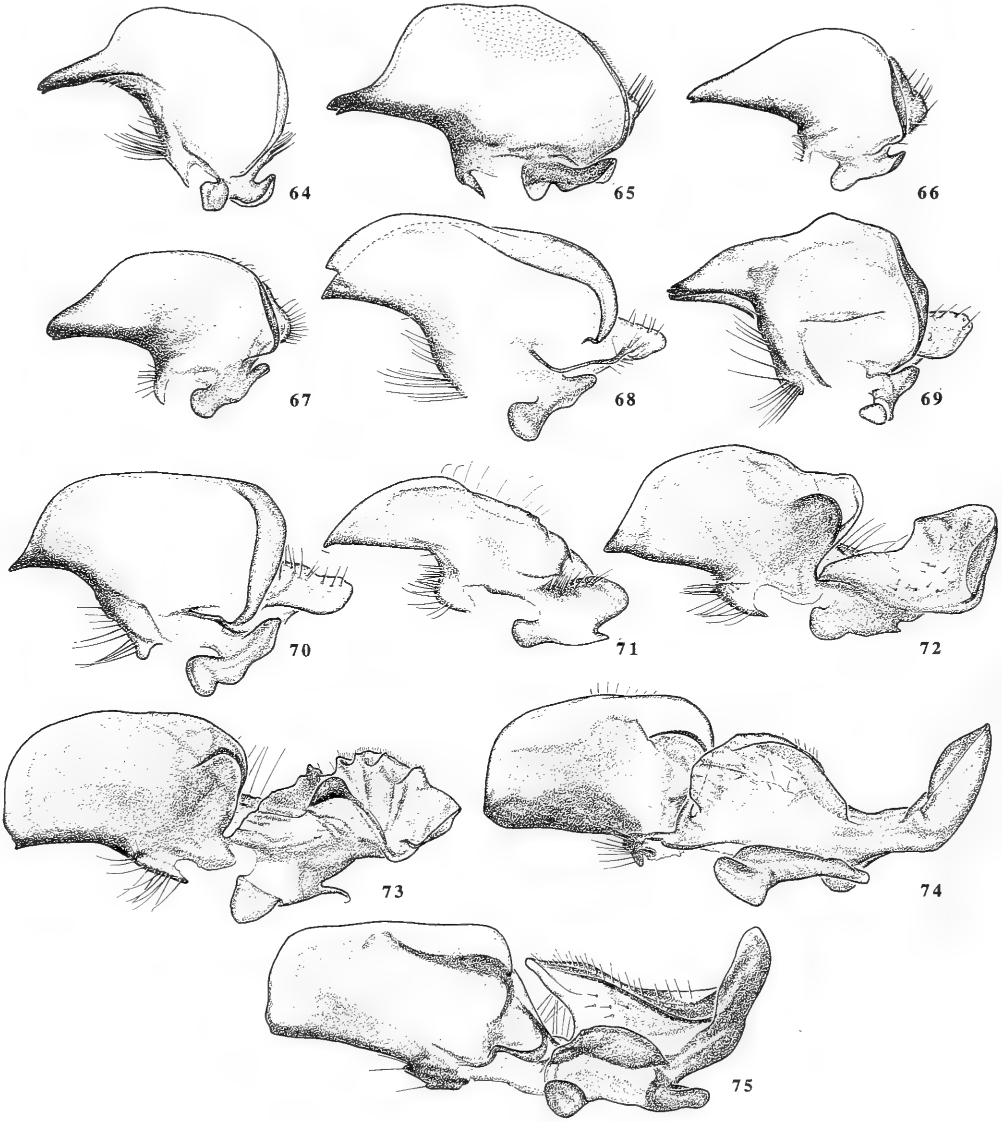
The majority of species of *Savtshenkia* are characterized by a gradually curved and pointed tip of the anterior part of the inner gonostylus (lateral view; see figs. 55-72). The same situation probably is the groundplan condition of the *Lunatipula* group and *Mediotipula.* Within *Savtshenkia,* the species of the clade *persignata* to *omega* are distinguished from the remainder of the subgenus by the broad, almost parallel-sided anterior part of the inner gonostylus which terminates in a rather steep front end (figs. 73-75, 181, 193).

32. – Inner gonostylus, base: (0) posteriorly rounded; (1) posteromedially terminating in pointed extension.

Usually, the base of the inner gonostylus is rounded at its posterior margin in the Tipulidae, a situation representing the presumed groundplan condition of the *Lunatipula* group and *Mediotipula.* It is also found in most species of *Savtshenkia* (dorsal view, fig. 52, arrow). A number of species of *Savtshenkia* are distinguished by the presence of an acute point at the posteromedial corner of the base of the inner gonostylus (figs. 53, arrow, 54). The species concerned constitute the clade *hartigiana* to *simulans.*

33. – Inner gonostylus, lateral ridge, ventral part: (0) without extensions; (1) with one or two acute blackish pointed extensions.

The ventral part of the lateral ridge of the inner gonostylus gradually merges with the main body of the inner gonostylus in most species of *Savtshenkia.* The three species *cheethami, goriziensis,* and *simulans* differ from the remainder of species of *Savtshenkia* by the presence of one or two acute blackish points at the end of the lower part of the lateral ridge of the inner gonostylus. The points are located near midheight of



Figs. 64-75. Left inner gonostylus, lateral view. – 64, *Tipula* (*Savtshenkia*) *limbata*; 65, *T.* (*S.*) *pechlaneri*; 66, *T.* (*S.*) *gimmerthali gimmerthali*; 67, *T.* (*S.*) *gimmerthali pteromaculata*; 68, *T.* (*S.*) *haennii*; 69, *T.* (*S.*) *corsosignata*; 70, *T.* (*S.*) *subsignata subsignata*; 71, *T.* (*S.*) *boreosignata*; 72, *T.* (*S.*) *benesignata*; 73, *T.* (*S.*) *persignata tofina*; 74, *T.* (*S.*) *signata*; 75, *T.* (*S.*) *mannheimsi*.

the body of the inner gonostylus. In *goriziensis*, a single point is present (fig. 54, arrow), while *cheethami* and *simulans* have two points, the posterior of which is bifid in *simulans*.

34. – Inner gonostylus, lateral ridge: (0) ventrally directed and terminating at about midlength of base of inner gonostylus; (1) in ventral part angularly bent and anteriorly extended, terminating in front of base of inner gonostylus.

The lateral ridge of the inner gonostylus is ventrally directed in the majority of species of *Savtshenkia*. The lateral ridge of *subsignata subsignata* and *subsignata cazorla* is present as a sharp edge directed towards the anterior margin of the inner gonostylus. The ridge makes a distinct angle in its posteroventral section near the base of the inner gonostylus (fig. 70).

Dufour (1991, character 3) recognized the presence of a ridge, on what he referred to as the median part of the inner gonostylus, as a synapomorphy of the subspecies *subsignata subsignata* and the then newly described *subsignata cazorla* and *subsignata haennii*. Furthermore, Dufour (1991, character 4) considered the continuity of the ventral and posterior parts of the ridge, as found in *subsignata subsignata* and *subsignata cazorla*, a synapomorphy of these two subspecies. Regarding the shape of the ridge in other species of *Savtshenkia*, it appears, however, that a continuous ridge should be judged a plesiomorphy in *subsignata subsignata* and *subsignata cazorla*. Consequently and contrary to Dufour, I regard the separation of the posterior and ventral parts of the ridge in *haennii* an autapomorphy of that species (fig. 68; see Appendix C).

35. – Inner gonostylus, posterior part: (0) variously shaped; (1) posterolaterally extended, cup-shaped, laterodorsal margin blackened and serrate.

The groundplan condition of the posterior part of the inner gonostylus in the *Lunatipula* group and *Mediotipula* is probably represented by a relatively simple and single structure. The posterior part is rounded and little developed in most species of *Savtshenkia*. The species *confusa*, *eugeni*, and *jeekeli* differ from the other species of *Savtshenkia* by the configuration of the posterior part. In these three species, it projects posterolaterally and carries acute processes along its blackish sclerotized laterodorsal margin (fig. 58). The species *confusa* has a serrate and blackened rim running medially of and parallel to the posterolateral margin (fig. 58; see Appendix C).

36. – Inner gonostylus, posterior part: (0) variously shaped; (1) a posteriorly projecting, often rather acute, structure.

As stated above, the posterior part of the inner gonostylus is moderately developed and rounded off in most species of *Savtshenkia*. The members of the clade *odontostyla* to *omega* are characterized by a more caudal development of the posterior part. In these species, the posterior part either is a rather slender and often somewhat acute structure (fig. 63), or a more enlarged and posteriorly produced extension (figs. 68-75, 181, 193; see also next character). A caudally produced posterior part of the inner gonostylus is also present in the species *ornata* (fig. 59).

37. – Inner gonostylus, posterior part: (0) a relatively small projection; (1) posteriorly extended, large.

As mentioned under the previous character, the posterior part of the inner gonostylus is usually little developed in the species of *Savtshenkia*. The species *benesignata*, *mannheimsi*, *omega*, *persignata*, *signata*, and *trinacria* are distinguished among the species of the subgenus by a strikingly large posterior part which is of about the same length as the anterior part (figs. 72-75, 181, 193). The posterior part in these species is vertically orientated and lies more or less in line with the anterior part.

38. – Inner gonostylus, posterior part: (0) dorsal surface even; (1) dorsal surface corrugated.

The dorsal surface of the posterior part of the inner gonostylus is even in the majority of species of *Savtshenkia*, as is the probable groundplan condition of the *Lunatipula* group and *Mediotipula*. Within *Savtshenkia* the dorsal surface of this part of the inner gonostylus is corrugated in both *persignata persignata* and *persignata tofina* (fig. 73).

39. – Inner gonostylus, posterior part: (0) variously shaped; (1) anterior section anterodorsally extended towards anterior part of inner gonostylus.

As noted under character 37, a number of species of *Savtshenkia* have a caudally produced and large posterior part of the inner gonostylus. The extended posterior part of the inner gonostylus is low in its anterior half in *benesignata*, *persignata persignata*, and *persignata tofina* (figs. 72, 73), as it is in the other species of *Savtshenkia*. In the species *mannheimsi*, *omega*, *signata*, and *trinacria* it is anterodorsally protruding (figs. 74, 75, 181, 193).

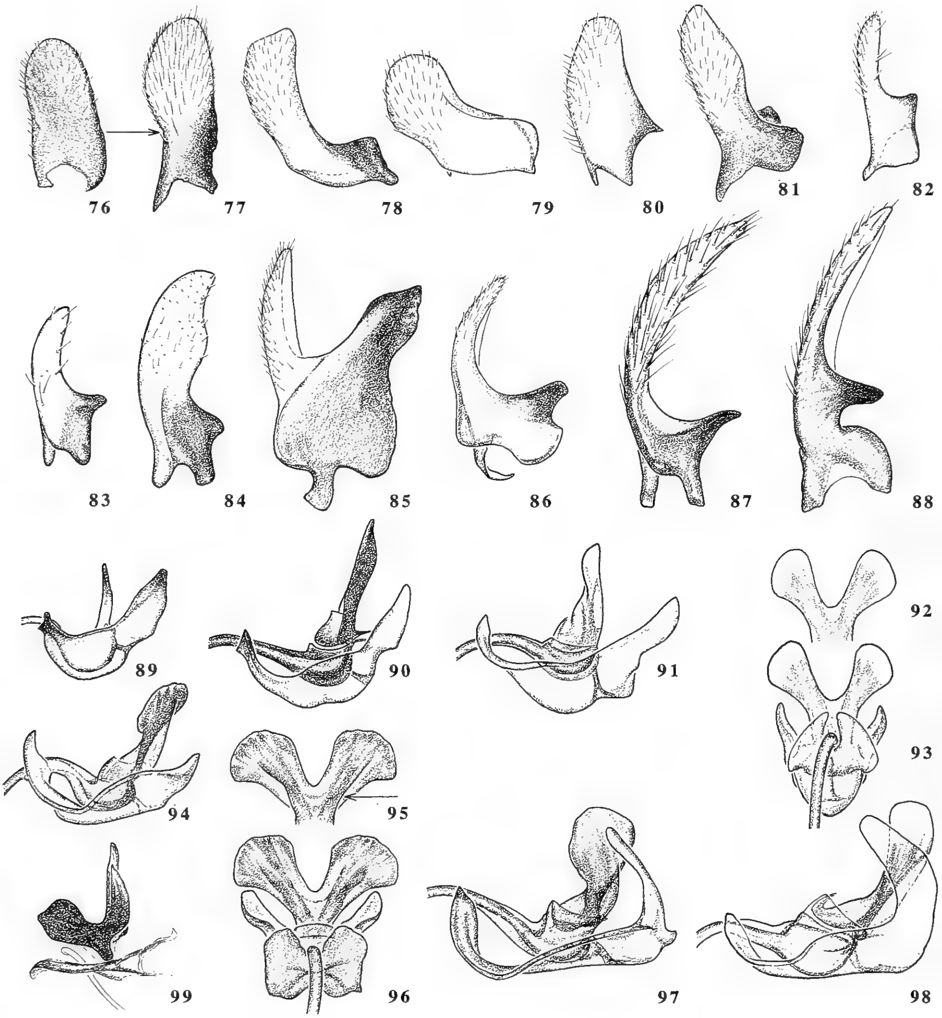
40. – Inner gonostylus: (0) variously shaped; (1) similarly shaped, with high anterior part and blackish sclerotized triangular projection posterolaterally.

The inner gonostylus shows a wide variety of forms throughout *Savtshenkia*. The two subspecies *rufina rufina* and *rufina maderensis* display a remarkable similarity in the structure of the inner gonostylus which differs most notably from that of other species of *Savtshenkia* by the shape of the anterior part and the location of the posterolateral projection (fig. 55).

41. – Inner gonostylus: (0) variously shaped; (1) similarly shaped, anterior part anterodorsally straightened, gradually narrowing towards bifid tip.

Throughout *Savtshenkia* a wide variety of forms of the inner gonostylus can be found. The three recognized subspecies of *gimmerthali* can be separated from the other species of the subgenus by the unique shape the inner gonostylus, of which the anterior part gradually narrows towards a bifid tip (figs. 66, 67).

42. – Inner gonostylus: (0) variously shaped; (1) similarly shaped, with long sloping caudodorsal margin.



Figs. 76-99. – 76-88, left outer gonostylus, lateral view; 76, *Tipula* (*Savtshenkia*) *grisescens*; 77, *T.* (*S.*) *hartigiana*; 78, *T.* (*S.*) *lundbladi*; 79, *T.* (*S.*) *multipicta*; 80, *T.* (*S.*) *jeekeli*; 81, *T.* (*S.*) *aspromontensis*; 82, *T.* (*S.*) *fragilis*; 83, *T.* (*S.*) *gimmerthali gimmerthali*; 84, *T.* (*S.*) *gimmerthali pteromaculata*; 85, *T.* (*S.*) *nielseni*; 86, *T.* (*S.*) *sardosignata*; 87, *T.* (*S.*) *signata*; 88, *T.* (*S.*) *mannheimsi*; 89-99, sperm pump and appendages; 89, *T.* (*S.*) *subnodicornis*, lateral view; 90, *T.* (*S.*) *baltistanica*, lateral view; 91-93, *T.* (*S.*) *alpium*, 91, lateral view; 92, compressor apodeme, posterior view; 93, anterior view; 94-96, *T.* (*S.*) *jeekeli*, 94, lateral view; 95, compressor apodeme, posterior view; 96, anterior view; 97, *T.* (*S.*) *confusa*, lateral view; 98, *T.* (*S.*) *graciae*, lateral view; 99, *T.* (*S.*) *boreosigata*, lateral view.

The species *boreosignata* and *eleonorae* are distinguished among the species of *Savtshenkia* by their uniquely shaped and very similar inner gonostyli. The overall structure is rather long, with a well developed anterior part and a long caudodorsal margin which gradually slopes towards the low posterior part (fig. 71).

43. – Outer gonostylus: (0) anterior margin convex or slightly and evenly concave; (1) concave, with distinct bend at about two-fifth of length from base.

The anterior margin of the outer gonostylus is either entirely convex or evenly concave in its lower half in the presumed groundplan condition of the *Lunatipula* group and *Mediotipula*, and in the majority of species of *Savtshenkia* (figs. 76, 78-88, 160, 180, 192). The three species *atlas*, *breviantennata*, and *hartigiana* have the anterior margin of the outer gonostylus angularly concave near two-fifth of its height (fig. 77, arrow).

44. – Outer gonostylus: (0) upright structure; (1) inclined forward.

The outer gonostylus in Tipulidae usually is an upright structure, as is the presumed groundplan condition of the *Lunatipula* group and *Mediotipula.* The majority of species of *Savtshenkia* are also distinguished by the presence of a vertically orientated outer gonostylus (figs. 76, 77, 80, 82-88, 160, 180, 192). The outer gonostylus of the species *aspromontensis, lundbladi,* and *multipicta* leans over anteriorly (figs. 78, 79, 81). The actual shapes of the outer gonostyli of the three pertaining species differ notably. The base of the outer gonostylus is low and elongate in *lundbladi* (fig. 78) and *multipicta* (fig. 79), whereas it is rather short in *aspromontensis* (fig. 81).

45. – Outer gonostylus: (0) anterior part rather broad; (1) slender and elongate.

In general, the outer gonostylus is present as a single oblong and rather broad structure in the Tipulidae, a situation which probably represents the groundplan condition of this character for the *Lunatipula* group and *Mediotipula.* A broad outer gonostylus is found in about half of the species of *Savtshenkia* (figs. 76-81, 160). The species of the clade *fragilis* to *omega* are distinguished by the presence of a rather slender and elongate anterior substructure of the outer gonostylus (figs. 82, 83, 85-88, 180, 192). A similar outer gonostylus with slender anterior section is found furthermore in the species *eugeni* and *ornata.* The subspecies *gimmerthali pteromaculata,* which is included in the clade *fragilis* to *omega,* has a relatively wide anterior part of the outer gonostylus (fig. 84).

46. – Outer gonostylus: (0) base variously shaped, usually relatively narrow; (1) broad, laterally concave and blackish sclerotized.

As noticed under the previous character, the outer gonostylus generally is an oblong structure in the Tipulidae. The base of the outer gonostylus is usually relatively narrow compared with the length of the structure, a situation present in the majority of species of *Savtshenkia* (figs. 76, 77, 80, 82-84, 87, 88, 160, 180, 192). The species *nielseni* (fig. 85) and *sardosignata* (fig. 86) differ from the remainder of *Savtshenkia* by the presence of a large base of the outer gonostylus. The base is laterally concave, partly blackish sclerotized and carries a strong posterior projection.

47. – Sperm pump, endophallic lumen: (0) bulbous, ventrally expanded; (1) small.

Throughout the Tipulidae, the sperm pump has a rather large and bulbous endophallic lumen, a situation which probably represents the groundplan condition of the *Lunatipula* group and *Mediotipula.* Within *Savtshenkia* a similar condition is found in the species *alpha, grisescens, ignobilis, subnodicornis,* and the species of the clade *hartigiana* to *simulans* (figs. 89, 163). The majority of species of *Savtshenkia,* however, have an endophallic lumen that is hardly ventrally expanded (figs. 5, 90, 91, 94, 97, 98, 183, 195). The species concerned include the members of the clade *baltistanica* to *omega.*

48. – Sperm pump, compressor apodeme: (0) a flattened blade; (1) posteriorly provided with U-shaped or V-shaped brace.

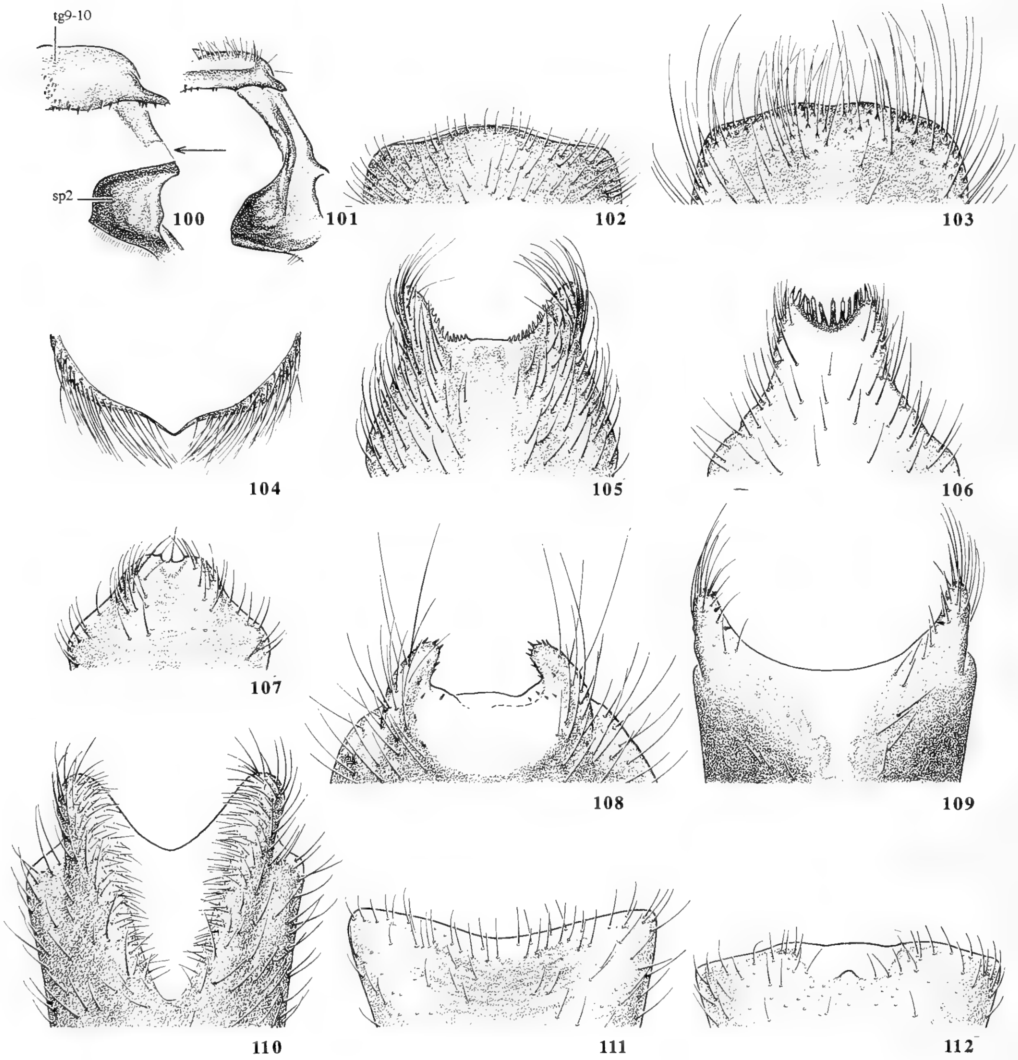
The groundplan condition of the compressor apodeme of the *Lunatipula* group and *Mediotipula* probably consists of a flattened blade with a more or less distinct dorsomedial emargination. Within *Savtshenkia* a similar compressor apodeme is found in the species that range from *alpha* to *macaronesica* (figs. 92, 93, 164). The other species of *Savtshenkia* are distinguished by the presence of a U-shaped or V-shaped support on the posterior side of the compressor apodeme (fig. 95, arrow, 96, 184, 196). The species involved constitute the clade *jeekeli* to *omega.*

49. – Sperm pump: (0) ventral wall convex; (1) ventral wall flattened or concave.

In Tipulidae, the body of the sperm pump usually is a bulbous structure which has a convex ventral wall. This situation probably reflects the groundplan condition of the *Lunatipula* group and *Mediotipula* and is found in about two-fifth of the species of *Savtshenkia* (the range *alpha* to *macaronesica*; frontal view, figs. 93, 164). Within *Savtshenkia* the bulb of the sperm pump has a flat or concave ventral wall in most species of the clade *jeekeli* to *omega* (figs. 96, 184, 196). There are, however, a few species within this latter clade which have a convex ventral wall of the sperm pump, viz. *aspromontensis, eugeni,* and *interserta.*

50. – Sperm pump, posterior apodemes: (0) well developed and posteriorly or posterodorsally directed; (1) elongate and anteriorly extended.

In Tipulidae, the posterior apodemes of the sperm pump are generally well developed, rather broad and posteriorly or posterodorsally directed. This character state probably represents the groundplan condition of the *Lunatipula* group and *Mediotipula.* The majority of species of *Savtshenkia* also display this character state (figs. 5, 89-91, 94, 163, 183, 195). In contrast, the members of the clade *confusa* to *aster* are distinguished by the presence of elongate and anteriorly extended posterior apodemes. The tips of the posterior



Figs. 100-112. – 100, 101, sp2 and part of tergite 9-10, posteromedial view; 100, *Tipula* (*Savtshenkia*) *odontostyla*; 101, *T.* (*S.*) *limbata*; 102-112, male sternite 8, posterior margin; 102, *T.* (*S.*) *grisescens*, ventral view; 103, *T.* (*S.*) *lundbladi*, ventral view; 104, *T.* (*S.*) *rufina rufina*, posterior view; 105, *T.* (*S.*) *alpium*, ventral view; 106, *T.* (*S.*) *obsoleta*, ventral view; 107, *T.* (*S.*) *holoptera*, ventral view; 108, *T.* (*S.*) *confusa*, ventral view; 109, *T.* (*S.*) *aster*, ventral view; 110, *T.* (*S.*) *limbata*, ventral view; 111, *T.* (*S.*) *pechlaneri*, ventral view; 112, *T.* (*S.*) *invenusta invenusta*, ventral view.
Abbreviations: sp2: lateral part of genital bridge; tg9-10: tergite 9-10.

apodemes in these species lie alongside the compressor apodeme (figs. 97, 98).

51. – Sperm pump, posterior apodemes: (0) well developed, broad; (1) slender.

As noticed under the previous character, the posterior apodemes of the majority of species of *Savtshenkia* are well developed and broad (figs. 5, 89-91, 94, 98, 163, 183, 195). Three species are distinguished from the remainder of the subgenus by their long and slender posterior apodemes, viz. *confusa*, *interserta*, and *ornata* (fig. 97). The posterior apodemes of these three species are anteriorly extended (see previous character).

52. – Sperm pump: (0) general shape of the standard

tipulid type; (1) general shape different, partly heavily sclerotized.

The sperm pump in Tipulidae usually consists of a bulbous main body, which is surrounded in the horizontal plane by a pair of anterior and a pair of posterior apodemes, and perpendicular and dorsal to these a single compressor apodeme. The anterior and posterior apodemes are attached to the main body of the sperm pump at about midheight and the aedeagus leaves the sperm pump in between the anterior apodemes. This configuration doubtlessly represents the groundplan condition of the *Lunatipula* group and *Mediotipula.* The majority of species of *Savtshenkia* also show a sperm pump of this form (figs. 5, 89-98, 163, 164, 183, 184, 195, 196). However, the species *boreosignata* and *eleonorae* possess a peculiarly built sperm pump, which has the heavily sclerotized main body lying just dorsal of (*boreosignata,* fig. 99) or on (*eleonorae*) a membranous disc-like structure which contains the remnants of the anterior and posterior apodemes. The heavily sclerotized compressor apodeme seems to be fused with the main body of the pump. In *boreosignata,* the short aedeagus appears to be attached to the ventral side of the main body, after which it makes a loop at the level of the disc-like structure containing the anterior and posterior apodemes. Compared with the sperm pump of the other species of *Savtshenkia,* the whole structure is small in both *boreosignata* and *eleonorae.*

53. – Sp2: (0) uniformly and moderately sclerotized; (1) medially blackish sclerotized.

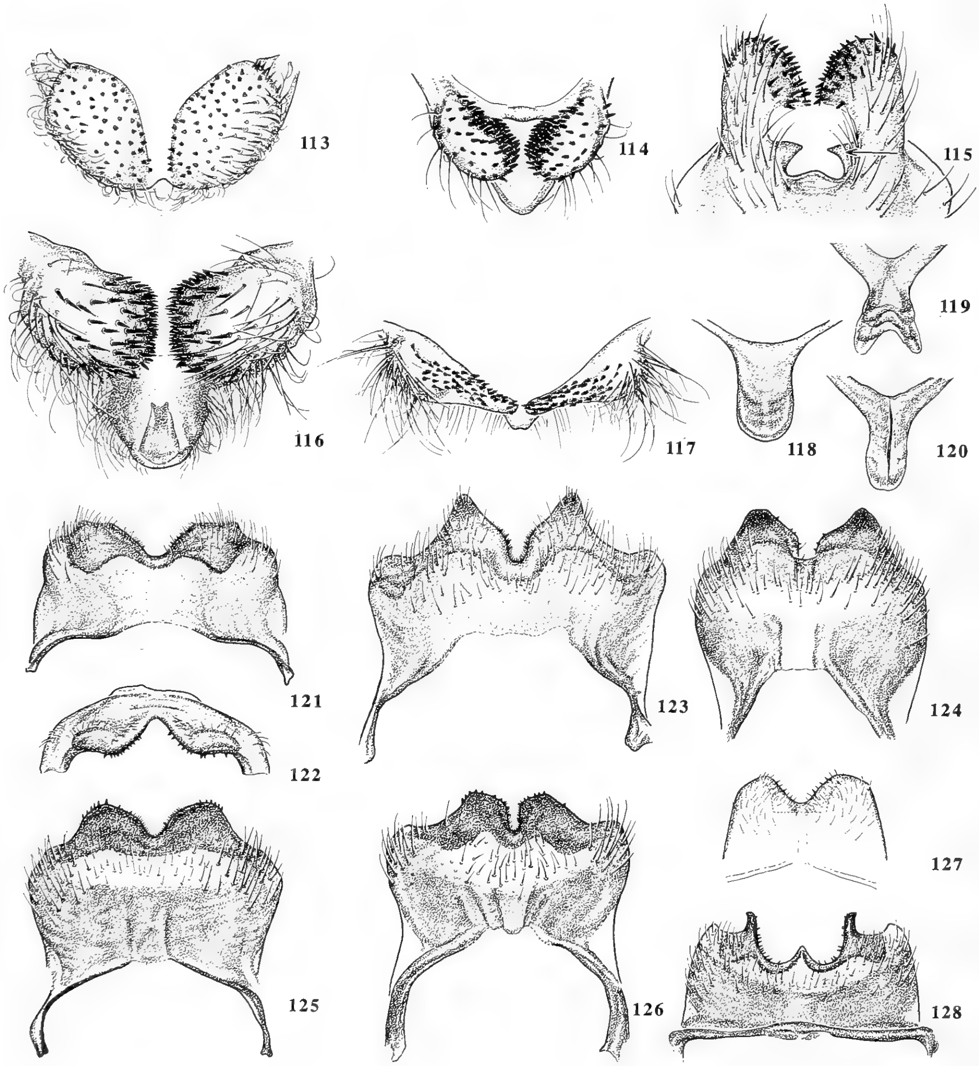
Throughout the Tipulidae, sp2 generally is uniformly sclerotized. This situation is found in the *Lunatipula* group and in *Mediotipula* and represents the groundplan state of this character for both taxa. All species of *Savtshenkia* as recognized in this paper have the medial margin of sp2 blackish sclerotized (figs. 100, 101, 159, 179, 191). The only other Tipulidae in which a similar situation was studied are species of the genus *Nephrotoma* Meigen and of the subgenus *Tipula* (*Schummelia* Edwards). In *Nephrotoma,* a partly blackish sclerotized sp2 can be found in for instance the Palaearctic *aurantiocincta* Alexander, *biarmigera* Alexander, *medioproducta* Alexander and the Oriental *citricolor* Alexander, *integra* Alexander, *progne* Alexander, *subumbonis* Alexander, and *umbonis* Alexander. In the pertaining species of *Nephrotoma,* the general shape of sp2 differs from that of the species of *Savtshenkia* in that sp2 is short and broad, anteriorly notched, and rather deeply concave. All species of *Schummelia* studied (viz. *ahrensi* Savchenko, *butzi* Edwards, *variicornis* Schummel, *yerburi* Edwards, *zernyi* Mannheims, and *zonaria* Goetghebuer) have the anteromedial margin of sp2 more or less darker sclerotized than the remainder of the structure. The general shape of sp2 in the species of *Schummelia* is similar to the elongate form as found in the majority of species of *Savtshenkia.* The phylogenetic positions of the pertaining species of *Nephrotoma* and *Schummelia* within the respective taxa are still unestablished. Except for the similar modification of sp2, there are at the moment, however, no indications to suggest that either *Nephrotoma* or *Schummelia,* or both combined, represent(s) the closest relative of *Savtshenkia* (see also next character).

54. – Sp2: (0) dorsally separate from tergite 9-10; (1) dorsally fused with ventromedial part of tergite 9-10.

Sp2 and tergite 9-10 are separate from each other in the greater majority of Tipulidae, a situation considered the groundplan condition of the *Lunatipula* group and *Mediotipula.* More than half of the species of *Savtshenkia* also show this character state (fig. 100, arrow). In the species of the clade *fragilina* to *omega,* sp2 is fused with the ventromedial sclerotization of tergite 9-10 (fig. 101). Both structures are firmly connected over their entire width. Outside *Savtshenkia,* I found a similar character state in species of the subgenus *Tipula* (*Schummelia*) only. In the examined species of *Schummelia* (see previous character), sp2 and the ventral sclerotization of tergite 9-10 are approximated. Some of these species show a partial fusion of sp2 and tergite 9-10 (viz. *ahrensi, variicornis,* and *yerburi*). In *zernyi,* both structures are more firmly connected. The studied species of *Schummelia* all have a western Palaearctic distribution and represent only a minor fraction of the subgenus which contains about 75 species distributed further in the Afrotropical, Nearctic and especially Oriental Regions. Fusion of tergite 9-10 with sp2 probably evolved independently in *Schummelia.* As stated under the preceding character, I do not consider *Schummelia* a potential sister group of *Savtshenkia.*

55. – Sternite 8, posterior margin: (0) unmodified; (1) caudally extended.

An unmodified sternite 8 in Tipulidae consists of a relatively short structure of which the posterior margin is evenly convex or slightly concave and lacks any trace of spinosity. This situation probably represents the groundplan condition of this character for the *Lunatipula* group and *Mediotipula.* In a number of species of *Savtshenkia,* a modification of the posterior margin of sternite 8 is found, which generally consists of a posterior elongation of the structure (figs. 103, 105-110, 112-117, 173, 177, 178, 185, 189, 190). Elongation of sternite 8 is usually combined with the presence of spines or strong setae along the posterior margin (character 57). A caudally produced posterior



Figs. 113-128. – 113-117, male sternite 8, posterior margin; 113, *T.* (*S.*) *cyrnosardensis*, posterior view; 114, 115, *T.* (*S.*) *haennii*, 114, posterior view; 115, ventral view; 116, *T.* (*S.*) *signata*, posterior view; 117, *T.* (*S.*) *mannheimsi*, posterior view; 118-120, male sternite 9, anteroventral appendage, dorsal view; 118, *T.* (*S.*) *sordidipes*; 119, *T.* (*S.*) *eugeni*; 120, *T.* (*S.*) *limbata*; 121-128, male tergite 9-10; 121, 122, *T.* (*S.*) *grisescens*, 121, dorsal view; 122, posterior view; 123, *T.* (*S.*) *hartigiana*, dorsal view; 124, *T.* (*S.*) *atlas*, dorsal view; 125, *T.* (*S.*) *goriziensis*, dorsal view; 126, *T.* (*S.*) *cheethami*, dorsal view; 127, *T.* (*S.*) *ignobilis*, dorsal view; 128, *T.* (*S.*) *subnodicornis*, dorsal view.

margin of sternite 8 is found in the species *lundbladi*, *multipicta*, *rufina*, and those of the clade *alpium* to *omega*. Within the latter clade a short sternite 8 is present in *aspromontensis*, *gimmerthali*, *interserta*, *pechlaneri*, *sordidipes*, and *venerabilis* (see fig. 111).

56. – Sternite 8, posterior margin: (0) variously shaped; (1) with V-shaped ventral carina.

Sternite 8 is present as an evenly curved sclerite in the presumed groundplan condition of the *Lunatipula* group and *Mediotipula*. Within *Savtshenkia* a variety of forms of the posterior margin of sternite 8 is found. The two subspecies *rufina rufina* and *rufina maderensis* are distinguished from the remainder of the subgenus by the presence of a midventral V-shaped carina in the posterior part of sternite 8 (posterior view, fig. 104).

57. – Sternite 8, posterior margin: (0) unarmed; (1) provided with strong setae or black spines.

In most Tipulidae, sternite 8 is unarmed, a situation considered to represent the groundplan state of this character for the *Lunatipula* group and *Mediotipula.* About half of the species of *Savtshenkia* have the posterior margin of sternite 8 provided with strong setae or short spines (figs. 105-109, 113-117, 177, 178, 189, 190). The number of spines or setae and their location varies among the different species of *Savtshenkia.* The species with an armed posterior margin of sternite 8 include *baltistanica, multipicta,* and most species of the clade *alpium* to *omega.* Within the latter clade a number of species show an unarmed sternite 8, viz. *interserta, macaronesica, ornata,* and the species of the clade *fragilina* to *invenusta* (see figs. 110-112).

58. – Sternite 8, posterior margin: (0) variously shaped; (1) with medial tongue-like extension, posteriorly concave.

As stated above, a number of species of *Savtshenkia* have a caudally produced posterior margin of sternite 8. The species *holoptera, obsoleta,* and *pagana* are distinguished among these by the peculiarly shaped posterior extension of sternite 8, which appears as a tongue-like blade which is caudally more or less emarginate (figs. 106, 107). In most specimens of *pagana,* the caudal margin of the posterior extension is nearly straight, in the species *holoptera* and *obsoleta* it is distinctly concave.

59. – Sternite 8, posterior margin: (0) unarmed or armed with more than 10 spinous setae; (1) number of spinous setae less, ranging from seven to one.

The number of strong setae or spines on the posterior margin of sternite 8 in the species of *Savtshenkia* which have this structure armed usually is (considerably) more than 10 (figs. 105, 113-117, 177, 178, 189, 190). In the species *obsoleta,* there are about 13 to 15 spines on the posterior margin of sternite 8 (fig. 106). The species *holoptera* and *pagana* have less than 10 spines along the posterior margin of sternite 8. Sternite 8 of *pagana* usually has about four to eight spinous setae, in *holoptera* the number varies between one and three (fig. 108; see Eiroa, 1987).

60. – Sternite 8, posterior margin: (0) medial membranous area absent, small or, if large, without rim of longish setae; (1) membranous area broadly V-shaped, anteriorly extending, its margins set with long slender setae.

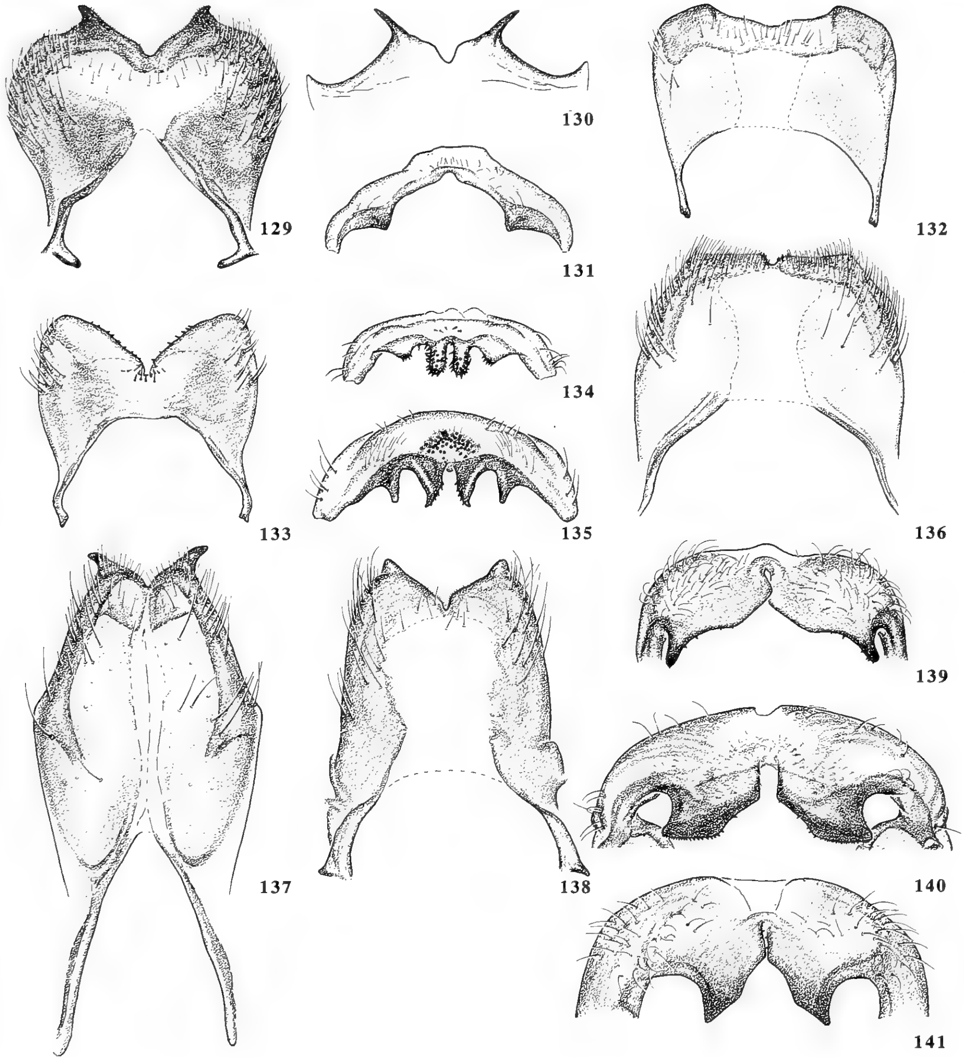
As noticed above, the groundplan condition of sternite 8 for the *Lunatipula* group and *Mediotipula* probably consists of an unmodified sclerite. The posterior margin of the sternite in this situation is uniformly sclerotized. In *Savtshenkia,* sternite 8 generally has no membranous area at its posterior margin or the membranous area is restricted to a narrow zone (figs. 102, 103, 105-107, 111, 112, 115, 158, 177, 189). The three species *fragilina, limbata,* and *subvafra* are distinguished from the remainder of *Savtshenkia* by a large and V-shaped membranous area which is bordered by a fringe of thickly set longish slender setae (fig. 110). The species *aster* and *confusa* are the only other species of *Savtshenkia* that also have a relatively large membranous area on the posterior margin of sternite 8. In *aster,* a V-shaped membranous area is present in between the caudolateral extensions, the extensions themselves are provided with a few black spines (fig. 109; see Appendix C). The species *confusa* has a broad and rounded membranous zone (fig. 108; see Appendix C). In both species, the margin of the membranous area is surrounded by scattered setae only.

61. – Sternite 8, posterior margin: (0) ventrally directed medial extension absent; (1) unarmed medial extension present rostrally of lateral extensions, or at this position with sclerotized edge.

In the majority of species of *Savtshenkia,* the posterior margin of sternite 8 medially either is unmodified or produced into a rather broad lobe provided with spines or strong setae (figs. 102, 103, 105-111, 158). An unarmed medial extension rostrally of a pair of lateral extensions on the posterior margin of sternite 8 can be found in the three subspecies of *invenusta* and in the species of the clade *nielseni* to *omega.* The size, shape and sclerotization of the medial extension varies among the species involved. In the subspecies of *invenusta,* and in *mannheimsi, omega,* and *trinacria* the medial extension is relatively small and moderately sclerotized (figs. 112, 117, 177, 178, 189, 190), it is large and partly membranous in *nielseni,* whereas it is more pronounced and heavily sclerotized in most other species involved (figs. 114, 116). It should be noted, however, that the species *benesignata, boreosignata,* and *eleonorae* lack a protruding medial extension. In these three species, a sclerotized rim marks the position of the medial extension.

62. – Sternite 8, posterior margin: (0) extension(s) absent or dorsoventrally flat; (1) lateral extensions appearing as bulbous structures, densely set with spines.

The extensions of sternite 8 are relatively flat and follow the curve of sternite 8 when seen in posterior view in about half of the species of *Savtshenkia* with a modified sternite 8. Most members of the clade *cyr-*



Figs. 129-141. Male tergite 9-10.– 129, *T.* (*S.*) *baltistanica*, dorsal view; 130, *T.* (*S.*) *elgonensis*, posterior margin, dorsal view, after celluloid preparation holotype; 131, 132, *T.* (*S.*) *aberdareica*, 131, posterior view; 132, dorsal view; 133, *T.* (*S.*) *sordidipes*, dorsal view; 134, *T.* (*S.*) *serrulifera*, posterior view; 135, *T.* (*S.*) *aspromontensis*, posterior view; 136, *T.* (*S.*) *invenusta invenusta*, dorsal view; 137, *T.* (*S.*) *nielseni*, dorsal view; 138, *T.* (*S.*) *boreosignata*, dorsal view; 139, *T.* (*S.*) *persignata tofina*, posterior view; 140, *T.* (*S.*) *signata*, posterior view; 141, *T.* (*S.*) *mannheimsi*, posterior view.

nosardensis to *omega* are characterized by the presence of bulbously swollen lateral extensions of sternite 8. In the majority of these species, the lateral extensions are thickly set with black spines (figs. 113-116), but in the species *boreosignata* only a few spines on the lateral lobes are found. Moreover, the three species *mannheimsi*, *omega*, and *trinacria* have a relatively flat pair of lateral extensions (figs. 117, 178, 190; character 65).

63. – Sternite 8, posterior margin: (0) lateral extensions absent, or, if present, dorsally not connected; (1) dorsally connected by a sclerotized bridge.

In most species of *Savtshenkia* which carry a pair of lateral extensions on the posterior margin of sternite 8, the extensions are dorsally separated by a membranous area (figs. 113, 116, 117, 178, 190). The species and subspecies *corsosignata*, *haennii*, *subsignata subsig-*

nata, and *subsignata cazorla* are distinguished by the presence of a sclerotized dorsal bridge that connects the lateral extensions of sternite 8 (fig. 114).

64. – Sternite 8, posterior margin: (0) variously shaped; (1) in between medial and lateral extensions a pair of medially directed projections.

The ventral margin of sternite 8 in between the medial and lateral extensions is straight or evenly curved in most species of *Savtshenkia* with a three-lobed sternite 8. As an extra feature, *corsosignata*, *haennii*, *subsignata subsignata*, and *subsignata cazorla* have an acute and dorsomedially directed sclerotized projection on each side of the medial extension (fig. 115, arrow).

65. – Sternite 8, posterior margin: (0) variously shaped; (1) lateral extensions dorsoventrally flattened, posterior margin straight, spines confined to posterior margin.

The bulbously swollen lateral extensions of sternite 8 in most species of the clade *cyrnosardensis* to *omega* are more or less circular in cross section and covered with spines on their posterior half, dorsally as well as ventrally (figs. 113-116). The species *mannheimsi*, *omega*, and *trinacria* have the lateral extensions of sternite 8 dorsoventrally flatter and straight along their posterior margins (figs. 117, 177, 178, 189, 190). The spines in these three species are concentrated along the posterior margin of the sternite.

66. – Sternite 9, midventral anterior appendage: (0) apically rounded; (1) apically bifid.

Sternite 9 often carries a more or less developed anterior midventral appendage in the Tipulidae. When present, this appendage has a rounded anterior margin, as it has in the majority of species of *Savtshenkia* (figs. 118, 120). In the species *aspromontensis*, *aster*, *eugeni*, and *serrulifera* the anterior appendage has a bifid apex (fig. 119).

67. – Sternite 9, midventral anterior appendage: (0) a plain structure; (1) dorsally provided with medial carina.

In the presumed groundplan condition of the *Lunatipula* group and *Mediotipula*, the ventromedial part of sternite 9, including the anterior appendage, is a dorsoventrally flattened structure. The majority of species of *Savtshenkia* show an anterior midventral appendage of sternite 9 which looks like a simple tongue-like extension without further modifications (fig. 118). A different form of this structure is present in the species of the clade *fragilina* to *omega*, where the appendage is provided with a medial carina on its dorsal side (fig. 120). Although the height of the carina varies among the pertaining species, it is usually well developed and clearly visible. A similar anterior appendage was also found in the species *hartigiana*. Within the clade *fragilina* to *omega* only *pechlaneri*, *sardosignata*, and *subsignata cazorla* lack a distinct medial carina.

68. – Tergite 9-10, posterior margin: (0) extensions variously shaped; (1) narrowing toward caudally produced tip.

In Tipulidae, tergite 9-10 often has a pair of low and rounded extensions at its posterior margin, a situation that probably represents the groundplan condition of the *Lunatipula* group and *Mediotipula*. Within *Savtshenkia*, only a few species show similar extensions (figs. 121, 122, 125, 126, 127, 156, 157). The species concerned lie in the range *alpha* to *ignobilis*, with the exception of the species *atlas*, *breviantennata*, and *hartigiana*. In the three latter species, the extensions are caudally produced and constricted before their tips. The medial margins of the extensions in these species are slightly concave in dorsal view (figs. 123, 124).

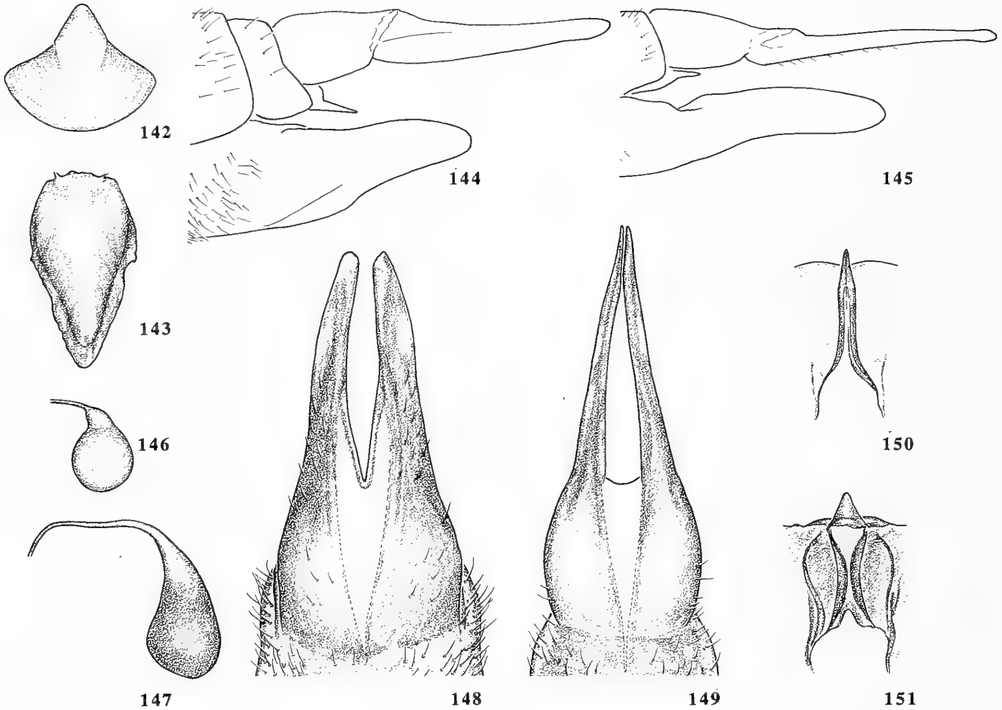
69. – Tergite 9-10, posterior margin: (0) posteroventral sclerotization uninterrupted along posterior margin; (1) separated into two parts by medial incision.

Tergite 9-10 in Tipulidae often has a sclerotized rim running along the ventral side of the posterior margin. An uninterrupted rim probably represents the groundplan state of this character for the *Lunatipula* group and *Mediotipula*. The majority of species of *Savtshenkia* also have a complete and broad posteroventral sclerotized rim along the posterior margin of tergite 9-10 (figs. 121, 123, 125-129, etc., after macerated specimens). Seen in dorsal view, this rim seems to be intersected by the narrow and deep medial incision of tergite 9-10 in the species *atlas* and *breviantennata* (fig. 124).

70. – Tergite 9-10, posterior margin: (0) tips of extensions broadly separate; (1) close together, separated by a narrow gap.

A broad emargination or medial notch usually separates the extensions on the posterior margin of tergite 9-10 in Tipulidae, a situation reflecting the presumed groundplan condition of the *Lunatipula* group and *Mediotipula*. In the majority of species of *Savtshenkia*, the posterior extensions of tergite 9-10 are separated by a broad V-shaped or U-shaped emargination (figs. 121-125, 127, 129, etc.). In *cheethami* and *simulans*, the extensions approach each other medially and are separated by a rather deep and narrow fissure (fig. 126).

71. – Tergite 9-10, posterior margin: (0) extensions



Figs. 142-151. – 142, 143, genital fork, dorsal view; 142, *Tipula* (*Savtshenkia*) *hartigiana*; 143, *T.* (*S.*) *atlas*; 144, 145, ovipositor, lateral view; 144, *T.* (*S.*) *grisescens*; 145, *T.* (*S.*) *hartigiana*; 146, 147, spermatheca; 146, *T.* (*S.*) *hartigiana*; 147, *T.* (*S.*) *villeneuvii*; 148, 149, female sternite 8 and hypogynial valves, ventral view; 148, *T.* (*S.*) *grisescens*; 149, *T.* (*S.*) *ignobilis*; 150, 151, female sternite 9, medial part, ventral view; 150, *T.* (*S.*) *jeekeli*; 151, *T.* (*S.*) *obsoleta*.

posteriorly directed and rounded at tip; (1) laterally curved and pointed at tip.

As noted above, the groundplan condition of tergite 9-10 for the *Lunatipula* group and *Mediotipula* probably shows a pair of broad and rounded extensions on the posterior margin of the tergite. The majority of species of *Savtshenkia*, however, have the tips of the extensions of tergite 9-10 pointed and outwardly curved when seen in dorsal view (figs. 128-130, 137, 139-141, 174, 175, 186, 187).

72. – Tergite 9-10, posterior margin: (0) provided with black spines; (1) spines absent.

The section of the family Tipulidae to which *Savtshenkia* and its outgroups belong, is, among other things, characterized by the presence of black spines on the posterior margin of tergite 9-10. Although such spines are absent in the majority of species of the *Lunatipula* group, there are several species within the group which have the posterior margin of tergite 9-10 armed with spines. For this reason I, putatively, consider this latter state the groundplan condition of the *Lunatipula* group. All species of *Mediotipula* and the majority of species of *Savtshenkia* also show a spinose posterior margin of tergite 9-10 (figs. 121-128, 133-136, 139, 140, 187). Within *Savtshenkia*, total absence of spines on the posterior margin of tergite 9-10 is found in the species *alpha* (figs. 156, 157) and the species of the clade *baltistanica* to *chrysocephala* (figs. 129-132). The species *glaucocinerea* has a few knob-like protuberances on the lower margin of the extensions of tergite 9-10, but lacks distinct spines. Spines along the ventral margin of the extensions of tergite 9-10 are absent in the species *mannheimsi* and *omega*, but in both species a few small spines are present in the dorsal part of the medial cleft (figs. 141, 175).

73. – Tergite 9-10, posterior margin: (0) extensions variously shaped, usually long and laterally directed; (1) extensions present as short spineless points.

The laterally directed extensions of the species of the clade *subnodicornis* to *omega* usually terminate in slender and elongate points (figs. 128-130, 137-141, 174, 175, 186, 187). A number of Afrotropical species of *Savtshenkia* are characterized by the presence of short and acute extensions, viz. the species *aberdareica, akeleyi, asbolodes, chrysocephala, draconis,* and *hancocki* (figs. 131, 132).

74. – Tergite 9-10, posterior margin: (0) spines confined to the extensions; (1) spines present above medial notch.

As is usual in Tipulidae which have tergite 9-10 provided with spines, the spines are concentrated on the posterior margin of the tergite in the majority of species of *Savtshenkia* (figs. 121-128, 139, 140, 175, 187). Spines are present also in the area above the medial notch of tergite 9-10 in the species *aspromontensis, aster, eugeni, odontostyla, serrulifera, sordidipes,* and *venerabilis* (figs. 133-135). In the latter five species, there are about 10 spines in this area (figs. 133, 134), while *aspromontensis* and *aster* carry 20 to 30 spines above the notch (character 78).

75. – Tergite 9-10, posterior margin: (0) variously shaped; (1) broadly V-shaped emarginate with rounded corners.

The Kashmirian species *sordidipes* and *venerabilis* differ from all other species of *Savtshenkia* by the shape of the posterior margin of tergite 9-10. Tergite 9-10 in both species has a broad V-shaped emargination with a small median notch, while the posterior corners are broadly rounded off (fig. 133). The species *sordidipes* and *venerabilis* resemble each other very much, including in details of the male terminalia. Differences are found in the colour of the legs and abdomen and in the height of the anterior part of the inner gonostylus.

76. – Tergite 9-10, posterior margin: (0) single pair of extensions present; (1) two pairs present.

As in most other Tipulidae, the standard number of extensions on the posterior margin of tergite 9-10 in *Savtshenkia* is two (figs. 121-127, 129-133, 136-141, 156, 157, 174, 175, 186, 187). The species *serrulifera, aspromontensis,* and *aster* differ from this by having a medial and a sublateral pair of extensions. Both pairs of extensions are provided with black spines in *aster* and *serrulifera* (fig. 134), in *aspromontensis* the sublateral pair is unarmed (fig. 135).

77. – Tergite 9-10, posterior margin: (0) dorsal surface of extensions rounded; (1) flattened.

In general, the extensions on the posterior margin of tergite 9-10 are rounded on their dorsal surface in Tipulidae, a situation found also in the majority of species of *Savtshenkia.* As a special trait, the species *aspromontensis* and *aster* have the medial pair of extensions of the posterior margin of tergite 10 flattened. The dorsal surface of the medial extensions of both species is glossy black.

78. – Tergite 9-10, posterior margin: (0) dorsal surface in between extensions unarmed or armed with up to 10 spines; (1) dorsal surface in between extensions armed with 20 to 30 spines.

As discussed under character 74, a few species of *Savtshenkia* have the area above the medial notch of tergite 9-10 armed with up to 10 spines (fig. 133, 134). The number of spines is higher in the species *aspromontensis* and *aster.* In *aspromontensis,* there are about 30 spines above the medial notch (fig. 135), in *aster* there are about 20.

79. – Tergite 9-10, posterior margin: (0) extensions present; (1) margin straightened, with small medial notch.

As discussed above, the majority of species of *Savtshenkia* have a pair of lateral extensions on the posterior margin of tergite 9-10, either low and rounded or elongate, diverging and pointed (figs. 128-130, 134, 135, 137-141, 174, 175, 186, 187). The species *interserta,* the three subspecies of *invenusta,* and the species *subvafra* are characterized by a straightened posterior margin of tergite 10 (fig. 136). In *subvafra,* a pair of small posteroventral projections flank the narrow medial notch; such projections are absent in *interserta* and *invenusta.*

80. – Tergite 9-10: (0) broader than long, or about as long as broad; (1) elongate, distinctly longer than broad.

In Tipulidae, tergite 9-10 usually is a relatively short and broad structure, a situation which probably reflects the groundplan condition of the *Lunatipula* group and *Mediotipula.* The majority of species of *Savtshenkia* also show a similar character state (figs. 121, 123-129, 132, 133, 136, 156). In the pertaining species, tergite 9-10 is broader than long and in most of the species shows a broad medial membranous zone. The species and subspecies of the clade *nielseni* to *omega* differ from this in having an elongate tergite 9-10 which is markedly longer than broad (fig. 137, 138, 174, 186). The medial membranous area of tergite 9-10 in these taxa is restricted to a narrow zone, with the exception of the species *boreosignata* which has a relatively wide membranous area (fig. 138).

81. – Tergite 9-10, posterior margin: (0) extensions variously shaped; (1) rather broad, ventral margin straightened, terminating in an acute lateral tip.

As noted above (character 71), most species of *Savtshenkia* have the extensions on the posterior margin of tergite 9-10 laterally directed and pointed at the tip. In the majority of these species, the ventromedial margin of the extensions is distinctly concave when seen in posterior view (fig. 139). The species *corsosignata*, *mannheimsi*, *omega*, *signata*, and *trinacria* are characterized by rather broad extensions of tergite 9-10 of which the ventral margin appears to be almost straight in posterior view (figs. 140, 141, 175, 187).

Female terminalia

82. – Genital fork: (0) broadest width in posterior half; (1) broadest width in anterior half.

In general, the genital fork in Tipulidae is a rather slender structure that widens in its apical posterior part. This situation probably represents the groundplan condition of the *Lunatipula* group. Within *Mediotipula*, the genital fork is slender throughout, with the widest portion lying in the anterior part. The general structure of the genital fork is rather uniform in the species of *Savtshenkia*, being broad with its greatest width lying in the anterior half (figs. 142, 169, 201; lower side in illustrations). The species *atlas* and *breviantennata* are the only studied representatives of *Savtshenkia* which have the broadest part of the genital fork situated in the posterior section (fig. 143; upper side in illustration).

83. – Hypogynial valve, dorsal margin: (0) not blackish sclerotized; (1) blackish sclerotized.

The hypogynial valves are usually uniformly sclerotized in Tipulidae and this condition probably represents the groundplan state of this character for the *Lunatipula* group and *Mediotipula*. All species of *Savtshenkia* of which the female was examined have the dorsal margin of the hypogynial valve blackish sclerotized.

84. – Ovipositor: (0) well developed, elongate; (1) short.

The ovipositor in Tipulidae generally is well developed and has elongate cerci and hypogynial valves, a situation which represents the groundplan condition of the *Lunatipula* group and *Mediotipula*. The same state occurs in the majority of species of *Savtshenkia* (figs. 145, 165, 197). Cerci and hypogynial valves are short in the females of *grisescens*, *holoptera*, *obsoleta*, *pagana*, and *subnodicornis* (fig. 144).

85. – Spermathecae: (0) globular; (1) elongate.

Table 2
Theowald's (1957, 1967) arrangement of species groups of *Tipula* (*Savtshenkia*) based on larvae and pupae (1957), and pupae (1967).

	1957	1967
rufina group	*cheethami*	*cheethami*
	rufina	*rufina*
subnodicornis group	*goriziensis*	(not filed)
	(not mentioned)	*grisescens*
	subnodicornis	*subnodicornis*
subvafra group	*atlas* (as *breviantennata*)	*atlas* (as *breviantennata*)
signata group	*alpium*	*alpium*
	confusa	*confusa*
	nielseni	(not mentioned)
	obsoleta	*obsoleta*
	(not mentioned)	*odontostyla*
	(not mentioned)	*pagana*
	signata	*signata*
	staegeri	*staegeri*

Table 3
Division of the Palaearctic species and subspecies of *Tipula* (*Savtshenkia*) into species groups according to Savchenko (1961) and Theowald (1973, 1978). Theowald's group numbering is given in parentheses, a '?' denotes a species placed by Theowald under restriction in the pertaining group.
Notes: 1: placed in miscellaneous group by Savchenko, under restriction in *convexifrons* group by Theowald; 2: referred to by Theowald only; 3: placed in *rufina* group by Savchenko, in *pagana* group by Theowald; 4: placed in miscellaneous group by Savchenko, under restriction in *pagana* group by Theowald; 5: placed in *cheethami* group by Savchenko, in *alpium* group by Theowald; 6: placed in *rufina* group by Savchenko, under restriction in *obsoleta* group by Theowald; 7: referred to by Savchenko only.

→

Savchenko 1961	Theowald 1973, 1978	Species and subspecies
subnodicornis group	*subnodicornis* group (1)	*postposita* *subnodicornis*
	convexifrons group (2)	*convexifrons* *interserta* ? *venerabilis*[1]
limbata group	*grisescens* group (3)	*goriziensis*[2] *grisescens* (as *macrocera* in Savchenko 1961) *villeneuvii*[2] (as *goriziensis villeneuvii*)
	invenusta group (4)	*invenusta invenusta* *invenusta subinvenusta* *subvafra*
	limbata group (5)	*limbata*
	pagana group (6)	*baltistanica*[3] *glaucocinerea* *holoptera* (as *pagana holoptera*) ? *kiushiuensis*[2] ? *koreana*[4] ? *minuscula*[2] (as *nana*) *nivalis* *pagana* (as *pagana pagana*)
	gimmerthali group (7)	*gimmerthali* *pechlaneri*[2]
rufina group	*rufina* group (8)	*rufina rufina* *rufina maderensis*
	alpium group (11)	*alpium* *subalpium* *macaronesica*[5] *baltistanica*[3] *odontostyla*[6]
cheethami group	*atlas* group (9)	*atlas*[2] *breviantennata* *cheethami* *macaronesica*[5]
marmorata group	*obsoleta* group (10)	*aspromontensis*[2] *lundbladi*[2] ? *mohriana* *multipicta*[2] *obsoleta* ? *odontostyla*[6] *serrulifera*
	marmorata group (12)	*confusa* (as *marmorata*) *eugeni*[2] *jeekeli*
	staegeri group (13)	*boreosignata*[2] *nielseni*[2] *sardosignata* *staegeri* *subsignata*
	signata group (14)	*benesignata* *mannheimsi*[2] *persignata persignata* *persignata tofina* *signata*
miscellaneous group		*koreana*[4] *letifera*[7] *venerabilis*[1]

The shape of the (three) spermathecae in Tipulidae is usually spherical to somewhat ovoid. The groundplan condition of this character for the *Lunatipula* group and *Mediotipula* is probably represented by this state. The majority of females of *Savtshenkia* examined also show this spermathecal form (figs. 146, 170, 202). Only the species *cheethami*, *goriziensis*, *simulans*, and *villeneuvii* are characterized by the presence of elongate spermathecae (fig. 147). It should be noted that the female of *tulipa* is not yet known.

86. – Sternite 8: (0) ventromedial membranous area near base of hypogynial valves V-shaped, encompassing base of medial margins of hypogynial valves; (1) posteriorly terminating in between hypogynial valves.

The ventromedial membranous area of sternite 8 broadens posteriorly and encompasses the bases of the hypogynial valves medially in the species of the *Lunatipula* group and *Mediotipula*, thus probably representing the groundplan condition of this character for the pertaining taxa. The same state is found in the species of *Savtshenkia* which lie in the range *alpha* to *simulans* (fig. 148). The membranous area lies in between the bases of the hypogynial valves in the species of the clade *ignobilis* to *omega* (fig. 149). In these species, the valves are usually broadly separate at the posterior end of the membrane.

87. – Sternite 9: (0) with long and slender medial projection; (1) with broad and short medial projection.

The medial projection of sternite 9 usually takes the form of an elongate slender and pointed structure in Tipulidae. This situation, which probably reflects the groundplan condition of the *Lunatipula* group and *Mediotipula*, is present in the majority of species of *Savtshenkia* (figs. 150, 168, 200). The species *benesignata*, *eugeni*, *holoptera*, *obsoleta*, and *pagana* have a differently built medial projection, which consists of a rather broad structure that is narrowed near midlength (fig. 151). In *eugeni*, the cavities next to the medial projection are restricted to the anterior part of sternite 9, whereas they run along the whole length of the medial projection in the four other species.

DISCUSSION OF ADOPTED PHYLOGENY

The character state matrix as given in table 4 was used to establish the phylogeny of the species and subspecies of *Savtshenkia*. The character states are binary coded, polymorphies are coded '–', absent data '?'. Initially all characters employed had the same weight 1. The character state matrix of table 4 was run under the command 'mh*; bb*;' of the parsimony program Hennig86. The first part of the command (mh*;) constructs several trees to which it applies branch-swapping, retaining one tree for each initial tree, while the second part of the command (bb*;) applies extended branch-swapping to each of the input trees, retaining all most parsimonious trees. Although it does not guarantee to find all trees of minimal length, applying 'mh*; bb*;' to extensive data sets offers a good alternative for the time-consuming implicit enumeration options of Hennig86 that definitely result in finding all trees of minimal length (Farris 1988). The procedure followed resulted in 28 equally most parsimonious trees with length 157, consistency index 55, and retention index 88.

Subsequently successive weighting was carried out under the command 'mh*; bb*; xs w; cc;'. This procedure uses the fit of the characters to the input trees to calculate the weights as the product of the character consistency and character retention indices, which are then scaled in the range 0-10 (Farris 1988). Successive weighting resulted in 14 equally most parsimonious trees with length 723, consistency index 84, and retention index 96. This result was obtained after a single weighting run and did not improve upon further repeats. The calculated weights for the characters are given in table 5, the strict consensus tree of the 14 equally most parsimonious trees is shown in fig. 2. The strict consensus tree of the 14 trees resulting of successive weighting (fig. 2) differs from the strict consensus tree of the 28 trees without successive weighting in the presence of the clade *baltistanica* to *chrysocephala* in the former. The internode leading to this clade is not recognized in the consensus tree of the 28 trees without weighting, lowering the grouping *baltistanica* to *chrysocephala* one level relative to its position in fig. 2. For the remainder the topologies of both consensus trees are identical. The results of the phylogenetic analysis will be discussed with reference to fig. 2.

At the base of the cladogram a trichotomy of the clades *alpha* and *grisescens*, *hartigiana* to *simulans*, and *ignobilis* to *omega* is found. The species pair *alpha* and *grisescens* probably are sister species as exemplified by two homoplasies and one reversal [characters 2 (length of male antenna), 9 (size of gonapophysis), and 4 (shape of cell m1), respectively].

The second clade seems to be better substantiated by the characteristic shape of the gonapophysis (character 10) and the acute posterior corner of the base of the inner gonostylus (character 32). The first lineage within this clade leads to a triplet containing the species *hartigiana* as the sister species of the pair *atlas* and *breviantennata*. In its original description, *hartigiana* was referred to the *atlas* group sensu Theowald (table 3) (Theowald, Dufour & Oosterbroek 1982). Besides the species *atlas*, *breviantennata*, and *hartigiana*, the *atlas* group sensu Theowald also included the species *cheethami*. As the present analysis shows, the latter species seems to be more closely related to the species of the second group within the clade *hartigiana* to *simulans*. This group, the clade *tulipa* to *simulans*, consists of the species *tulipa*, *villeneuvii*, *goriziensis*, and the pair *cheethami* and *simulans*. Dufour (1983), on describing the species *tulipa*, placed it in the *grisescens* group sensu Theowald which by then contained the species *goriziensis*, *grisescens*, and *villeneuvii* (table 3). Dufour (1983) suggested that *grisescens* stands apart from the other three species, including *villeneuvii*, thus countering Theowald & Oosterbroek's (1981) contention that *villeneuvii* should be regarded a subspecies of *grisescens*. The results of the present analysis endorse Dufour's views.

The third basal clade in fig. 2 contains the remainder of *Savtshenkia*. It opens with the successive branching off of the species *ignobilis* and *subnodicornis*, followed by the remainder of species of *Savtshenkia* which constitute the monophyletic group *baltistanica* to *omega*. The species *subnodicornis* was placed either near *goriziensis*, *grisescens*, or *postposita* by Savchenko (1961) and Theowald (1957, 1967, 1973, 1978) (tables 2, 3). The species listed belong to the phylogenetically more basal species of *Savtshenkia*, but none of them appears to be the actual sister species of *subnodicornis*.

The clade *baltistanica* to *chrysocephala* contains the majority of species of *Savtshenkia* with a non-spinous posterior margin of tergite 9-10 (character 72). The only other species of *Savtshenkia* in which the spines on the extensions of tergite 9-10 are absent, are the phylogenetically basal species *alpha* and the derived species *mannheimsi* and *omega*. The basal trichotomy of the clade *baltistanica* to *chrysocephala* is constituted of the species *baltistanica*, the species pair *glaucocinerea* and *postposita*, and the clade *lundbladi* to *chrysocephala*. The clade *lundbladi* to *chrysocephala* contains almost all strictly Atlantic (viz. *lundbladi*, *multipicta*, and *rufina maderensis*), and all Afrotropical species of *Savtshenkia* (viz. *nephrotomoides* to *chrysocephala*). (The only remaining Atlantic species of *Savtshenkia* is *macaronesica* from the Azores, a species closely related to *alpium*, see below.) As table 3 shows, the Palaearctic species of the clade *baltistanica* to *chrysocephala* were placed in various groupings by Savchenko (1961) and Theowald (1973). (The phylogeny of the Afrotropical species presented here should be regarded as preliminary only. Most species are known of just a few specimens, thus giving the strong impression that the Afrotropical fauna is poorly known. Furthermore, the species are in general very similar to each other and homoplasy in this group seems to be rather common. As the present study is primarily concerned with the western Mediterranean species of *Savtshenkia*, this issue is not further explored here.)

Modifications of the posterior margin of the male sternite 8 (characters 55, 57) suggest that the remainder of species of *Savtshenkia*, the clade *alpium* to *omega*, constitute a monophyletic group. The contours of this group were recognized by Theowald (1957, 1967) in his *signata* group (table 2), by Savchenko (1961) in his *marmorata* group, and by Theowald (1973) in his *obsoleta*, *alpium*, *marmorata*, *staegeri*, and *signata* groups (table 3). Within the clade *alpium* to *omega*, the basal lineage is composed of the species pair *alpium* and *macaronesica*. Theowald (1973) correctly grouped both species in his *alpium* group, but Savchenko (1961) placed *macaronesica* in his *cheethami* group (table 3). The species *subalpium* is probably closely related to *alpium* and *macaronesica* (see Appendix B). The sister group of *alpium* and *macaronesica* is substantiated by apomorphies of the sperm pump (characters 48, 49). The basal phylogeny of this clade (*jeekeli* to *omega*) could not be fully resolved. Four lineages constitute a polytomy, with the first containing the single species *jeekeli*, the second the clade *obsoleta* to *pagana*, the third the clade *confusa* to *aster*, and the fourth the clade *fragilis* to *omega*. The species of the clade *obsoleta* to *pagana* are most readily distinguished from the other species of *Savtshenkia* by the peculiar form of sternite 8 (character 58). Notwithstanding this, Savchenko (1961) as well as Theowald (1973) placed *obsoleta* in a species group different from *holoptera* and *pagana* (table 3). [I here retain *holoptera* as a taxon separate from *pagana*. Both taxa are usually distinguished by the length of the wing and build of the legs in the female (macropterous with slender legs in *holoptera*, brachypterous with stoutish legs in *pagana*), and the shape of the posterior margin of male sternite 8 and the number of setae it carries (more deeply emarginate with one seta on tubercle in *holoptera*, less emarginate to truncate with about five to seven setae on tubercles in *pagana*) (Coe 1950; Edwards 1939). However, numbers of setae on the posterior margin of sternite 8 intermediate to those of typical *holoptera* and *pagana* can be found in certain specimens (Eiroa 1987; see also Hutson & Vane-Wright 1969). The occurrence of intermediate stages of fully winged and brachypterous forms has been recorded within *Savtshenkia* for the female of *gimmerthali* (Dufour & Brunhes 1984). As long as a similar variability of wing length is not recorded for females of the pair *holoptera* and *pagana*, I prefer to keep them apart. This the more so as the studied male specimens of *holoptera* show a slight difference with those of *pagana* in the presence of a small acute and blackish sclerotized extension at the posterior end of the dorsal edge of the inner gonostylus.]

The clade *confusa* to *aster*, which is substantiated by the elongate aedeagus (character 15) and the presence

Table 4. Character state matrix of *Tipula* (*Lunatipula*), *T.* (*Mediotipula*), and the species and subspecies of *T.* (*Savtshenkia*).

Character		10		20		30		
Lunatipula	00000	00000	00000	00000	00000	00000	00000	000
Mediotipula	00010	00000	00000	00000	00010	00000	00000	000
aberdareica	01010	00000	10000	00000	00001	00000	00000	000
akeleyi	01010	10000	10000	00001	00001	01000	00000	000
alpha	01000	00010	00000	00000	00000	00000	00000	000
alpium	00010	00010	00000	00000	10000	00000	00000	000
asbolodes	01010	00000	10000	00000	00001	00000	00000	000
aspromontensis	00010	00000	00001	000–0	00000	00110	00000	000
aster	00010	00000	00001	00000	00000	00110	00000	000
atlas	10010	01001	00000	00010	00000	00000	01000	000
baltistanica	00010	00000	00000	00000	00000	00000	00000	000
benesignata	00010	00000	00001	00000	01100	00000	00000	110
boreosignata	00010	00010	00000	00000	01000	00000	00000	100
breviantennata	10010	01001	00000	00010	00000	00000	01000	000
caligo	01010	10000	10000	00001	00001	01000	00000	000
cheethami	00011	00001	00000	00010	00100	00000	01100	000
chrysocephala	01010	10000	10000	00001	00001	01000	00000	000
confusa	00010	00000	00001	00000	00000	00000	00001	000
corsosignata	00010	00100	00101	00100	01010	10001	00000	100
cyrnosardensis	10010	00000	01001	00000	00010	00000	00000	100
draconis	01010	00000	00000	00000	00001	00000	00000	000
eleonorae	00010	00000	00000	00000	01000	00000	00000	100
elgonensis	01010	00000	00000	00000	0000?	00000	00000	000
eugeni	00010	00000	00001	00000	00000	00000	00001	000
fragilina	00010	00000	00001	01000	00010	00001	00000	100
fragilis	00010	00000	01001	00000	00000	10000	00000	000
gimmerthali	00010	00000	00001	00000	00010	00001	00000	100
g. mattheyi	00010	00000	00001	00000	00010	00001	00000	100
g. pteromaculata	00010	00000	00001	00000	00010	00001	00000	100
glaucocinerea	00000	00000	00000	00000	00000	00000	00000	000
goriziensis	00010	00001	00000	00000	00100	00000	01100	000
graciae	00010	00000	00001	00000	00000	00000	00000	000
grisescens	01000	00010	00000	00000	00000	00000	00000	000
haennii	00010	00000	00101	00100	01010	10000	00000	100
hancocki	00010	00000	10000	00000	00001	00000	00000	000
hartigiana	00010	00001	00000	00010	00000	00000	01000	000
holoptera	01010	00000	00000	10000	00000	00000	00000	000
ignobilis	00010	00000	00000	00000	00000	00000	00000	000
interserta	00010	00010	00001	00000	00000	00000	00000	000
invenusta	00010	00000	00001	00000	00010	00000	00000	100
i. microinvenusta	00010	00000	00001	00000	00010	00000	00000	100
i. subinvenusta	00010	00000	00001	00000	00010	00000	00000	100
jeekeli	00010	00000	00000	00000	00000	00000	00001	000
limbata	00010	00000	00001	01000	00000	00001	00000	100
lundbladi	00110	00000	00001	00000	00001	00000	00000	000
macaronesica	00010	00010	00000	00000	10000	00000	00000	000
mannheimsi	00010	00000	00001	00000	01100	00000	10000	110

	50		60		70		80		
000	00000	00000	00000	00000	00000	00000	00000	00000	00
000	00000	00000	00000	00000	00000	00000	00000	01000	00
000	01000	00100	00000	00000	00000	11100	00000	0????	??
000	01000	00100	00000	00000	00000	11100	00000	0????	??
000	00000	00100	00000	00000	00000	01000	00000	01100	00
000	01000	00101	01000	00000	00000	10000	00000	01100	10
000	01000	00100	00000	00000	00000	11100	00000	0????	??
010	01101	00100	01000	00000	10000	00010	11100	01100	10
000	01111	00101	01000	00000	10000	00010	11100	0????	??
100	00000	00100	00000	00000	00110	00000	00000	00100	00
000	01000	00100	01000	00000	00000	11000	00000	01100	10
001	01110	00111	01000	11000	01000	10000	00001	01100	11
001	01010	01111	01000	11000	01000	00000	00001	0????	??
100	00000	00100	00000	00000	00110	00000	00000	00100	00
000	01000	00100	00000	00000	00000	11000	00000	01100	10
000	00000	00100	00000	00000	00001	00000	00000	01101	00
000	01000	00100	00000	00000	00000	11100	00000	0????	??
000	01111	10101	01000	00000	00000	10000	00000	01100	10
001	01110	00111	01000	11110	01000	10000	00001	11100	10
001	01110	00111	01000	01000	01000	10000	00000	01100	10
000	01000	00100	00000	00000	00000	11100	00000	0????	??
001	01010	01111	01000	11000	01000	10000	00001	0????	??
000	01000	00100	00000	00000	00000	11000	00000	0????	??
001	01101	00101	01000	00000	10000	10010	00000	01100	11
001	01110	00111	00001	00000	01000	10000	00000	01100	10
001	01110	00101	01000	00000	00000	10000	00000	01100	10
001	01110	00110	00000	00000	01000	10000	00000	01100	10
001	01110	00110	00000	00000	01000	10000	00000	0????	??
000	01110	00110	00000	00000	01000	10000	00000	0????	??
000	01000	00100	00000	00000	00000	11000	00000	01100	10
000	00000	00100	00000	00000	00000	00000	00000	01101	00
000	01111	00101	01000	00000	00000	00000	00000	0????	??
0000	00000	00100	00000	00000	00000	00000	00000	01110	00
0001	01110	00111	01000	11110	01000	10000	00001	0????	??
0000	01000	00100	00000	00000	00000	11100	00000	0????	??
0100	00000	00100	00000	00000	01100	00000	00000	01100	00
0000	01110	00101	01110	00000	00000	10000	00000	01110	11
0000	00000	00100	00000	00000	00000	00000	00000	01100	10
0000	01101	10100	00000	00000	00000	00000	00010	01100	10
0001	01110	00111	00000	10000	01000	00000	00010	0????	??
0001	01110	00111	00000	10000	01000	00000	00010	01100	10
0001	01110	00111	00000	10000	01000	10000	00010	01100	10
0000	01110	00101	01000	00000	00000	10000	00000	01100	10
0001	01110	00111	00001	00000	01000	10000	00000	01100	10
0010	01000	00101	00000	00000	00000	11000	00000	01100	10
0000	01000	00101	00000	00000	00000	10000	00000	0????	??
0001	01110	00111	01000	11001	01000	11000	00001	1????	??

Table 4. (continued) Character state matrix of *Tipula* (*Lunatipula*), *T.* (*Mediotipula*), and the species and subspecies of *T.* (*Savtshe*

Character		10		20		30		
multipicta	00110	00000	00001	00000	00001	00000	00000	00
nephrotomoides	00010	00000	00000	00001	00001	00000	00000	00
nielseni	00010	00000	00001	00000	00010	00001	00000	10
obsoleta	00010	01000	00001	10000	00000	00000	00000	00
odontostyla	00010	00000	00001	00000	00010	00000	00000	10
omega	00010	00000	00001	00000	01100	00000	10000	11
ornata	00010	00000	00001	00000	00000	10000	00000	10
pagana	01010	00000	00000	10000	00000	00000	00000	00
pechlaneri	00010	00000	00001	00000	01010	00001	00000	10
persignata	00010	00000	00001	00000	01100	00000	10000	111
p. tofina	00010	00000	00001	00000	01100	00000	10000	111
phoroctenia	00010	00000	01001	00000	00000	00000	00000	00
postposita	00000	00000	00000	00000	00000	00000	00000	00
rufina	00010	00000	00000	00000	00001	00000	00000	00
r. maderensis	00010	00000	00001	00000	00001	00000	00000	00
sardosignata	00010	00000	00001	00000	00010	00000	00000	10
serrulifera	00010	00000	00001	00000	00000	00110	00000	00
signata	00010	00000	00001	00000	01100	00000	10000	11
simulans	00011	00001	00000	00010	00100	00000	01100	00
sordidipes	00010	00000	00001	00000	00000	00000	00000	00
staegeri	00010	00000	00001	00000	00010	00000	00000	10
subnodicornis	000-0	00000	00000	00000	00000	00000	00000	00
subsignata	00010	00100	00111	00100	01010	10000	00010	10
s. cazorla	00010	00100	00111	00100	01010	10000	00010	10
subvafra	00010	00000	00001	01000	00010	00001	00000	10
trinacria	00010	00000	00001	00000	01100	00000	10000	11
tulipa	00010	00001	00000	00000	00100	00000	01000	00
venerabilis	00010	00000	00001	00000	00000	00000	00000	00
villeneuvii	10010	00001	00000	00000	00100	00000	01000	00

of elongate and anteriorly directed posterior apodemes of the sperm pump (character 50), contains as its first lineage the triplet *confusa*, *interserta*, and *ornata*. Although differing in most genital features, these three species share the presence of the quite remarkable slender elongate and anteriorly extended posterior apodemes of the sperm pump (character 51). In fig. 2, the remainder of the clade *confusa* to *aster* is depicted as a monophyletic group which is substantiated by a single reversal only. The reversal concerns the redirection and reduction of the extensions of the posterior margin of tergite 9-10 (character 71). The extensions are rather differently shaped in the species of this grouping and its actual monophyly is open to question. The species *eugeni*, which is included in this grouping, has the extensions of tergite 9-10 well developed and laterally extended.

Theischinger (1983) correctly considered his species *aster* to be the closest relative of *aspromontensis*.

Theowald (1973) placed the species *confusa* (as *marmorata*), *eugeni*, and *jeekeli* in his *marmorata* group on account of the peculiar shape of their inner gonostyli (character 35). When other characters are taken into consideration, the three species appear not to be closely related, forcing the conclusion that the characteristic shape of the inner gonostylus must be due to homoplasy.

Next in fig. 2 is the clade *fragilis* to *omega*, in which the Nearctic species pair *fragilis* and *phoroctenia* branch off first, followed by the species *odontostyla*.

The remainder of species of *Savtshenkia* constitute the monophyletic group *fragilina* to *omega* of which the first lineage leads to the clade *fragilina* to *invenusta microinvenusta*. This latter clade contains species which are characterized by the presumably secondary absence of spines on the posterior margin of male sternite 8 (character 57). It is composed of species which Theowald (1973) arrayed in his *gimmerthali*, *invenusta*, and *limbata* groups (table 3), together with the Nearctic species *fragilina* (the species *mohriana*

	5		6		7		8		
	0		0		0		0		
0010	01000	00101	01000	00000	00000	11000	00000	01100	10
0000	01000	00100	00000	00000	00000	11000	00000	01100	10
0001	11110	00111	01000	11000	01000	10000	00001	01100	10
0000	01110	00101	01100	00000	00000	10000	00000	01110	11
0001	01110	00101	01000	00000	00000	10010	00000	0????	??
0001	01110	00111	01000	11001	01000	11000	00001	1????	??
0001	01111	10101	00000	00000	00000	10000	00000	01100	10
0000	01110	00101	01110	00000	00000	10000	00000	01110	11
0001	01110	00110	00000	00000	00000	10000	00000	01100	10
0001	01110	00111	01000	11000	01000	10000	00001	0????	??
0001	01110	00111	01000	11000	01000	10000	00001	0????	??
0001	01110	00101	01000	00000	00000	10000	00000	01100	10
0000	01000	00100	00000	00000	00000	11000	00000	0????	??
0000	01000	00101	10000	00000	00000	11000	00000	01100	10
0000	01000	00101	10000	00000	00000	11000	00000	01100	10
0001	11110	00111	01000	11000	00000	10000	00001	01100	10
0000	01111	00101	01000	00000	10000	00010	10000	01100	10
0001	01110	00111	01000	11000	01000	10000	00001	11100	10
0000	00000	00100	00000	00000	00001	00000	00000	01101	00
0000	01111	00100	01000	00000	00000	00011	00000	01100	10
0001	01110	00111	01000	01000	01000	10000	00000	01100	10
0000	00000	00100	00000	00000	00000	10000	00000	01110	10
0001	01110	00111	01000	11110	01000	10000	00001	01100	10
0001	01110	00111	01000	11110	00000	10000	00001	0????	??
0001	01110	00111	00001	00000	01000	10000	00010	01100	10
0001	01110	00111	01000	11001	01000	10000	00001	11100	10
0000	00000	00100	00000	00000	00000	00000	00000	0????	??
0000	01111	00100	01000	00000	00000	00011	00000	0????	??
0000	00000	00100	00000	00000	00000	00000	00000	01101	00

and *productella* probably also belong here; see Appendix B).

The clade *fragilina* to *invenusta microinvenusta* contains two trichotomies. The exact relationships of the species *fragilina, limbata* and *subvafra* as well as those between the three subspecies of *gimmerthali* are hard to establish. The subspecies *gimmerthali pteromaculata* was described as differing from the nominotypical subspecies by its darker colour, spotted wings, and relatively short second flagellomere (Theowald, Dufour & Oosterbroek 1982). Examination of material of the nominotypical form of *gimmerthali*, however, revealed that the length of the second flagellomere varies considerably within this subspecies. The relative length of the second flagellomere thus offers no arguments to distinguish *gimmerthali pteromaculata* from the nominotypical subspecies. [The length of the second male flagellomere has also been used to distinguish *gimmerthali* from *pechlaneri* (Mannheims & Pechlaner 1963). Considering the variability of this character within *gimmerthali* it has proved to be non-applicable here. The species *gimmerthali* and *pechlaneri* are more easily distinguished on account of the structure of the inner gonostylus and the shape of male tergite 9-10 (see also Appendix C). The monophyly of the three subspecies of *gimmerthali* could be demonstrated by the shape of the inner gonostylus only (character 41)]. Useful differences between *gimmerthali gimmerthali* and *gimmerthali pteromaculata* are found in the autapomorphous larger outer gonostylus and relatively plump anterior tip of the inner gonostylus of *gimmerthali pteromaculata* (cf. figs. 66 and 67, and 83 and 84). The subspecies *gimmerthali mattheyi*, known of the male holotype only (not examined), apparently differs from the other subspecies by the autapomorphous absence of a posterior projection on the outer gonostylus and the reduced armature of the posterior margin of tergite 9-10 (Theowald & Dufour 1983). [The females of both *gimmerthali mattheyi* and *gimmerthali pteromaculata*

Table 5. Weights of characters after single weighting run using the command 'mh*; bb*; xs w; cc;' of Hennig86.

Character	Weight	Character	Weight	Character	Weight
1	1	31	10	61	4
2	1	32	10	62	10
3	10	33	10	63	10
4	1	34	10	64	10
5	10	35	0	65	10
6	10	36	4	66	10
7	2	37	10	67	1
8	10	38	10	68	10
9	1	39	10	69	10
10	10	40	10	70	10
11	10	41	10	71	1
12	2	42	10	72	2
13	10	43	10	73	4
14	10	44	2	74	4
15	1	45	2	75	10
16	10	46	10	76	10
17	10	47	10	77	10
18	10	48	4	78	10
19	3	49	2	79	1
20	3	50	10	80	10
21	10	51	10	81	3
22	4	52	10	82	2
23	4	53	10	83	10
24	2	54	10	84	1
25	10	55	1	85	10
26	2	56	10	86	10
27	10	57	1	87	1
28	10	58	10		
29	10	59	10		
30	2	60	10		

remain unknown. Those of *gimmerthali gimmerthali* are usually brachypterous, but populations of the nominotypical form of *gimmerthali* are known from Switzerland which have female wing lengths ranging from the brachypterous to the fully winged condition (Dufour & Brunhes 1984). Dufour (1990) furthermore recorded hemipterous females of *gimmerthali* from the eastern side of the Sierra Nevada, Spain.]

The species *invenusta* presently contains three subspecies. Differences between the subspecies can be found in details of the male terminalia and in the ventral distance between the eyes. The examined specimens of *invenusta invenusta* conform to Riedel's (1919) description of the species as having rounded posterolateral corners on tergite 9-10 ['Lam. term. sup. (...) mit abgerundeten Ecken']. However, illustrations of the terminalia of '*invenusta invenusta*' by Savchenko (1961) and Theowald (1973) depict tergite 9-10 with acute posterior extensions. Examination of material present in ZMAN showed that Theowald actually figured a specimen that can only be identified as *invenusta subinvenusta*. However, considering Savchenko's illustration there still is a possibility that the structure of the posterior margin of tergite 9-10 varies within *invenusta invenusta*. [All three described subspecies bear spines on the posteroventral margin of tergite 9-10. Having examined several of its paratypes, I can not corroborate Dufour's (1990) observation that spines are absent from the posterior margin of tergite 9-10 in his *invenusta microinvenusta*.] Another complicating factor in maintaining the three recognized subspecies is the observation that Tipulidae occurring at high geographical latitudes or high altitudes usually have smaller eyes than their relatives living under more moderate ecological conditions. Therefore, the size of the eyes in specimens of *invenusta* might well be an ecotypic differentiation in response to local environmental conditions and thus would be of little value in separating the subspecies. The complicated nature of the taxonomy of *invenusta* is furthermore illustrated by the fact that Alexander described *invenusta invenusta* under three different names, viz. *docilis* (correctly synonymized with *invenusta* by Savchenko 1961), and *insignifica* and *packardi* (synonymized in this paper; see Appendix A, synonymy). Hancock (1988) suggested that yet another subspecies might be introduced to accommodate a morphologically slightly deviating population from Andorra (Pyrenees). I here would like to stress the need to study the variability of this taxon over its immense Holarctic range before even considering to introduce new formal names for single isolated populations. [The most recently published map showing the Palaearctic distribution of *invenusta* is the one given by Dufour (1992).]

The clade *cyrnosardensis* to *omega* contains the species of Theowald's (1973) *staegeri* and *signata* species groups (table 3). Most species of this clade are easily recognized by the presence of the bulbous and spinous extensions on the posterior margin of sternite 8 (character 62). The clade opens with a trichotomy consisting of the species *cyrnosardensis* and *staegeri* in combination with a clade which includes the remainder of the species. Both *cyrnosardensis* and *staegeri* are species distinguished by a number of autapomorphies but apparently lack any further character states that could enable the resolution of their exact phylogenetic position.

The species *nielseni* and *sardosignata* are depicted here as sister species as is suggested by their broad based outer gonostyli, although the overall shape of this structure differs remarkably in both species (character 46). The two species are, moreover, distinguished from each other by the autapomorphous form of the inner gonostylus and the shape of sternite 8. Their tentative sister species relationship could not be substantiated by other apomorphies.

Although on quite different grounds, the clade *haennii* to *subsignata cazorla* contains the four taxa which were recognized as a monophyletic group by Dufour (1991). The characters employed in the present analysis result in a sequence of relationships between these taxa which differs from the solution provided by Dufour. Compared with Dufour's cladogram, *corsosignata* and *haennii* have changed places in the present phylogeny, necessitating the elevation in rank of *haennii* from subspecies of *subsignata* to species (see Appendix A). Dufour substantiated his concept of a monophyletic group containing *corsosignata*, *haennii*, *subsignata subsignata*, and *subsignata cazorla* by the degree of sclerotization and shape of the ventromedial appendage of male sternite 8 and the degree of sclerotization of female sternite 9 (Dufour 1991, characters 1 and 2). I can see no essential differences between the sclerotization and shape of the ventromedial extension of male sternite 8 in this clade of four taxa and that of other derived members of *Savtshenkia* such as *persignata*, *sardosignata*, and *signata*, and prefer to consider it a plesiomorphy at this level. The presence of an unsclerotized female sternite 9 as a synapomorphy for the members of the clade *haennii* to *subsignata cazorla* has not been employed in this paper because it is not always clear whether sternite 9 should be valued as sclerotized or not in species of *Savtshenkia*. Moreover, the female of *subsignata cazorla* remains unknown. Dufour considered *haennii* the sister species of the pair *subsignata subsignata* and *subsignata cazorla* because of the presence of a ridge on what he denoted as the median part of the inner gonostylus (Dufour 1991, character 3). As discussed under character 34, I consider the presence of the anteriorly extended part of the lateral ridge of the inner gonostylus an apomorphy of the pair *subsignata subsignata* and *subsignata cazorla*. Of the three apomorphies of Dufour supporting the monophyly of *subsignata subsignata* and *subsignata cazorla*, two appear to be invalid (Dufour 1991, characters 4 and 5). The continuity of the posterior and ventral parts of the lateral ridge of the inner gonostylus in these two subspecies (Dufour 1991, character 4) probably is a plesiomorphy (see discussion under character 34). The relatively broad base of the outer gonostylus in *subsignata subsignata* and *subsignata cazorla* (Dufour 1991, character 5) probably also represents a plesiomorphy considering the situation in most related species. The width of the base of the outer gonostylus furthermore varies within the species and subspecies and differs only slightly from that in *haennii*. Dufour's third argument for the monophyly of the pair *subsignata subsignata* and *subsignata cazorla* (Dufour 1991, character 6, shape of the gonapophysis) is employed in this paper as well (character 14).

Following on his description of *eleonorae*, Theischinger (1978) suggested that this species is most closely related to *benesignata*. I am, however, convinced that the sister species of *eleonorae* is *boreosignata*, which is substantiated by the almost identical shape of the inner gonostylus (character 42) and the bizarre modification of the aedeagal complex (character 52). Both *boreosignata* and *eleonorae* are known of their holotypes only, with the type localities lying about 2500 kilometers apart, that of *boreosignata* in northern Sweden and that of *eleonorae* in western Rumania!

The clade *benesignata* to *omega* contains the species which Theowald (1973) included in his *signata* group, with the addition of the species *omega* and *trinacria* described herein as new.

DISTRIBUTION

In this section I will give a brief account on the distribution of the species and subspecies of *Savtshenkia*. As noted above, more detailed information on the distribution of the western Mediterranean species and subspecies and their closest relatives will be given in a forthcoming paper on the historical biogeography of the western Mediterranean area. A survey of the distribution of the species and subspecies of *Savtshenkia* is given for the Afrotropical Region by Hutson (1980, under *Pterelachisus*), the Nearctic Region by Alexander (1965b), the Oriental Region by Alexander &

Alexander (1973), and the Palaearctic Region by Oosterbroek & Theowald (1992). The sequence of taxa in the summary below follows that of fig. 2.

The two species of the pair *alpha* and *grisescens* differ considerably in their ranges. The first species is known of its type locality in the Rodna Mountains of northern Rumania only, while *grisescens* is distributed over the central belt of Europe eastwards to the Altai Mountains in central Asia.

The species of the clade *hartigiana* to *simulans* are confined to the western Palaearctic, with most of them having a restricted range. The species *hartigiana* is known from Corsica and Sardinia only, *atlas* is recorded from Algeria and Morocco, and *breviantennata* from Spain, southern Switzerland, Corsica, Italy, including Sardinia, and northern Algeria. The species *tulipa* was described from two localities in southern Switzerland, *villeneuvii* is known from central Spain, while *goriziensis*, *cheethami* and *simulans* are more widely distributed over the mountainous areas of central Europe. The species *ignobilis* has an eastern Nearctic distribution between about 35° and 50°N latitude. The species *subnodicornis* has a wide range extending from the Faeroes and Ireland in the west over central Europe towards Lake Baykal in the east.

The clade *baltistanica* to *chrysocephala* contains species which cover a wide geographic area. The species *baltistanica* occurs in the Caucasus, Tadzhikistan and Kashmir, *glaucocinerea* has an arctic Siberian distribution, as does its presumed sister species *postposita*, which is furthermore known from northern Finland, the Altai Mountains and Mongolia. The species *lundbladi* is an endemic of Madeira, the species *multipicta* is presently recorded from the Canary Islands only. The nominotypical form of *rufina* is widespread, ranging from Iceland and north-west Africa towards Tadzhikistan in the east, while the subspecies *rufina maderensis* is endemic to Madeira. The majority of species of the grouping *nephrotomoides* to *chrysocephala* is distributed in the mountainous areas surrounding Lake Victoria in eastern Africa. The only member of this group that does not occur in this region is the species *draconis* from South Africa (Natal).

The species *alpium* has a wide distribution which includes most of Europe. It also occurs along the east-coast of the Nearctic Region between about 42° and 55° N latitude (see Appendix A, synonymy, under *nebulipennis*). The species *macaronesica* is endemic to the Azores.

As is presently known, the phylogenetically rather isolated species *jeekeli* has a disjunct distribution throughout the Mediterranean, ranging from Galicia in north-west Spain to Cyprus in the east.

The species *obsoleta* is distributed over most of Europe, extending its range towards Georgia in the south-east, while the pair *holoptera* and *pagana* is confined to the central belt of Europe, with *holoptera* having a disjunct distribution in south-west England, north-west Spain, and Czechia.

Of the species of the clade *confusa* to *aster*, *confusa* occurs over most of Europe, including the Faeroes and Ireland in the north-west. The species *interserta* has a distribution ranging from the central European mountains in the west towards the Tuva in the east. The beautiful *ornata* was described on the basis of a single male from northern Israel, but a series of this species, including females, was collected recently on Cyprus by Pjotr Oosterbroek and Cita Hartveld. It seems that the species *graciae* still is known from its type locality in southern California only. Both *sordidipes* and *venerabilis* are restricted to Kashmir. The species *eugeni* is presently known from Corsica, Sicily, and southern Italy. The species *serrulifera* has a more extensive distribution, occurring in mountainous areas from the Pyrenees in the west to the Caucasus in the east. Theowald (1973) described *aspromontensis* from southern Italy (Aspromonte), but more recently it was collected also in Greece (Peloponnisos, Crete). The species *aster* still is known of its holotype only, originating from the Greek island Thasos in the northern Aegean Sea.

The presumed sister species *fragilis* and *phoroctenia* have a Nearctic distribution which extends across the continent in the region of the 50th degree of latitude. The species *odontostyla* is known from the north-eastern coastal areas of the Black Sea and the Greek island Thasos.

The species *fragilina* has a Nearctic distribution, being recorded from the north-western part of the continent, ranging from Alaska to Colorado, as well as from Maine on the east coast (under its synonym *broweri*). The species *limbata* is widespread in the mountainous areas of Eurasia, *subvafra* seems to be confined to continental western Europe. The members of the clade *pechlaneri* to *gimmerthali pteromaculata* are distributed in the mountainous areas of the western Palaearctic Region, with *pechlaneri* having a disjunct distribution from Andorra in the Pyrenees to northern Iran, *gimmerthali gimmerthali* ranging from the Sierra Nevada of Spain in the south towards northern Scandinavia and eastwards to the Caucasus, *gimmerthali mattheyi* being restricted to southern France, and *gimmerthali pteromaculata* to Corsica.

The three subspecies of *invenusta* differ considerably in the extent of their distribution area. The subspecies *invenusta microinvenusta* is presently known only from southern Spain (Sierra Nevada), the subspecies *invenusta subinvenusta* has a wider range in the mountains of central Europe, while the nominotypical subspecies disjunctly ranges across Eurasia and also occurs in eastern North America (see Appendix A, synonymy, under *insignifica* and *packardi*).

The species *cyrnosardensis* is endemic to Corsica and Sardinia, *staegeri* occurs in Europe from the Faeroes to northern Spain in the west towards the coastal areas of the Baltic Sea in the east. Both species of the pair *nielseni* and *sardosignata* have a restricted range, with *nielseni* being confined to the Alps, and *sardosignata* occurring on Corsica and Sardinia, as well as in southern France.

The four members of the clade *haennii* to *subsignata cazorla* are also restricted to Europe, with *haennii* being recorded from the French and Spanish Pyrenees, *corsosignata* occurring on Corsica, *subsignata cazorla* in northern Spain, and *subsignata subsignata* being more widely distributed in the mountains of central Europe. As mentioned above, both *boreosignata* and *eleonorae* are known of their holotypes only, with the type localities lying in northern Sweden and western Rumania respectively. The distribution area of the species *benesignata* consists of widely separated populations ranging from the Alps towards northern Scandinavia and eastwards to the Tien Mountains. The original descriptions of the two subspecies *persignata persignata* and *persignata tofina* were based on material originating from North Korea, to which area the distribution range of the nominotypical form seems to be restricted. Later records of *persignata tofina,* however, showed that this subspecies ranges across all of northern Eurasia.

The species *signata* is widespread in Europe, covering most of the area. The triplet *trinacria* to *omega* is restricted to Italy, with *trinacria* occurring on Sicily, *mannheimsi* in the north of Italy, and *omega* on Sardinia.

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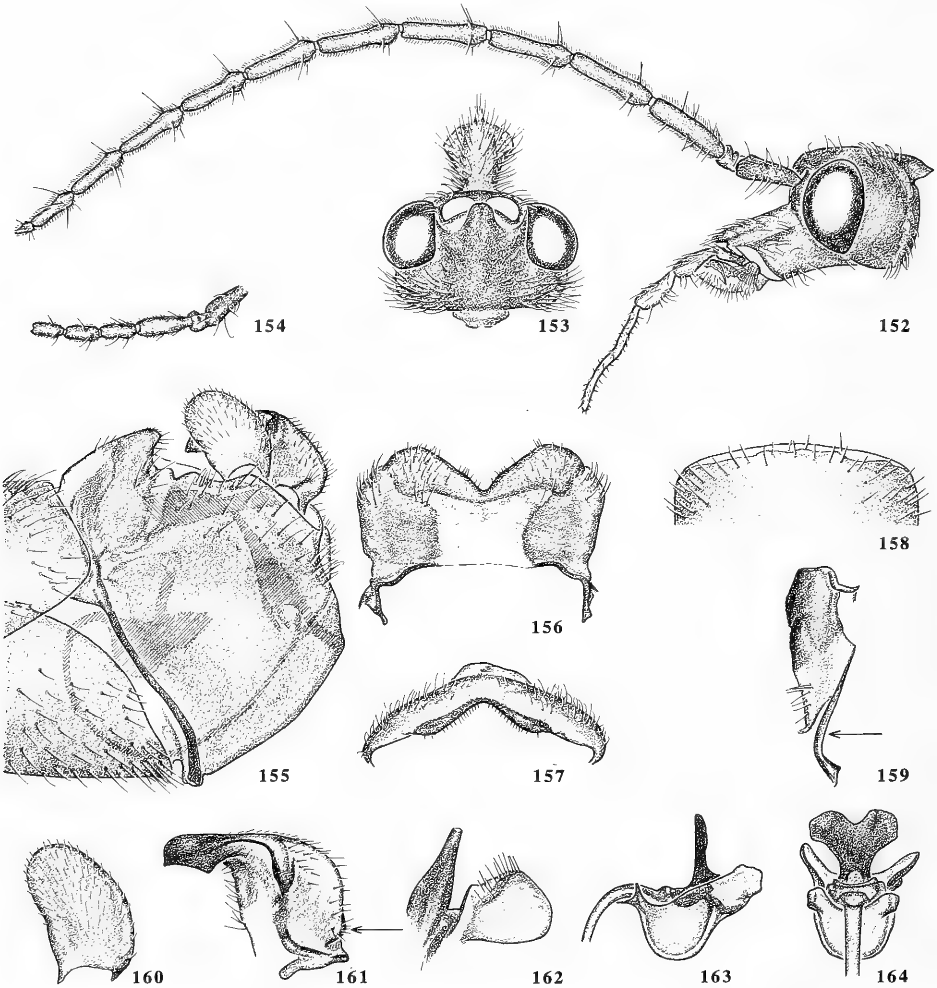
APPENDIX A

In this appendix taxonomic changes pertaining to *Savtshenkia* are dealt with. The changes include the description of three new western Palaearctic species of the subgenus, the establishment of five synonymies, the elevation of one subspecies to species rank, and the removal of one species from *Savtshenkia*.

Descriptions of new species

Tipula* (*Savtshenkia*) *alpha sp. n.
(figs. 152-170)

Type material. – Holotype ♂: Rumania, Mara-



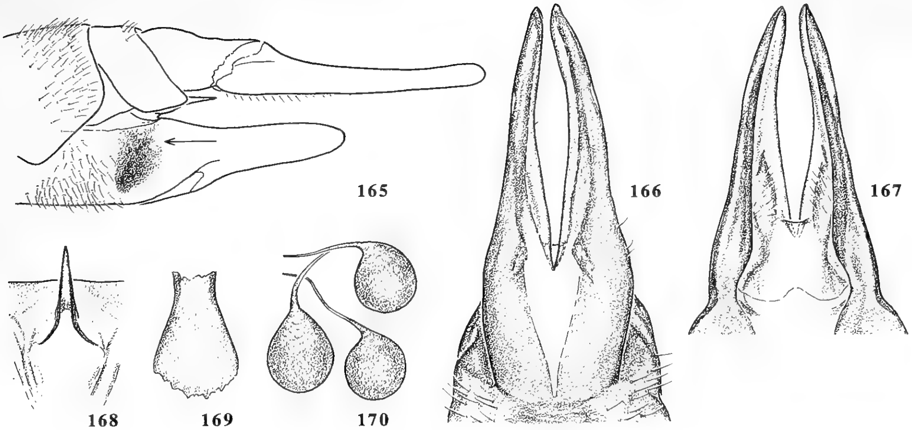
Figs. 152-164, *Tipula* (*Savtshenkia*) *alpha* sp. n. – 152, male head and appendages, lateral view; 153, male head, dorsal view, antennae and mouthparts omitted; 154, female antenna, basal segments; 155, male terminalia, lateral view; 156, male tergite 9-10, dorsal view; 157, male tergite 9-10, posterior view; 158, male sternite 8, posterior margin, ventral view; 159, right sp2, dorsal view; 160, left outer gonostylus, lateral view; 161, left inner gonostylus, lateral view; 162, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 163, sperm pump and appendages, lateral view; 164, sperm pump and appendages, anterior view.

mures, Muntii Rodnei, Borsa, subalpine lake 'Stiolul', main sources of river Bistrita Aurie, 1700-1800 m, 31.V.1974, L. Botosaneanu (ZMAN). – Paratypes 5♂, 1♀, same data as holotype (ZMAN). Material preserved in alcohol.

Description

Body length 10-12 mm (♂), 14 mm (♀); wing length 12-13.5 mm (♂), 13.5 mm (♀); antennal length 5-5.5 mm (♂), ? mm (♀; antenna broken, fig. 154).

Colour. – Ground colour greyish brown. Head and thorax dark greyish. Antenna with scapus dark greyish, remainder of segments dark brown. Palpus dark brown. Prescutum with single broad medial and pair of lateral dark stripes. Wing veins brown; pterostigma brown, distinct; membrane unpatterned. Haltere yellowish brown, including knob. Trochanters of same dark greyish colour as coxae, femora yellowish brown in basal section, from about half length darkening towards tip, remainder of legs dark brown. Abdomen dark brown, terminalia slightly darker. (Colour de-



Figs. 165-170. *Tipula* (*Savtshenkia*) *alpha* sp. n., female. – 165, ovipositor, lateral view; 166, sternite 8 and hypogynial valves, ventral view; 167, sternite 8 and hypogynial valves, dorsal view; 168, sternite 9, medial part, ventral view; 169, genital fork, dorsal view; 170, spermathecae.

duced by approximation, material preserved in alcohol).

Head (figs. 152-154). – Rostrum shorter than remainder of head, nasus well developed; eyes small, dorsally and ventrally separated by about four times diameter of scapus; occiput perpendicular to lateral sides of head (dorsal aspect, fig. 153); male antenna about four times as long as head, longest verticils about one and a half times as long as diameter of flagellomeres at base; female antenna shorter (flagella of both antennae broken beyond basal flagellomeres in female paratype, fig. 154).

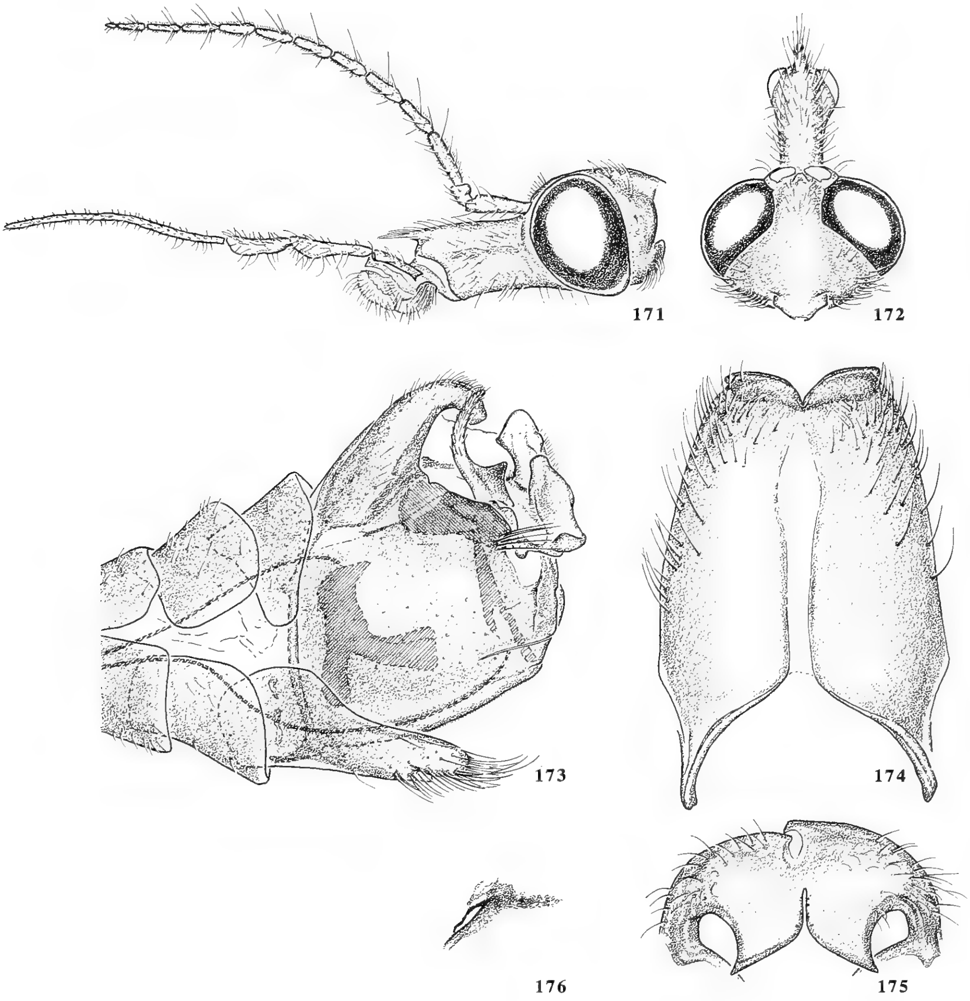
Thorax. – Wing fully developed in both sexes, squama devoid of macrotrichia; cell m1 gradually widening towards wing margin. Tarsal claws toothless in both sexes.

Male terminalia (figs. 155-164). – Compactly built, tergite 9-10 and gonocoxites separated by membranous zone (fig. 155). Tergite 9-10 (figs. 156, 157) broad and short, with medial membranous area occupying about one third of total width; posterior margin widely V-shaped, with shallow emargination near median line; margin ventrally set with scattered hairs, without spines; lateral corners broadly rounded. Posterior margin of sternite 8 unmodified (fig. 158). Gonocoxites ventrally separated by membranous area, membrane with pair of weakly sclerotized bands extending anteriorly from base of aedeagal guide. Suture x narrow, about one fourth length of gonocoxite (fig. 155). Sp2 (fig. 159) long, medial blackish sclerotized margin moderately serrate; dorsally separate from tergite 9-10; connexion between sp2 and posterior margin of foramen of gonostyli short (fig. 159, arrow). Outer gonostylus (fig. 160) broad, its tip anteriorly inclined, posterior margin only moderately blackened. Inner gonostylus (fig. 161) with relatively slender blackish sclerotized anterior part; lateral rim in its ventral part directed towards base of gonostylus; posterolaterally near base with blackened rim (fig. 161, arrow). Aedeagal guide (fig. 162) a short and plump blackish sclerotized structure, gonapophysis reduced to a sclerotized strip (fig. 162, arrow). Fragmentum (fig. 162) a rounded lobe with a few long hairs dorsomedially. Sperm pump (figs. 163, 164) with anterior apodemes short, posterior apodemes well developed and obliquely placed, compressor apodeme dorsally emarginate, blackish; lumen of endophallus well developed; ventral wall convex. Aedeagus short, anteriorly reaching segment 8 (fig. 155), tubular throughout, gradually narrowing towards tip.

Female terminalia (figs. 165-170). – Cercus and hypogynial valve well developed, robust, relatively short (fig. 165). Sternite 8 dorsolaterally near base of hypogynial valve with concavity (fig. 165, arrow); ventral membrane in posterior part of sternite 8 enclosing medial base of hypogynial valves (fig. 166). Dorsomedial margin of hypogynial valve only moderately blackened (fig. 167). Sternite 9 with slender medial projection (fig. 168). Genital fork elongate, anteriorly broader (fig. 169). Three spermathecae, globular to oblong, of about same size, moderately sclerotized (fig. 170).

Etymology. – The name of this species was prompted by its phylogenetic position within *Savtshenkia* and is the pendant of *Tipula* (*Savtshenkia*) *omega* sp. n. A noun in apposition.

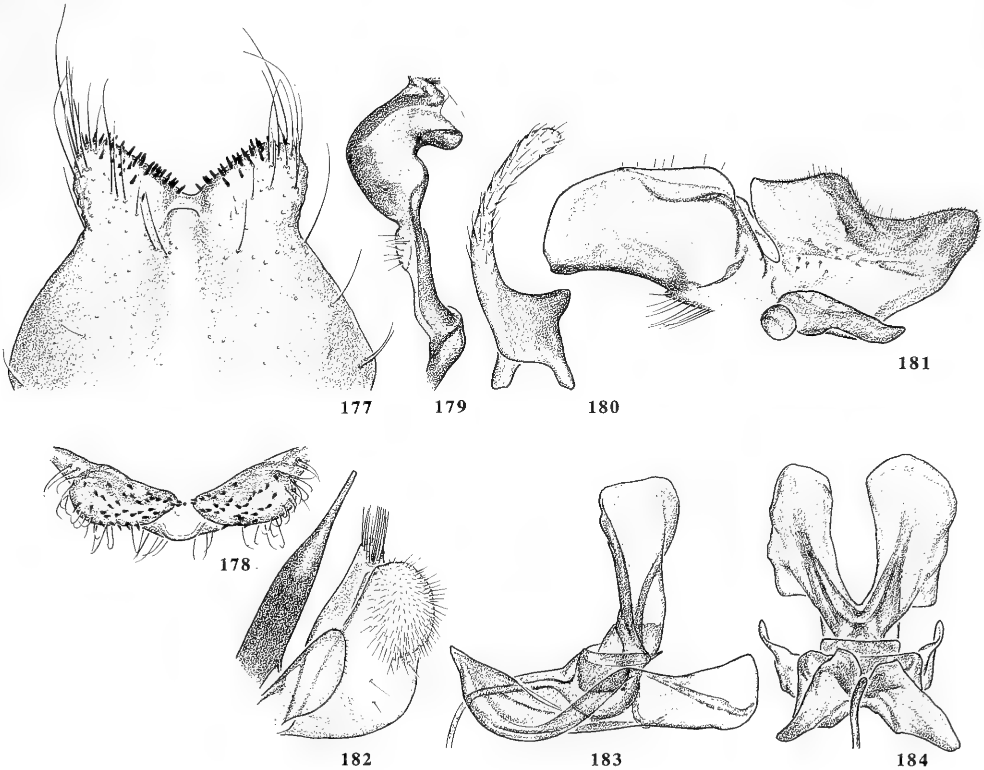
Remarks. – *Tipula* (*Savtshenkia*) *alpha* differs from its presumed sister species *T.* (*S.*) *grisescens* by the



Figs. 171-176. *Tipula* (*Savtshenkia*) *omega* sp. n., male. – 171, head and appendages, lateral view; 172, head, dorsal view, antennae and mouthparts omitted; 173, terminalia, lateral view; 174, tergite 9-10, dorsal view; 175, tergite 9-10, posterior view; 176, left sclerotization proctiger, lateral view.

colour of the coxae (dark greyish in *alpha*, yellowish brown in *grisescens*), the less elongate male antenna (see figs. 9 and 152), the separated gonocoxites (fused in *grisescens*), the broader outer gonostylus (see figs. 76 and 160), the more slender anterior part of the inner gonostylus and the presence of a sclerotized rim posterolaterally at the base of the same structure, the shallowly emarginate compressor apodeme of the sperm pump (deeply emarginate in *grisescens*), the rounded body of the sperm pump (with conical anteroventral extension in *grisescens*).

The type locality of *alpha* lies above the tree line on the subalpine plain at an altitude of 1700-1800 m. The locality has a characteristic vegetation of *Pinus mugo* Turra and the grass *Nardus stricta* Linnaeus. At the end of May thaw has set in, but the surface of the area is still extensively snow- and ice-covered. Under sunny conditions *alpha* emerges in large numbers as soon as holes begin to appear in the ice-covering. Although fully winged, the insects tend to crawl around on the ice and surrounding grasses. Under cloudy conditions *alpha* shows no sign of activity, suggesting that the behaviour of the species is largely influenced by the environmental temperature. In these aspects, the biology of *alpha* resembles that of the trichopteron *Chionophylax czarnohoricus* Dziedz.,



Figs. 177-184. *Tipula* (*Savtshenkia*) *omega* sp. n., male. – 177, sternite 8, posterior margin, ventral view; 178, sternite 8, posterior margin, posterior view; 179, right sp2, dorsal view; 180, left outer gonostylus, lateral view; 181, left inner gonostylus, lateral view; 182, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 183, sperm pump and appendages, lateral view; 184, sperm pump and appendages, anterior view.

a species which occurs in the same locality (Dr Botosaneanu, pers. comm.).

Tipula (*Savtshenkia*) *omega* sp. n.
(figs. 171-184)

Type material. – Holotype ♂: Italy, Sardinia, Fiume Taloro, 670 m, 9°31'/40°06', 21.X.1981, H. Malicky (ZMAN). – Paratypes: 1♂, Italy, Sardinia, Rio Aratu, 970 m, 9°15'/40°02', 22.X.1981, H. Malicky (ZMAN). Material preserved in alcohol.

Description

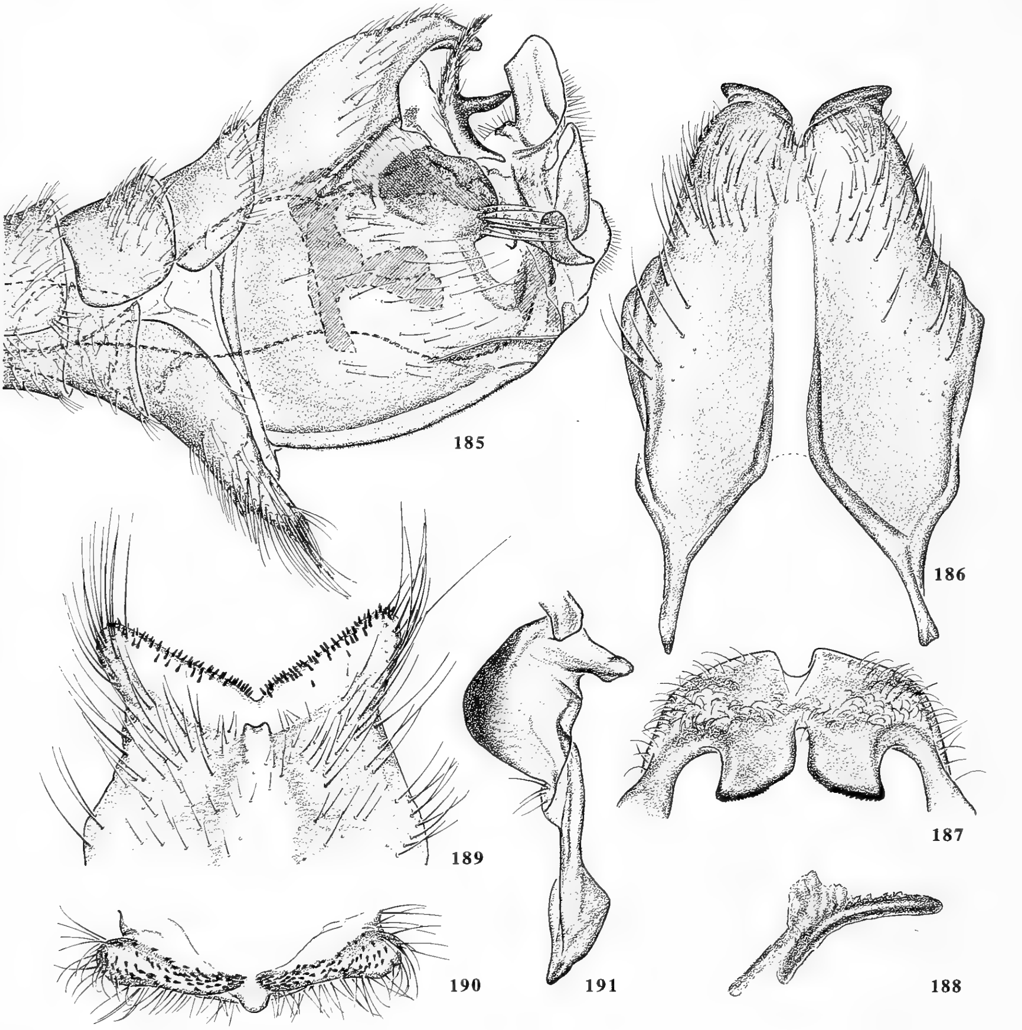
Body length 12-14.5 mm (♂); wing length 14-15.5 mm (♂); antennal length 5-6 mm (♂).

Colour. – Ground colour yellowish brown. Vertex of head and dorsal and lateral sides of thorax darker, probably slightly greyish pruinose in dry specimens. Antenna yellowish brown, scapus and pedicel somewhat lighter coloured than flagellum. Palpus yellowish brown. Presutum with confluent medial and pair of lateral dark stripes indicated. Wing veins yellowish brown; pterostigma yellowish brown, distinct; membrane vaguely patterned. Halteres yellowish brown, including knob. Legs yellowish brown, femora and tibiae darkened at extreme tip, tarsi darkening towards tip. Abdomen yellowish at base, darkening towards tip. (Colour deduced by approximation, material preserved in alcohol).

Head (figs. 171, 172). – Rostrum about as long as remainder of head, nasus well developed; eyes well developed, dorsally separated by about two and a half times diameter of scapus, ventrally by about two times diameter of scapus; occiput gradually narrowing towards cervix (dorsal aspect, fig. 172); male antenna just less than two times length of head, longest verticils about as long as flagellomeres (fig. 171).

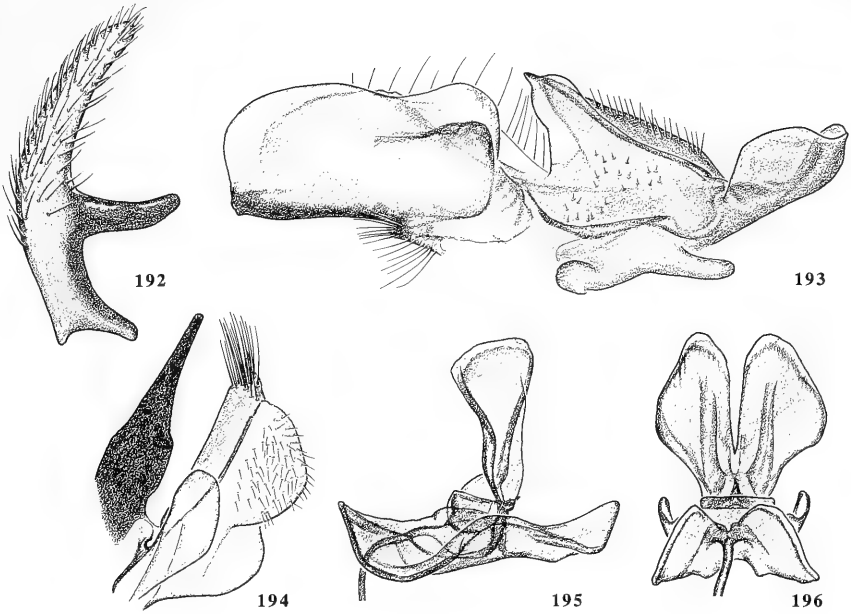
Thorax. – Wing fully developed, squama devoid of macrotrichia; cell m1 elongate bell-shaped, narrowing towards wing margin. Tarsal claws with small medial teeth in male.

Male terminalia (figs. 173-176). – Large, tergite 9-



Figs. 185-191. *Tipula* (*Savtshenkia*) *trinacria* sp. n., male. – 185, terminalia, lateral view; 186, tergite 9-10, dorsal view; 187, tergite 9-10, posterior view; 188, left sclerotization proctiger, lateral view; 189, sternite 8, posterior margin, ventral view; 190, sternite 8, posterior margin, posterior view; 191, right sp2, dorsal view.

10 and gonocoxites separated by membranous zone (fig. 173). Tergite 9-10 (figs. 174, 175) elongate, with narrow medial membranous area; posterior margin with pair of broad laterally diverging extensions; extensions not blackish sclerotized, devoid of spines along ventral margin. Proctiger with rather diffuse and narrow lateral sclerotization (fig. 176). Sternite 8 (figs. 173, 177, 178) posteriorly with diverging broad dorsoventrally flattened lobes, each lobe carrying about 35-40 black spines. Gonocoxites ventrally fused with narrow medial carina; at level of insertion of inner and outer gonostyli with concentration of long and strong setae (fig. 173). Suture x narrow, about two-fifth length of gonocoxite (fig. 173). Sp2 (fig. 179) medially protruding, blackish sclerotized medial margin entire; sp2 fused with tergite 9-10; connexion between sp2 and posterior margin of foramen of gonostyli long. Outer gonostylus (fig. 180) with elongate slender anterior part, posterior blackish sclerotized part relatively broad, with short posterodorsal extension, slightly concave. Inner gonostylus (fig. 181) with anterior and posterior parts about as long, posterior part caudally terminating in a densely pubescent lobe. Aedeagal guide (fig. 182) long and



Figs. 192-196. *Tipula* (*Savtshenkia*) *trinacria* sp. n., male. – 192, left outer gonostylus, lateral view; 193, left inner gonostylus, lateral view; 194, aedeagal guide with right gonapophysis and fragmentum, posteromedial view; 195, sperm pump and appendages, lateral view; 196, sperm pump and appendages, anterior view.

slender, blackish sclerotized, gonapophysis short, dorsally directed. Fragmentum (fig. 182) anteriorly with sclerotized bar which dorsally carries a bundle of long hairs, posteriorly weakly sclerotized. Sperm pump (figs. 183, 184) with large anterior apodemes, posterior apodemes caudally directed, compressor apodeme dorsally deeply emarginate, wings broad; lumen endophallus small, body wall ventrally concave. Aedeagus elongate (fig. 173), anteriorly reaching segment 3, tubular throughout.

Etymology. – The phylogenetic position of this species within *Savtshenkia* suggested its name. A noun in apposition.

Remarks. – The species *omega* very much resembles the species *mannheimsi* and *trinacria* sp. n. It differs from these species by the number of spines on the posterior lobes of male sternite 8 (ca. 35-40 in *omega* to ca. 50 in *mannheimsi* and ca. 65 in *trinacria*), the absence of spines on the ventral margin of male tergite 10 in *omega* (spines absent also in *mannheimsi*, present in *trinacria*), and in the shape of the inner and outer gonostyli.

The female of *omega* remains unknown.

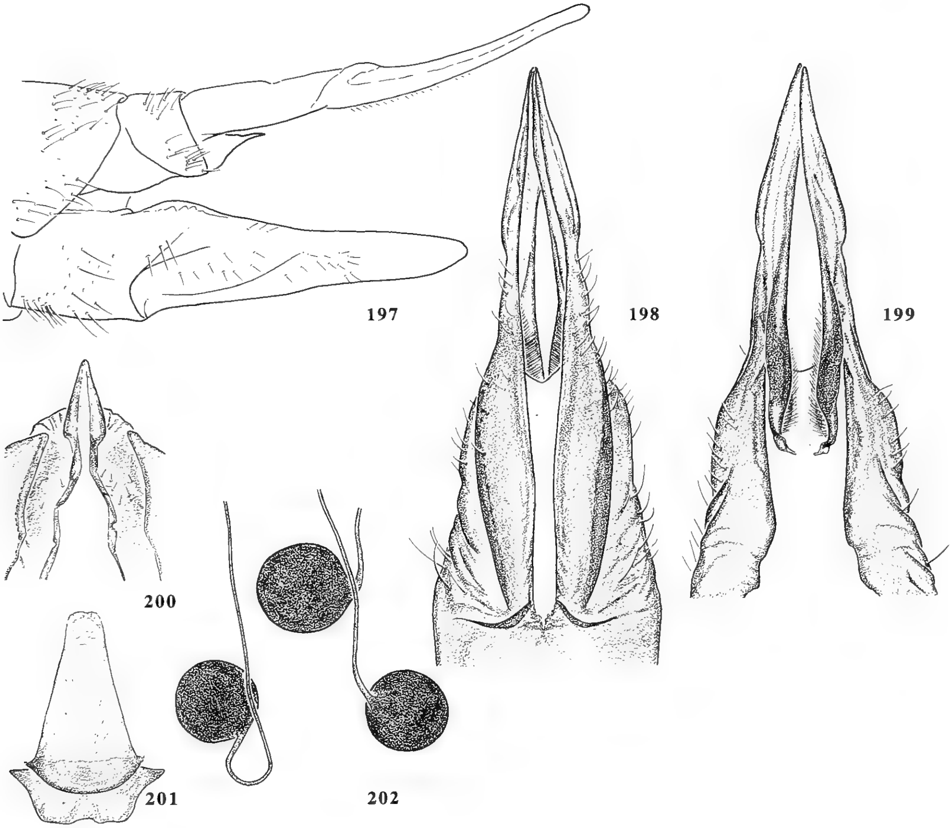
Tipula* (*Savtshenkia*) *trinacria sp. n.
(figs. 185-202)

Type material. – Holotype ♂: Italy, Sicily, Nébrodi, 10 km north of Capizzi, Fiume Troina, 1200-1400 m, 11-14.X.1993, P. Oosterbroek & C. Hartveld (ZMAN). – Paratypes: 13♂, 3♀, same data as holotype; 4♂, Italy, Sicily, Nébrodi, 5 km north of Monte Soro, Biviere di Cesaro, 1300 m, 12.X.1993, P. Oosterbroek & C. Hartveld; 2♂, Italy, Sicily, Nébrodi, 6 km east of Serra del Re, Foresta Vécchia, Fiume di Saracena, 1100 m, 13.X.1993, P. Oosterbroek & C. Hartveld; 4♂, 3♀, Italy, Sicily, Madonie, 6 km north of Monte San Salvatore, Torrente Vicaretto, 1300 m, 15-21.X.1993, P. Oosterbroek & C. Hartveld, (ZMAN).

Description

Body length 13.5-16 mm (♂), 15.5-17 mm (♀); wing length 16-19 mm (♂), 16.5-18 mm (♀); antennal length 6-7 mm (♂), 5-5.5 mm (♀).

Colour. – Ground colour yellowish brown. Excepting rostrum, head greyish pruinose. Antenna with yellowish scapus and pedicel, flagellum almost uniformly brownish, basal flagellomeres somewhat lighter. Palpus yellowish brown. Dorsal and lateral sides of thorax slightly greyish pruinose. Presutum



Figs. 197-202. *Tipula* (*Savtshenkia*) *trinacria* sp. n., female. – 197, ovipositor, lateral view; 198, sternite 8 and hypogynial valves, ventral view; 199, sternite 8 and hypogynial valves, dorsal view; 200, sternite 9, medial part, ventral view; 201, genital fork, dorsal view; 202, spermathecae.

with pair of approximating slender medial and pair of lateral dark stripes, medial stripes anteriorly lighter coloured. Wing veins brown; pterostigma brown, distinct; membrane vaguely patterned and iridescent. Halteres with yellowish brown pedicel, knob brown. Legs yellowish brown, femora and tibiae darkened at extreme tip, tarsi largely dark brown. Abdomen yellowish at base, darkening towards tip.

Head. – Very much as that of *omega* sp. n. (see figs. 171, 172; see for description of head under that species, above).

Thorax. – Wing fully developed in both sexes, squama devoid of macrotrichia; cell m1 elongate bell-shaped, narrowing towards wing margin. Tarsal claws with small medial teeth in the male, female claws toothless.

Male terminalia (figs. 185-196). – Large, tergite 9-10 and gonocoxites separated by membranous zone (fig. 185). Tergite 9-10 (figs. 186, 187) elongate, with narrow medial membranous area; posterior margin with pair of broad laterally diverging extensions; extensions blackish sclerotized along ventral margin, ventral margin set with small black spines. Proctiger with rather well demarcated slender lateral sclerotization (fig. 188). Sternite 8 (figs. 189, 190) posteriorly with diverging broad flattened lobes, each lobe carrying about 65 slender black spines. Gonocoxites ventrally fused with narrow medial carina. Suture x narrow (fig. 185). Sp2 (fig. 191) medially protruding, blackish sclerotized medial margin entire; sp2 fused with tergite 9-10; connexion between sp2 and posterior margin of foramen of gonostyli long. Outer gonostylus (fig. 192) with elongate slender anterior part, posterior blackish sclerotized part elongate, upcurved. Inner gonostylus (fig. 193) with anterior and posterior parts about as long, posterior part anteriorly extended, posteriorly terminating in cup-shaped structure. Aedeagal guide (fig. 194) long and slender, blackish sclerotized, gonapophysis short, dorsally directed. Fragmentum (fig. 194) anteriorly with sclerotized bar which dorsally carries a bundle of long hairs, posteriorly weakly sclerotized. Sperm pump (figs. 195, 196) with large anterior apodemes, posterior apodemes caudally directed, at tip somewhat upturned, compressor apodeme dorsally deeply emarginate, with narrow cleft, wings broad; lumen endophallus small, wall ventrally concave. Aedeagus elongate (fig. 185), anteriorly reaching segment 4, tubular throughout.

Female terminalia (figs. 197-202). – Cercus and hypogynial valve well developed, cercus approximately straight (fig. 197). Ventral membrane in posterior part of sternite 8 terminating in between bases of hypogynial valves (fig. 198). Dorsomedial margin of hypogynial valve only moderately blackened (fig. 199), ventrally at base with concavity (figs. 197, 198). Sternite 9 with relatively narrow and slender medial projection, concave lateral of this structure (fig. 200). Genital fork short and broad, broadest at anterior side (fig. 201). Three spermathecae, globular, of about same size, blackish sclerotized (fig. 202).

Etymology. – Trinacria is an old name of Greek origin for Sicily. A noun in apposition.

Remarks. – The species *trinacria* very much resembles *mannheimsi* and *omega* sp. n. For distinguishing characters see under *omega.* The type specimens of *trinacria* were captured along rivers and a lake in deciduous forests. The specimens collected in the period from 15-21 October were taken from the moss covered river banks of the Torrente Vicaretto. Among these latter specimens was one pair in copula.

Synonymy

insignifica Alexander, 1924 = *invenusta invenusta* Riedel, 1919 **syn. n.**

Alexander (1924) described *insignifica* as a new species based on a single male originating from Mount Washington, New Hampshire, U.S.A. Alexander (loc. cit.) recorded the collection of BSNH as the depository of the holotype (holotype not examined). I have studied specimens labelled by Alexander as metatypes, i.e. specimens compared with the type specimen(s), originating from Mount Katahdin, Maine and Mount Madison, New Hampshire (-USNM). Examination of these specimens revealed only slight differences between the Nearctic *insignifica* and the Palaearctic *invenusta invenusta* in the distance of the eyes on the ventral side of the head (see also 'Discussion of adopted phylogeny'). No other structural differences between *insignifica* and *invenusta invenusta* were found and I therefore consider *insignifica* a junior synonym of *invenusta invenusta.* [Contrary to Alexander's (1942, 1966b) assertion, the posterior margin of tergite 9-10 is posteroventrally armed with small black spines in *insignifica*, as it is in *invenusta*].

broweri Alexander, 1940 = *fragilina* Alexander, 1919 **syn. n.**

Alexander (1940) described *broweri* based on 12 males and two females from Mount Katahdin, Maine, U.S.A. (types in USNM). Despite Alexander's claim that *broweri* should be entirely distinct from its relatives, examination of type material of *broweri* showed that it is morphologically identical with *fragilina.* I therefore consider *broweri* a junior synonym of *fragilina.*

nebulipennis Alexander, 1919 = *alpium* Bergroth, 1888 **syn. n.**

Alexander (1919a) introduced *nebulipennis* as a new species based on two males from Battle Harbour, Labrador, Canada (holotype in Brooklyn Museum, New York, U.S.A., paratype in USNM). Later, *nebulipennis* was also recorded from Quebec and New Hampshire (Alexander 1965b). Examination of material of *nebulipennis* in the Alexander collection (USNM) revealed no significant morphological differences between these specimens and the European species *alpium.* I therefore consider *nebulipennis* a junior synonym of *alpium.* The larvae of *alpium* were recorded from terrestrial mosses (Brindle 1958, 1959, 1960). Theowald (1957, 1967) recorded the larvae furthermore from the litter layer beneath oaks. Possibly *alpium* has been introduced into North America in a way similar to the European species *Tipula (Tipula) paludosa* Meigen (see Alexander 1965a).

packardi Alexander, 1928 = *invenusta invenusta* Riedel, 1919 **syn. n.**

Alexander (1928) described *Tipula packardi* based on a single male from Hopedale, Labrador, Canada. The holotype of *packardi* is preserved in CNCI (holotype not examined). An additional male specimen originating from the type locality of *packardi* is present in USNM. This latter specimen was compared by Alexander with the holotype of *packardi* and considered conspecific. Examination of the metatype of *packardi* in USNM showed that it has the eyes on the ventral side of the head slightly more approximate than the examined specimens of *invenusta invenusta* (see also 'Discussion of adopted phylogeny', and *insignifica*, this section). No other structural differences were found and I therefore consider *packardi* a junior synonym of *invenusta invenusta.*

perparvula Alexander, 1926 = *ignobilis* Loew, 1863 **syn.n.** (partim?)

Loew (1863) described the species *ignobilis* based on the female sex from material captured by Osten-Sacken in the District of Columbia, U.S.A. (holotype in MCZC, not examined). According to its labels, Alexander compared a male specimen captured by Osten Sacken in Catskill, New York, with the type specimen of *ignobilis* and considered the two conspecific. Examination of this inferred male specimen of *ignobilis* and the paratype male of the species *perparvula* (both in USNM) revealed that these two specimens belong to the same species. Alexander (1926), describing *perparvula* based on two males originating from Aweme, Manitoba, Canada (holotype in CNCI, paratype in USNM), explicitly stated that *perparvula* has a relatively stout nasus. Examination of the paratype of *perparvula* shows that this structure is entirely absent in the specimen, as it is in the species *ignobilis*. Either the holotype and paratype of *perparvula* belong to two different species, with the paratype being conspecific with *ignobilis*, or both type specimens are conspecific and belong to *ignobilis*. Examination of the holotype of *perparvula* should settle this question.

Subspecies raised to species rank

haennii Dufour, 1991

This taxon was originally described as a subspecies of *subsignata* (Dufour 1991). The tip of the aedeagal guide of *haennii* does not show the abrupt constriction which probably represents a synapomorphy of a monophyletic group containing *corsosignata*, *subsignata subsignata* and *subsignata cazorla* (character 8, above). Because of its phylogenetic position next to this clade, *haennii* is elevated from subspecific to specific rank.

Species removed from *Savtshenkia*

convexifrons Holmgren, 1883

Savchenko (1961) placed the species *convexifrons* Holmgren in his *subnodicornis* group of *Pterelachisus* sensu Savchenko, nec Rondani. Savchenko (1961: 223) based its membership of the *subnodicornis* group on the shape of the inner gonostylus, and its incorporation in *Pterelachisus* sensu Savchenko on the proximal position of the fork of vein M3+4. At the same time, Savchenko underlined the isolated position of *convexifrons* within this grouping. As noticed in the introduction to the present paper, the name *Savtshenkia* replaces *Pterelachisus* sensu Savchenko. Theowald (1973) followed Savchenko in considering *convexifrons* a species of *Savtshenkia*, but split the *subnodicornis* group sensu Savchenko into two species groups (table 3). I remove *convexifrons* from *Savtshenkia* because of the absence of the defining apomorphies 53 and 83 of *Savtshenkia*. Furthermore, the species *convexifrons* differs from the species of *Savtshenkia* by the shape of male tergite 9-10, the ventral structure of the fused gonocoxites, the shape of the elongate aedeagal guide and its gonopophyses, and, most noteworthy, by the presence of a complete genital bridge (a plesiomorphy; the medial part of the genital bridge is absent in all species of *Savtshenkia*). The fork of vein M3+4 is located proximally in many genera and subgenera of Tipulidae other than *Savtshenkia*. The resemblance of the inner gonostylus of *convexifrons* to the inner gonostyli of plesiomorphous species of *Savtshenkia* is only superficial. At the moment I am unable to establish the actual phylogenetic relationships of *convexifrons* and can not allocate it to any other subgenus or species group of Tipulidae.

Appendix B

In this appendix are listed the species and subspecies of *Savtshenkia* which, because of deficiency of data, were not incorporated in the character state matrix given in table 4. Incompleteness of data resulted of several causes. For some of the pertaining taxa no material was examined, for others the material examined was incomplete as regards the structures of the male terminalia, for others again only the female is known, thus excluding their incorporation in a phylogeny which is largely based on characters of the male terminalia. Where possible, the presumed phylogenetic position of the species and subspecies concerned is indicated. For the deposition of the type material of species described by Savchenko see Kandybina, Lantzov & Savchenko (1987).

Unexamined

imperfecta Riedel, 1914. – Description based on single brachypterous male specimen from Kenya (Mount Kenya) and single brachypterous female specimen, possibly belonging to the same species, from Tanzania (Mount Kilimanjaro). Types in MNHN. Species doubtfully belongs to *Savtshenkia*. Distribution: Kenya, Tanzania.

letifera Alexander, 1951. – Description based on single male from China (Tibet, Shugden Gompa a.k.a. Hsiu-teng). Type in BMNH. Inner and outer gonostyli quite similar to those of Kashmirian *sordidipes* and *venerabilis*. Differences with these species in structures of posterior margins of tergite 9-10 and sternite 8. Shape of sternite 8 suggests relationship with Nearctic *graciae* and Palaearctic *kiushiuensis* and *koreana*. Alexander (1953) illustrated details male terminalia of *letifera*. Distribution: China (south-east Tibet).

minuscula Savchenko, 1971. – Originally described as *Tipula* (*Savtshenkia*) *nana* by Savchenko (1968a) based on two males and single female from USSR (Kamchatka). Types in ZIAS. Savchenko, probably correctly, considered *minuscula* closely related to Nearctic *ignobilis*, with which it should differ in colour characteristics. Details male terminalia of *minuscula* illustrated by Savchenko (1968a). Distribution: Russia (Kamchatka).

nivalis Savchenko, 1961. – Description based on three males and four females from USSR (Stavropolskiy kray and Gruzinskaya SSR). Types in ZIAS. Savchenko (1961) compared *nivalis* with *glaucocinerea*. Theowald (1973) considered both very closely related and suggested that *nivalis* might be considered a subspecies of *glaucocinerea*. Details male terminalia of *nivalis* illustrated by Savchenko (1961) and Theowald (1973). Distribution: Russia (Stavropolskiy kray), Georgia.

productella Alexander, 1928. – Description based on single male from Canada (Labrador). Type in CNCI. According to Alexander (1928) most closely allied to Nearctic *fragilina*. Structure of sternite 8 of *productella* of same build as found in clade *fragilina* to *subvafra* of present paper; *productella* probably belongs to this clade; synonymy with one of its species possible. Distribution: Canada (Labrador).

subalpium Savchenko, 1961. – Description based on single male from USSR (Krasnodarskiy kray, Glavniy Mountains). Type in ZIAS. Savchenko (1961) compared *subalpium* with *alpium*, with which it shares same general colour and structure of inner and outer gonostyli and to which it is probably closely related. Differs quite remarkably from *alpium* in structure of posterior margin of sternite 8: whereas posterior margin of sternite 8 is U-shaped emarginate and carries spines along its edge in *alpium* (fig. 105), emargination is filled up with membrane covered with short setae in *subalpium*. According to Savchenko, there is a short pubescent extension in between what he denotes sternites 8 and 9. This structure could well be homologous with midventral extension found in *alpium* and *macaronesica*, which in dry material is often hardly visible or seems to originate from posterior margin of sternite 8 (see fig. 39). Savchenko (1969) depicted male terminalia of *subapium* in lateral and posterior view. Distribution: Russia (Krasnodarskiy kray), Georgia.

tetragramma Edwards, 1928. – Description based on single male from China (Yunnan). Type in BMNH. Edwards (1928) was of the opinion that *tetragramma* must bear a rather strong resemblance to *kiushiuensis*. Distribution: China (Yunnan).

Incomplete male terminalia

kiushiuensis Alexander, 1925. – Description based on single male and single female from Japan (Kyushu, Mount Kirishima). Types in USNM. Glass slides with terminalia male holotype and additional male specimen (USNM) do not allow study of all relevant structures. Related to species in range *jeekeli* to *aster* of cladogram fig. 2. Posteriorly produced unarmed medial part of posterior margin male sternite 8 suggests relationship with *koreana*. Savchenko (1968b) illustrated details male terminalia of *kiushiuensis*. Distribution: Russia (Primorskiy kray), Japan (Kyushu, Shikoku).

koreana Alexander, 1934. – Description based on single male and four females from North Korea (Mount Kongo). Types in USNM. Glass slide with terminalia male holotype does not allow study of all relevant structures. Related to species in range *jeekeli* to *aster* of cladogram fig. 2. Posteriorly produced unarmed medial part of posterior margin male sternite 8 suggests relationship with *kiushiuensis*. Alexander (1934) illustrated details male terminalia and wing of *koreana*. Distribution: Russia (Sakhalin), North Korea, Japan (Shikoku).

mohriana Alexander, 1954. – Description based on single male and single female from Japan (Shikoku, Mount Ishizuchi). Types in USNM. Glass slide with terminalia male holotype does not allow study of all relevant structures. Most probably sister species of clade *fragilina* to *subvafra* of present paper as implied by fused sp2 and tergite 9-10 (character 54), slender anterior part outer gonostylus (character 45), bifid tip of anterior part of inner gonostylus (character 30), and widely emarginate bilobed and unarmed posterior margin of male sternite 8 (cf. character 60). Differing most notably from species of clade *fragilina* to *subvafra* by presence of spinous gonapophysis (autapomorphy) and absence of blackened dorsal margin of fragmentum (cf. character 17). Details male terminalia and wing of *mohriana* illustrated by Alexander (1955). Distribution: Japan (Shikoku).

sciadoptera Alexander, 1964. – Described as *guttulifera* by Alexander (1961) based on two males from India (Himalayas). Types in USNM. Glass slides with terminalia male holotype and paratype do not allow study of all relevant structures. Probably related to species in range *baltistanica* to *chrysocephala* of cladogram in fig. 2. Alexander (1961) illustrated details male terminalia of *sciadoptera* (as *guttulifera*). Distribution: India (Sikkim).

Known in female sex only

aberdareica ulugurica Alexander, 1962. – Description based on single female from Tanzania (Uluguru Mountains). Type in MRAC, not examined. According to Alexander (1962) closely related to nominotypical form, sharing several colour characteristics with *chrysocephala*. Distribution: Tanzania.

nephrotomoides invariegata Alexander, 1956. – Description based on single female holotype from Uganda (Ruwenzori Range). Type in BMNH. Agreeing in its dark colour with the nominotypical form from Zaire and Uganda. Distribution: Uganda.

Appendix C

Autapomorphies of the species and subspecies of *Savtshenkia*

aberdareica: no autapomorphy recognized.

aberdareica ulugurica: no autapomorphy recognized (known of female holotype only).

akeleyi: inner gonostylus with dorsal margin anterior part undulating.

alpha: posterior rim of inner gonostylus ventrally blackish sclerotized (fig. 161, arrow).

alpium: shape of posterior margin of male tergite 9-10; shape of posterior margin of male sternite 8 (fig. 105); shape of extension of midventral area (long; fig. 39).

asbolodes: inner gonostylus with anterior part rather slender.

aspromontensis: shape of inner gonostylus (crest, fig. 61); shape of male tergite 9-10 (two pairs of pointed extensions, fig. 135).

aster: shape of aedeagal guide; gonapophysis slender, downcurved and pointed; shape of male tergite 9-10; shape of posterior margin of male sternite 8 (fig. 109).

atlas: extensions of male tergite 9-10 mediolaterally compressed.

baltistanica: arrangement of setae on posterior margin of male sternite 8.

benesignata: shape of inner gonostylus (fig. 72).

boreosignata: broad membranous zone of tergite 9-10 (fig. 138); reduction of spines on lobes on posterior margin male sternite 8; fragmentum with low anterior part; shape of aedeagal complex (fig. 99).

breviantennata: anterior part of inner gonostylus widening towards apex, lateral ridge of inner gonostylus short and angled.

caligo: shape of posterior margin of male tergite 9-10.

cheethami: midventral area posteriorly with long conical extension (fig. 35).

chrysocephala: anterior part of inner gonostylus constricted before tip (lateral view).

confusa: inner gonostylus with two blackish sclerotized dentate ridges on lateral side of posterior part (fig. 58); male tergite 9-10 with truncate extensions close together; shape of posterior margin of male sternite 8.

corsosignata: shape of inner (fig. 69) and outer gonostyli.

cyrnosardensis: inner gonostylus caudodorsally with posteriorly produced pubescent lobe; outer gonostylus with slender extension on posterior margin at about two-thirds from base; apex of elongate fragmentum medially curved.

draconis: shape of inner gonostylus; reduced nasus.

eleonorae: no autapomorphy recognized.

elgonensis: no autapomorphy recognized.

eugeni: extensions of male tergite 9-10 upcurved (lateral view); shape of inner gonostylus; anterior apodemes sperm pump elongate and dorsally directed, compressor apodemes mediolaterally flattened in apical part.

fragilina: inner gonostylus with acute sclerotized extension at ventral tip of posterior ridge.

fragilis: aedeagal guide elongate and slender (fig. 22); suture x broad, sigma-shaped.

gimmerthali: inner gonostylus with anterior part gradually sloping towards bifid apex (fig. 66).

gimmerthali mattheyi: outer gonostylus without posterior sclerotized appendage (present in both other subspecies).

gimmerthali pteromaculata: inner gonostylus with relatively broad anterior part (fig. 67); outer gonostylus broadened above midlength (fig. 84).

glaucocinerea: shape of extensions of tergite 9-10.

goriziensis: shape of inner gonostylus (fig. 54).

graciae: posterior margin of male sternite 8 medially with rounded extension set with long and strong setae.

grisescens: extensions of male tergite 9-10 dorsoventrally flattened (figs. 121, 122).

haennii: fragmentum 3-lobed (fig. 27); inner gonostylus with ridge separated in posterior and ventral part, ventral part ridge extended over posterior part of inner gonostylus, and dorsal crest anteriorly abruptly terminating (fig. 68).

hancocki: male antenna reduced in length.

hartigiana: shape of inner gonostylus (long anterior part, strongly protruding lateral ridge); extension of midventral area gonocoxites (fig. 33).

holoptera: posterior margin of male sternite 8 with a few strong setae (fig. 107).

ignobilis: shape of outer gonostylus; shape of sp2.

imperfecta: wings reduced in both sexes.

interserta: shape of inner gonostylus; outer gonostylus large, posteriorly inclined.

invenusta: shape of posterior margin of male tergite 9-10 (fig. 136).

invenusta microinvenusta: inner gonostylus anteriorly more curved forward than in both other forms; differing primarily in smaller size and darker colour from both other forms.

invenusta subinvenusta: inner gonostylus relatively slender.

jeekeli: shape of inner gonostylus; shape of outer gonostylus (fig. 80); shape of posterior margin of male sternite 8; sperm pump with sclerotized sperm duct; apex of aedeagus with spines.

kiushiuensis: shape of posterior margin of male sternite 8.

koreana: shape of posterior margin of male sternite 8.

letifera: no autapomorphy recognized (probably very similar to *sordidipes* and *venerabilis*).

limbata: anterior part of inner gonostylus produced into long and bifid extension (fig. 64).

lundbladi: shape of inner gonostylus (elongate, with short crest); shape of outer gonostylus (fig. 78); shape of posterior margin of sternite 8 (fig. 103); surface of sp2 anterodorsally with cone-shaped extension.

macaronesica: shape of extension of midventral area (short).

mannheimsi: outer gonostylus with incision ventral of posterior sclerotized spur.

minuscula: no autapomorphy recognized (probably very similar to *ignobilis*).

mohriana: gonapophysis as slender curved spine.

multipicta: shape of inner gonostylus (high anterior part with long and slender anterior apex); shape of outer gonostylus (oblong).

nephrotomoides: blackish species.

nephrotomoides invariegata: no autapomorphy recognized (known of female holotype only).

nielseni: shape of inner gonostylus; shape of outer gonostylus (fig. 85); shape of medial extension of male sternite 8.

nivalis: no autapomorphy recognized (probably very similar to *glaucocinerea*).

obsoleta: shape of inner and outer gonostyli; shape of posterior margin of male sternite 8 (fig. 106); spinous extensions on posterodorsal part fragmentum (fig. 21).

odontostyla: shape of male tergite 9-10; inner gonostylus dorsally with long and dense pubescence (fig. 63); apical part of fragmentum bent and posteriorly directed; gonapophysis twisted.

omega: inner gonostylus with hump in anterior half of posterior part (fig. 181).

ornata: wing cell a2 almost symmetrical in distal tip; posterior extensions male tergite 9-10 dorsoventrally flattened, laterally curved, ventrally carrying long thin spinous setae; shape of posterior margin of male sternite 8; midventral anterior extension of male sternite 9 elongate, membranous; shape of appendage of midventral area gonocoxites (fig. 40); suture x broad, enclosing isolated sclerite; female tergite 9 medially reduced to strip.

pagana: female brachypterous.

pechlaneri: male tergite 9-10 with pair of low extra extensions lateral of usual extensions on posterior margin; shape of inner gonostylus (fig. 65).

persignata: posterior part of inner gonostylus corrugated (fig. 73).

persignata tofina: differing in details of male terminalia from nominotypical form.

phoroctenia: shape of male tergite 9-10; shape of posterior margin of male sternite 8; lateral ridge of inner gonostylus posterodorsally angular; suture x of gonocoxite Y-shaped; shape of extension of midventral area gonocoxites (fig. 41).

postposita: shape of outer gonostylus.

productella: no autapomorphy recognized.

rufina: extensions of tergite 9-10 extremely long and slender; shape of inner gonostylus; tip of gonapophysis medially curved; posterior margin of male sternite 8 bulbously curved.

rufina maderensis: larger than nominotypical species.

sardosignata: shape of inner gonostylus; shape of outer gonostylus (fig. 88); shape of posterior margin of male sternite 8.

sciadoptera: shape of inner gonostylus.

serrulifera: shape of inner gonostylus (fig. 60); shape of outer gonostylus; shape of posterior margin of male sternite 8.

signata: posterior part of inner gonostylus anteriorly rounded (fig. 74); midventral extension on posterior margin male sternite 8 large, with dorsal sclerite (fig. 116).

simulans: inner gonostylus with lateral ridge dorsally produced into pointed extension; shape of extension of midventral area.

sordidipes: legs extensively blackened.

staegeri: extensions of male tergite 9 widely separate, mediolaterally flattened; male sternite 8 midventrally conical; posterior extensions of male sternite 8 elongate; aedeagal guide posteriorly curved; shape and length of gonapophysis; shape of inner gonostylus; female sternite 8 dorsally extended; base of hypogynial valve laterally bulging.

subalpium: shape of posterior margin of male sternite 8.

subnodicornis: tergite 9-10 with extension in between lateral pair (fig. 128).

subsignata: together with next subspecies distinguished by lateral ridge being acutely bent and anteriorly produced in ventral part (fig. 70); differing from *subsignata cazorla* in details of inner gonostylus.

subsignata cazorla: differing from nominotypical subspecies by shape of inner gonostylus (anterior part dorsally abruptly narrowed, lateral view).

subvafra: shape of male tergite 9-10; shape of inner gonostylus.

tetragramma: wing pattern.

trinacria: outer gonostylus with extremely long posterior sclerotized appendage (fig. 192); sclerotization of proctiger well demarcated (fig. 188).

tulipa: inner gonostylus with relatively short lateral ridge; midventral area gonocoxites broad and long pubescent.

venerabilis: no autapomorphy recognized (very similar to *sordidipes*).

villeneuvii: small and posteriorly curved outer gonostylus; gonocoxite posterodorsally acutely angled.

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THREE NEW SPECIES OF *PSEUDEXECHIA* TUOMIKOSKI FROM TANZANIA AND THAILAND (DIPTERA: MYCETOPHILIDAE)

Kjærandsen, J., 1994. Three new species of *Pseudexechia* Tuomikoski from Tanzania and Thailand (Diptera: Mycetophilidae). – Tijdschrift voor Entomologie 137: 325-330, figs. 1-4. [ISSN 0040-7496]. Published 15 December 1994.

Pseudexechia longistylus sp. n. and *P. lanceostylus* sp. n. from Tanzania and *P. inthanonensis* sp. n. from Thailand are described, based on adult males. The terminalia are figured. The presence of a pair of medium sized bristle-like dorsocentral setae on scutum in the two African species and an aberrant wing venation in *P. inthanonensis* sp.n. is commented on.

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Key words. – Diptera; Mycetophilidae; *Pseudexechia*; Tanzania; Thailand; taxonomy.

Pseudexechia Tuomikoski, 1966 constitutes one of 14 genera in the tribus Exechiini, subfamily Mycetophilinae (Tuomikoski 1966). The genus is characterised by the absence of large discal setae on the mesoscutum, by the ovate clypeus and on characters in the male terminalia such as the bud-like sternal process. Chandler (1978) treated all eight holarctic species known at that time. Three palaearctic species were added later; viz. *P. trilobata* Ostroverkhova, 1979, *P. ussurensis* Zaitzev, 1982 and *P. altaica* Zaitzev, 1988. Matile (1970) revised the Afrotropical *Pseudexechia* comprising four species. A fifth species, *P. tanganyikae* (Lindner, 1958) originally described as *Exechia,* was later referred to this genus as well (Matile 1980). No species of *Pseudexechia* are hitherto known from the oriental region. Thus, 16 species of the genus *Pseudexechia* were known: 9 palaearctic, 2 nearctic and 5 afrotropical. Of only one of the five Afrotropical species both sexes were described, the four other were all described on single females. Female holotypes make it difficult to describe new species from the region as certain association of the sexes is not easy to establish without large samples or reared specimens. However, based on differences in external characters as coloration and wing venation the present specimens can not belong to any of the described species.

MATERIAL

The material consists of two males collected in the West Usambara Mountains in Tanzania in 1990, and one male collected in the Doi Inthanon mountain in Thailand in 1991. The holotypes are deposited in the Museum of Zoology, Bergen (ZMBN).

METHODS AND TERMINOLOGY

The specimens were cleared and slide mounted in Canada balsam. The general terminology follows McAlpine (1981).

Wing measurements (fig. 1): Total wing length is measured from the extreme base of the distal median plate. A = distance between the points where R_1 and R_{4+5} reach wing margin. B = distance between the points where R_{4+5} and M_1 reach wing margin. C = width of M-fork at wing margin. D = width of Cu-fork at wing margin. E = distance from extreme base of the distal median plate to base of M-fork. F = distance from extreme base of the distal median plate to base of Cu-fork. Other measurements are self-explanatory and indicated in Fig. 1.

The tibial spur formula is the length of each spur in relation to the apical diameter of tibia in the following order: fore tibial spur; the two mid tibial spurs; the two hind tibial spurs.

SYSTEMATIC PART

Pseudexechia longistylus sp. n.
(figs. 1 - 2)

Type material. – Holotype male, TANZANIA: Tanga region, W. Usambara Mts, Mazumbai, 1440 m a.s.l., 22.XI.1990, G. E. E. Søli, sweep net (ZMBN No. 179).

Diagnostic characters. – The male imago is charac-

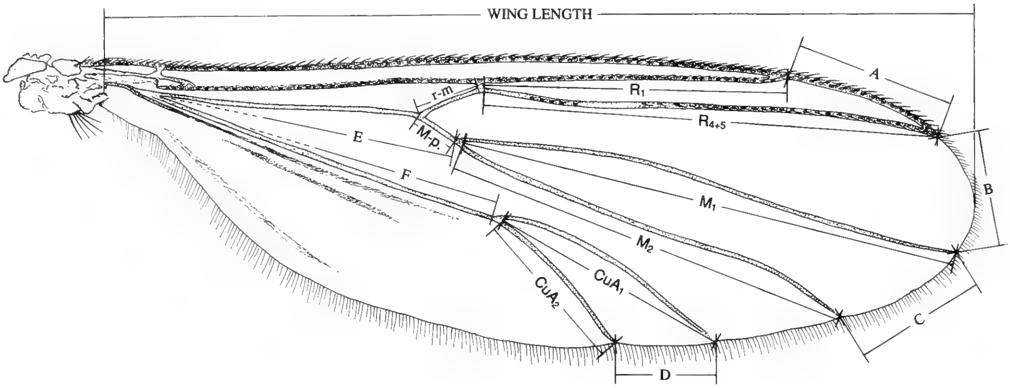
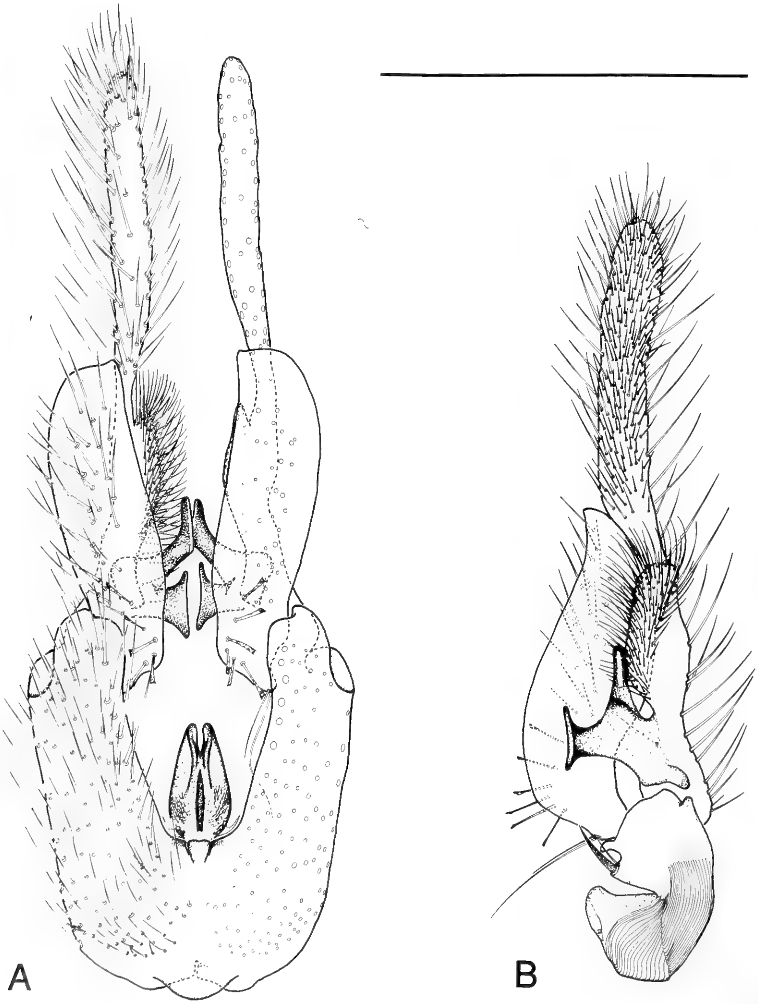


Fig. 1. *Pseudexechia longistylus* sp. n., right wing showing measuring points. – Total wing length is measured from the extreme base of the distal median plate to tip of wing. A = distance between the points where R_1 and R_{4+5} reaches wing margin. B = distance between the points where R_{4+5} and M_1 reaches wing margin. C = width of M-fork at wing margin. D = witdh of Cu-fork at wing margin. E = distance from extreme base of the distal median plate to point of M furcation. F = distance from extreme base of the distal median plate to point of Cu furcation. M-p. = M-petiole.

Fig. 2. *Pseudexechia longistylus* sp. n., male terminalia. – A, ventral view; B, internal face of the gonostylus. Scale 0.50 mm.



terised by the enlarged terminalia in which the dorsal lobe of gonostylus ends in a very elongated lobe with a setose cushion basally, and by the shape of the bifurcate internal process. The ventral lobe of the gonostylus also is enlarged compared to other species.

Etymology. – From Latin, *longus,* long, and *stylus,* style, referring to the elongated gonostylus. A noun in apposition.

Description of male holotype. – Length of thorax 0.86 mm. Wing length 2.62 mm. Wing length / length of thorax 3.1. Wing length / length of fore femur 3.1.

Coloration. Antenna with scape, pedicel and basal part of flagellum yellow, gradually becoming darker and more greyish dusted towards tip. Head yellow. Maxillary palp greyish yellow. Thorax mainly yellow; scutum with narrow pale yellow or somewhat silvery shining stripe along lateral margin, delimited by darker margins below and above; scutellum darker yellow. Wing unmarked, yellow tinted, paler towards tip and hind margin. Wing veins yellow with dark setae. Halter greyish yellow. Legs mainly yellow; coxae paler yellow, hind coxa posteriorly with darker stripe. Abdominal tergites mainly yellowish brown; tergite 1 and 2 with pale lateral markings; tergite 3 to 5 with pale posterolateral markings, almost reaching middle; tergite 6 almost entirely dark. Terminalia mainly yellow, darker apically on gonocoxite, on sternal process and on parts of dorsal lobe of gonostylus.

Head. Total length of flagellum 1.35 mm. First flagellomere 1.5 times as long as second flagellomere. Second flagellomere 2.2 times as long as wide. Five large orbital setae. Small round median ocellus present. Diameter of lateral ocellus / diameter of median ocellus 1.7. Clypeus bearing 31 setae; width / length 0.8. Fourth palpomere about 1.5 times as long as third palpomere.

Thorax. Pronotum with vertical row of 3 erect setae. Scutum with pair of medium sized bristle-like dorsocentral setae posteromedially in front of scutellum (prescutellar setae); anterior and lateral margin with large setae; otherwise uniformly clothed with small setae (but larger and fewer than in other *Pseudexechia* except in *P. lanceostylus* sp. n.). Scutellum with pair of strong scutellar setae and pair of very short incurved setae basad of them. Proepisternum with 1 strong, 1 medium sized and 5 small setae. Laterotergite with 6–7 large and about 50 small setae.

Wing (fig. 1). Crossvein h with 1 ventral seta. R_1 with 11 ventral setae apically. R_{4+5} with 26–27 ventral setae apically. Wing length / length of R_1 2.6. Wing length / length of R_{4+5} 1.9. R_{4+5} nearly straight. Length of r-m / length of M-petiole 1.7. A / B 1.4. E / length of M_1 0.7. E / length of M_2 0.8. Base of Cu–fork well beyond base of M–fork. M-fork veins distaly divergent. Cu-fork veins divergent. F / E 1.3. F / length of CuA_1 1.7. F / length of CuA_2 2.5. C / D 1.4. Vein CuP reaching as far as base of Cu–fork. Vein A_1 weak, shorter.

Legs. Length of fore basitarsus / length of fore tibia 1.3. Tibial spur formula 3.4; 8.8, 5.6; 4.6, 4.6. Fore tibia with 1 ad, 36 p and 3 v setae. Mid tibia with 40 a, 5 pd and 11 p setae. Hind tibia with 8 a, 5 pd and 3 p setae. Posterior sensillae placodea on basal part of tibia 3; 3; 3.

Terminalia (fig. 2A, B). Length of gonocoxite 0.60 mm. Sternal process narrow with about 40 tiny setae; length / width 1.9. Dorsal lobe of gonostylus 0.84 mm long with very elongated lobe, basally with strongly setose cushion. Sclerotized internal process bifurcate with both prongs widening apically. Ventral lobe of gonostylus large, bearing 6 fan-tipped setae basally. One lobe of the inner lamellate parts of the gonostylus apically with a slightly curved, spine-like seta thus forming a hook. Cerci thin and slender, reaching to about apical level of gonocoxite, with two short but strong apical setae (not figured).

Pseudexechia lanceostylus sp. n.
(fig. 3)

Type material. – Holotype male, TANZANIA: Tanga region, W. Usambara Mts., Mazumbai, 1530 m a.s.l., 02.–03.XI.1990, G. E. E. Søli, Malaise tent (ZMBN No. 180).

Diagnostic characters. – The male imago is characterised by the shape of the dorsal lobe of gonostylus which ends in a slender lobe, and by the shape of the bifurcate internal process.

Etymology. – From Latin, *lancea,* a small light spear, and *stylus,* style, referring to the slender lance-like dorsal lobe of gonostylus.

Description of male holotype. – Length of thorax 0.98 mm. Wing length 3.02 mm. Wing length / length of thorax 3.1. Wing length / length of fore femur 3.1.

Coloration. Antenna with scape, pedicel and basal part of flagellum yellow, gradually becoming darker and more greyish dusted towards tip. Head and maxillary palp yellow. Thorax mainly yellow; scutum uniformly brownish yellow with pale yellow or somewhat silvery shining stripe along lateral margin, delimited by darker margins below and above; scutellum brownish yellow with faint paler median stripe. Wing unmarked, yellow tinted, slightly paler towards hind margin. Wing veins yellow with dark setae. Halter pale yellow with three darker yellow stripes.

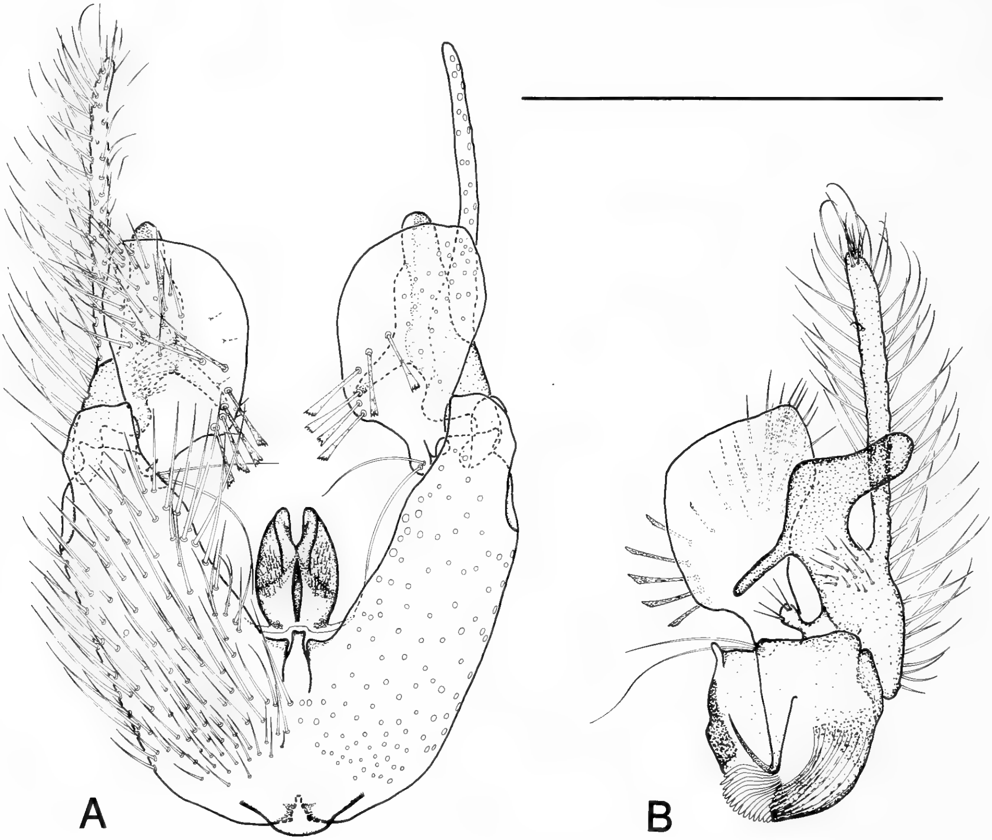


Fig. 3. *Pseudexechia lanceostylus* sp. n. male terminalia. – A, ventral view; B, internal face of the gonostylus. Scale 0.50 mm.

Legs mainly yellow; coxae paler yellow, fore coxa anteriorly with darker stripe. Abdominal tergites mainly yellowish brown; tergite 1 to 3 with pale lateral markings; tergite 4 and 5 with pale posterolateral markings, almost reaching middle; tergite 6 almost entirely dark. Terminalia mainly yellow, darker on sternal process and on parts of dorsal lobe of gonostylus.

Head. Total length of flagellum 1.53 mm. First flagellomere 1.7 times as long as second flagellomere. Second flagellomere 2.3 times as long as wide. Six large orbital setae. Tiny median ocellus present. Diameter of lateral ocellus / diameter of median ocellus 2.4. Clypeus bearing about 60 setae; width / length 0.8. Fourth palpomere about 1.5 times as long as third palpomere.

Thorax. Pronotum with vertical row of 3 erect setae. Scutum with pair of medium sized bristle like dorsocentral setae present posteromedially in front of scutellum (prescutellar setae); anterior and lateral margins with large setae; otherwise uniformly clothed with small setae (but larger and fewer than in other *Pseudexechia* except in *P. longistylus* sp. n.). Scutellum with pair of strong scutellar setae and 2 pairs of very short posteriorly curved setae basad of them. Proepisternum with 1 strong, 2 medium sized and 8 small setae. Laterotergite with 8–10 large and about 60 small setae.

Wing. Crossvein h with 1-2 ventral setae. R_1 with 5-8 ventral setae apically. R_{4+5} with 3-4 ventral setae basally and 36-39 ventral setae apically. Wing length / length of R_1 2.6. Wing length / length of R_{4+5} 1.8. R_{4+5} nearly straight. Length of r-m / length of M-petiole 1.6. A / B 1.5. E / length of M_1 0.7. E / length of M_2 0.8. Base of Cu–fork well beyond base of M–fork. M-fork veins distaly divergent. Cu-fork veins divergent. F / E 1.3. F / length of CuA_1 1.5. F / length of CuA_2 2.3. C / D 1.1. Vein CuP reaching as far as base of Cu–fork. Vein A_1 strong, shorter.

Legs. Length of fore basitarsus / length of fore tibia 1.8. Tibial spur formula 3.7; 9.8, 7.5; 5.4, 5.3. Fore tibia with 1 ad, 39 p and 3 v setae. Mid tibia with 41 a, 5 pd and 7 p setae. Hind tibia with 9 a, 5 pd and 4

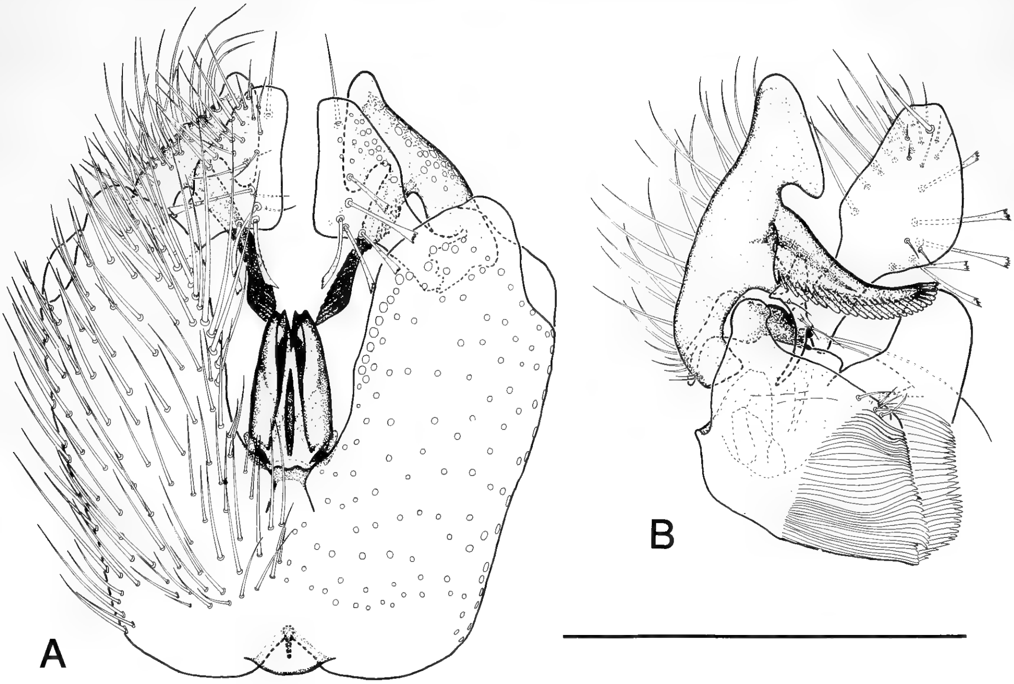


Fig. 4. *Pseudexechia inthanonensis* sp. n. male terminalia. – A, ventral view; B, internal face of the gonostylus. Scale 0.50 mm.

p setae. Posterior sensillae placodea on basal part of tibia 3; 4; 3.

Terminalia (Fig. 3A, B). Length of gonocoxite 0.57 mm. Sternal process rounded with about 55 tiny setae; length / width 1.4. Dorsal lobe of gonostylus 0.51 mm, ending in slender lobe. Sclerotized internal process bifurcate, the the prongs pointing in almost opposite directions. Ventral lobe of gonostylus broad and rounded, bearing 6 fan-tipped setae. Inner lamellate parts of gonostylus with lobe ending in strong seta–like hook. Cerci thin, not reaching apical level of gonocoxite, with two strong apical and one strong subapical setae (not figured).

Pseudexechia inthanonensis sp. n.
(fig. 4).

Type material. – Holotype male, THAILAND: Chiang Mai province, Doi Inthanon, about 2200 m a.s.l., 12.IV.1991, J. Kjærandsen, sweep net (ZMBN No. 181).

Diagnostic characters. – The male imago is separable from other species by the shape of the dorsal lobe of gonostylus, which has a smooth rounded hook at the tip and a large internal process with 25 teeth, by the shape of the sternal process and by the short stem of the cubital fork.

Etymology. – From Doi Inthanon, a mountain in northern Thailand. A noun in genitive case.

Description of male holotype. – Length of thorax 1.20 mm. Wing length 3.82 mm. Wing length / length of thorax 3.2. Wing length / length of fore femur 3.3.

Coloration. Antenna with scape, pedicel and first flagellomere for half of its length pale yellow, rest of flagellum greyish yellow. Head mainly brown, frons and sides yellowish. Maxillary palp yellow. Pronotum yellowish brown. Scutum brown with three yellow stripes, median stripe broadening to fore margin, and narrow yellow lateral margins. Scutellum brown with yellowish lateral margins. Pleura yellowish brown. Wing unmarked, greyish yellow tinted, paler on basal half posterior of R-stem. Wing veins yellowish brown with dark setae. Halter pale yellow with three greyish yellow stripes. Legs mainly yellow; coxae paler yellow, each coxa with yellowish brown stripe. Abdominal tergites mainly brown; tergite 2 to 5 with pale posterolateral markings, reaching middle; tergite 6 dark brown. Terminalia mainly yellow, darker on sternal process and on parts of dorsal lobe of gonostylus. Tip of dorsal lobe of gonostylus whitish.

Head. Total length of flagellum 1.84 mm. First flagellomere 1.7 times as long as second flagellomere.

Second flagellomere 2.0 times as long as wide. Four to five large orbital setae. Small median ocellus present. Diameter of lateral ocellus / diameter of median ocellus 2.1. Clypeus bearing about 40 setae; width / length 0.8. Fourth palpomere about 1.4 times as long as third palpomere.

Thorax. Pronotum with vertical row of 2 strong and 2 medium sized upcurved setae. Anterior and lateral margin of scutum with setae of different sizes; scutum otherwise uniformly clothed with small dark setae. Scutellum with pair of strong scutellar setae and pair of short posteriorly curved setae basad of them. Proepisternum with 1 large, 2 medium sized and 24 small setae. Anepisternum with 6 small setae. Laterotergite with 12–14 large and about 200 tiny setae.

Wing. Crossvein h without ventral setae. R_1 with 9 ventral setae apically. R_{4+5} with 4-5 ventral setae basally and 58-65 ventral setae apically. Wing length / length of R_1 2.3. Wing length / length of R_{4+5} 1.7. R_{4+5} distinctly downcurved. Length of r-m / length of M-petiole 1.0. A / B 1.9. E / length of M_1 0.7. E / length of M_2 0.8. Base of Cu–fork not beyond base of M–fork. M-fork veins only slightly divergent apically. Cu-fork large, veins divergent. F / E 0.98. F / length of CuA_1 1.2. F / length of CuA_2 1.7. C / D 0.9. Vein CuP reaching well beyond base of Cu–fork. Vein A_1 strong, shorter.

Legs. Length of fore basitarsus / length of fore tibia 1.2. Tibial spur formula 3.5; 6.7, 6.4; 4.6, 4.5. Fore tibia with 6 ad, 45p and 8 v setae. Mid tibia with 49 a, 5 pd and 4 p setae. Hind tibia with 6 a, 5 pd and 8 p setae. Posterior sensillae placodea on basal part of tibia 3; 3; 3.

Terminalia (Fig. 4A, B). Length of gonocoxite 0.67 mm. Sternal process narrow without setae; length / width 1.8. Dorsal lobe of gonostylus 0.67 mm long with smooth rounded hook at tip and relativly large sclerotized internal process with 25 teeth. Ventral lobe of gonostylus bearing 4-5 fan-tipped ventral setae and one strong dorsal setae apically. Inner lamellate parts of gonostylus with 5 small setae. Cerci thin and slender, reaching to about apical level of gonocoxite, without strong setae (not figured).

Discussion

The presence of a pair of medium sized bristle-like dorsocentral setae posteromedially above scutellum in *Pseudexechia longistylus* sp. n. and *P. lanceostylus* sp. n. is not in accordance with the generic description. Tuomikoski (1966) used absence of 'discal bristles' as one of the main diagnostic characters for *Pseudexechia.* The other setae on the scutal disc in these two species are also relatively strong, erect and bristle-like when compared with other species in the genus, and they are fewer in numbers. Hence, this character should be used with care. However, other generic characters clearly place these species within *Pseudexechia.*

P. inthanonensis sp. n. is evidently closely related to the Palaearctic *P. trisignata* (Edwards, 1913) based on the structure of the male terminalia. However, *P. inthanonensis* sp. n. is rather different in coloration (yellow thoracic stripes on brown ground) and shows an aberrant and interesting wing venation. The short Cu-stem places the base of Cu-fork slightly before base of M-fork (F / E = 0.98). A long Cu-stem (short Cu-fork) has been used to group the species of *Exechia* s.l. (including *Exechiopsis* and *Pseudexechia*) (e.g. Edwards 1925).

These findings strengthen the view of Tuomikoski (1966) that *Pseudexechia* is more closely related to *Allodiopsis* and *Allodia* than to *Exechia* and *Exechiopsis.*

Acknowledgements

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SYNONYMICAL NOTES ON THE *NEPA CINEREA* LINNAEUS COMPLEX (NEPIDAE: HETEROPTERA)

Polhemus, J. T., N. Nieser & S. L. Keffer, 1994. Synonymical notes on the *Nepa cinerea* Linnaeus complex (Nepidae: Heteroptera). – Tijdschrift voor Entomologie 137: 331-336. [ISSN 0040-7496]. Published 15 December 1994.

The *Nepa cinerea* Linnaeus complex is distributed over Europe, North Africa, the Middle East and northern Asia. Within this complex we recognize three species, *N. cinerea, N. sardiniensis* Hungerford and *N. anophthalma* Décu, Gruia, Keffer & Sarbu. The following are considered to be junior synonyms of *N. cinerea* Linnaeus, 1758: *Nepa rubra* Linnaeus, 1758; *Nepa scorpioaquaticus* De Geer, 1773; *Nepa cinerea* var. *minor* Puton, 1886, **syn. n.**; *Nepa seurati* Bergevin, 1926, **syn. n.**; *Nepa cinerea* var. *major* Bergevin, 1926, **syn. n.**; *Nepa dollfusi* Esaki, 1928, **syn. n.**; *Nepa cinerea* var. *orientalis* Esaki, 1928, **syn. n.**; *Nepa rubra meridionalis* Poisson, 1961, **syn. n.**; *Nepa remyi* Poisson, 1961, **syn. n.**; *Nepa cinerea poissoni* Tamanini, 1973.

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Key words. – Heteroptera; Nepidae; *Nepa cinerea*; synonymy.

The *Nepa cinerea* Linnaeus complex is a tightly knit and very widespread species group in the Old World, distributed throughout Europe, the Mediterranean region, and as far east as northwest China and the Amur region of Siberia. *Nepa cinerea* was one of the earliest water bugs to be studied (Hoefnagel 1592, Moufet 1634, Frisch 1728, Swammerdam 1737-38), and the morphology has been extensively investigated, with an excellent treatment and summary of earlier studies by Hamilton (1931). Despite of this wealth of knowledge, the species group nomenclature concerning this insect remains unsettled. A definitive synonymical treatment is needed for the Catalogue of Palearctic Heteroptera (B. Aukema & C. Rieger, editors) now being prepared for publication.

The early nomenclatural dilemma regarding the priority and synonymy of *Nepa cinerea* versus *Nepa rubra* Linnaeus, 1758, first addressed in detail by Esaki (1926), then by Tamanini (1973), was finally resolved by the ICZN (Opinion 1335/1985) in response to a petition by Kerzhner (1981). Tamanini (1973) has declared the type locality to be Sweden, because the first specimens were collected there; he cites inclusion in Linnaeus' Fauna Svecica (1761) as evidence for this. Over the years however, a number of additional taxa have been proposed, as species, subspecies and varietal forms, that are either synonymous or very closely allied with *N. cinerea.* Esaki (1928), Poisson (1961) and Tamanini (1973) addressed this species-group problem, however, far from resolving the status of these species-group taxa, each of these authors exacerbated the situation by adding at least one additional variety.

The following is a brief summary of the taxa and their supposed differences from *Nepa cinerea* sensu stricto, with comments on the validity of the characters used for differentiation.

Nepa cinerea var. *minor* Puton, 1886 and *Nepa cinerea* var. *major* Bergevin, 1926 were established solely on the basis of size differences, which is not a differentiating characteristic, as it varies widely within single populations. Jaczewski (1934) examined specimens of *N. cinerea minor* from Algeria, and stated that 'they seem to be conspecific with the typical *N. cinerea* L.' We therefore synonymize both varieties.

Bergevin (1926) established *Nepa seurati* n. sp. from Tunisia on the basis of a number of somatic differences, which he compared, in a table, with *Nepa cinerea* var. *minor* Puton. Esaki (1928) provided a photograph of the type of *seurati* which does indeed have a slightly different shape than the *cinerea* specimens he illustrates, with the lateral abdominal margins straight along much of the basal part, widening posteriorly, and abruptly incurved beyond, as noted by Poisson (1961: 631). Also the fore femur basally is wider than the *N. cinerea* specimens illustrated. This taxon would therefore seem to be separable from *Nepa cinerea cinerea*, however in long series taken from single populations in Morocco (nr. Tangier border, 8.VIII.1955, D. R. Lauck, Polhemus Coll.) and Portugal (nr. Portinas, Riba la Banho, 15.IV.1976, N. Nieser, Nieser and Polhemus Collns.) all of these character states are present along with intermediates. If considered as a valid subspecies, then many of the populations from north Africa would probably be attributable to this taxon.

Esaki (1928) described *Nepa dollfusi* from a single female collected in Morocco. Some of the differences from *N. cinerea* he cited may be attributable to alary polymorphism (see Larsén 1949, 1955), as the flightless forms, such as *dollfusi*, have an altered morphology, e. g. straighter hind margin of the pronotum, and reduced hemelytral membrane. Esaki provided a photograph of the type of *dollfusi* which appears to represent a malformed specimen, quite possibly resulting from damage during emergence from the last nymphal stage. The specimen also has reduced antennae, discussed below, that may have also resulted from a traumatic ecdysis. The red abdominal dorsum noted for European specimens of *N. cinerea* in contrast to *dollfusi* is unreliable, as it varies from grey brown to yellowish to pink or red in individual series from Europe and the Mediterranean region. Theiry (1981) noted the great variation in size and coloration (of both ground colour and abdominal tergites) in the 100+ specimens of *Nepa* collected over a wide range of elevation in Morocco, all of which he assigned to *N. cinerea*, noting that the parameres and antennae of all forms were of the 'type *cinerea*.' Lindberg (1929) considered *N. dollfusi* to be only an aberrant specimen of *N. cinerea*.

Nepa cinerea var. *orientalis* Esaki, 1928 was founded on the basis of size and slight differences in antennal and head morphology, all unreliable. We have not been able to study a long series from the Far East to determine if there is any discernable difference in the male genitalia from the western European stock, but for the present the available evidence leads us to synonymize this form with *N. cinerea*.

Hungerford (1928) described *Nepa sardiniensis* from the island of that name. He separated it from related taxa by the lack of a prolongation on the second antennal segment and slender fore femur. These alone are questionably enough to justify the status of a separate species for the populations of Sardinia and Corsica, however Mazza (1971, 1978) has given additional evidence for separate species status (see below). *Nepa sardiniensis* is the only geographically isolated taxon in the *N. cinerea* complex, aside from the unique spatially isolated cavernicolous *N. anophthalma* Décu et al (in press). Linnavuori (1960) reported this species from Israel, Transcaspica and Turkestan, but according to Tamanini (1973) these records refer instead to *N. cinerea cinerea*.

For the Palearctic region, Stichel (1955) listed as species *Nepa seurati* Bergevin, *Nepa dollfusi* Esaki, *Nepa sardiniensis* Hungerford, and *N. cinerea* (as *Nepa rubra*), with *minor* Puton, *major* Bergevin and *orientalis* Esaki clearly designated as forms of the latter.

Linnavuori (1960) claimed separation of *N. cinerea* and *N. sardiniensis* on the basis of the short second antennal segment, broader sternite VII, and differently formed male clasper of the latter. He stated that *N. cinerea* does not occur in Palestine. He also stated that the anterior femora of *Nepa seurati* are much broader basally than in *N. sardiniensis*.

Poisson (1961) gave figures of the antennae, female subgenital plate and male genitalia of *N. dollfusi* Esaki, *N. cinerea cinerea* (as *N. rubra rubra*), *N. cinerea meridionalis* (as *N. rubra meridionalis*), and *Nepa remyi* Poisson, 1961 from Morocco. *N. remyi* was separated on the basis of slight differences in the shapes of the male subgenital plate ('opercule génital'), male paramere, and the base of the fore femur, all of which have been seen to be somewhat variable within populations. We consider this variety to fall within the variability of *N. cinerea*, thus a synonym. Poisson also gave a key to separate all of the forms and species known in 1961 (including *Nepa apiculata* Uhler from North America and *Nepa hoffmanni* Esaki from China), based on differences in the antennae, the respiratory siphon, shape of the anterior femur, overall body length.

Seidenstücker (1963) investigated the status of *N. dollfusi*, *N. sardiniensis* and *N. seurati*, relying mainly on the antennal structure to conclude that *Nepa seurati* is a good species, and that *Nepa sardiniensis* Hungerford, 1928 (June) is a junior synonym of *Nepa dollfusi* Esaki, 1928 (April), and occurs in Turkey as well as Corsica and Sardinia. If Seidenstücker's analysis were accepted, the *N. cinerea* complex would include *N. anophthalma*, *N. cinerea*, *N. dollfusi* (= *N. sardiniensis*), and *N. seurati*. Later authors have not accepted the synonymy of *N. sardiniensis* (see below).

Mazza (1968) studied the variability of the number of respiratory horns of 5081 eggs of *N. cinerea* from Italy. He noted that the modal number of horns documented by Hinton (1961) for a British population (7) was different than the modal number (6) for the Italian population from La Spezia Province. Later he analyzed many specimens and concluded that the geographical forms were impossible to delimit, and that they form a continuum (Mazza 1974). This evidence suggests clines within *N. cinerea*.

Mazza (1971) noted constant differences in the number of respiratory horns (without giving details) between *N. sardiniensis* collected on Corsica and *N. cinerea* collected in Toscana (Italy), and further stated that these two populations were reproductively isolated, as cross breeding produced sterile F1 hybrids. Later he (Mazza, 1978) examined about 1000 specimens of each species, and using several somatic characters in first order equations he showed consistent separation, therefore *N. sardiniensis* and *N. cinerea* are presently accepted as distinct species.

Tamanini (1973) discussed all of the previously mentioned forms except *Nepa remyi* Poisson, 1961, and proposed yet another subspecies, *Nepa cinerea poissoni* Tamanini from the Pyrenees Mountains of France and Spain, based on differences in pronotal morphology and antennae. He compared his new taxon to *N. sardiniensis* and *N. cinerea cinerea.* The differences he cites are not sufficient to separate this taxon from the latter, and it was synonymized with the latter by Nieser & Montes (1984). Tamanini claims that *N. sardiniensis* is endemic to Corsica and Sardinia, and states that *N. cinerea dollfusi* and *N. cinerea meridionalis* are of 'uncertain systematic rank.' For all of Europe and North Africa, Nieser (1978) listed only *Nepa sardiniensis* Hungerford and *Nepa cinerea,* and recognized as subspecies of the latter *N. c. poissoni* Tamanini and *N. c. seurati* Bergevin. Later Nieser & Montes (1984) synonymized *N. c. poissoni* with *N. cinerea,* without comment.

Nepa anophthalma Décu, Gruia, Keffer & Sarbu (in press) is separable from all other species of the *cinerea* complex by five characters; 1. A yellow ground color (vs. dark), 2. Eyes absent (vs. present), 3. Hemelytra brachypterous, posterior margin sinuate (vs. macropterous, posterior margin rounded), 4. Midlongitudinal groove of mesosternum absent (vs. present), 5. Paraterga hirsute (vs. glabrous except for hairs ringing stigmata). This is clearly the most annectant species of the complex, yet the male genitalia are very similar to the other members of the group. It is endemic to the Movile cave system in Romania.

As discussed above, most of the characters used by various authors to separate species-group taxa in the *Nepa cinerea* complex are as variable within populations as they are between populations, thus must be considered unreliable for the separation of taxa, especially when dealing with single specimens or small series. The antennae have been extensively cited as a separating characteristic notwithstanding their variability. Tamanini (1973) has shown that the antennal morphology is quite variable, even in a single specimen, thus the antennal morphology is not a completely reliable specific character in this genus, although their form may indicate trends, certainly vary between some populations, and seem to have a norm within certain populations (vide Seidenstücker, 1963; Tamanini, 1973). Esaki (1928) illustrated the antennae of a topotypic specimen of *N. seurati,* the type of *N. dollfusi,* and of *N. cinerea* (no provenance given). In *dollfusi* the prolongation of the second segment is lacking and segments two and three are fused and short; in this regard it is very similar to *N. sardiniensis,* in fact so similar that Seidenstücker (1963) proposed the synonymy of the two taxa. In *seurati* the prolongation of the second segment is moderately long, and segments two and three are separated and moderately long, very similar to *cinerea* except in the latter the prolongation of the second segment is slightly longer. Tamanini (1973) studied many specimens from various localities, and illustrated the antennal forms most frequently encountered as well as aberrant forms rarely seen. The range of morphology within the species essentially covers the spectrum of differences used to separate the three species group taxa discussed above, although the 'normal' form of each conforms roughly to those illustrated by Esaki (1928). Mancini (1936), who tentatively identified specimens from Libya as *N. cinerea minor,* questioned whether the shape of the antennal segments was a valid character.

One of us (SLK) has studied the male genitalic structure of several populations of the *Nepa cinerea* complex from Finland, Morocco, Sardinia, Romania, and Iran and can find only one significant genitalic difference in any of the taxa (see below), although the genitalia of the *cinerea* complex are considerably different than the genitalia of the *apiculata* group which contains *Nepa apiculata* and *Nepa hoffmanni* (Keffer et al. 1990). However, this general lack of male genitalic difference should not be taken as evidence that species or subspecies designations within the *cinerea* complex are invalid. Keffer (1991 and personal observation) has found that male genitalia are often of little taxonomic value at the species level in the Nepidae. For example, in his revision of the New World waterscorpion genus *Curicta,* Keffer (1991) found male genitalia to be diagnostic for the genus but largely invariant throughout the range of the genus. Similarly, Keffer (in prep.) has studied a majority of the species across the family Nepidae and found that male genitalic characters often have generic or species group significance but are often of little value for species determination. One genitalic character, paramere shape, has been used extensively by two nepid taxonomists of the recent past, Jose De Carlo and Raymond Poisson, in their numerous new species descriptions. Keffer, however, has found that parameres may vary either little or else randomly across species groups, or even genera, and thus are not generally valid as a species specific character.

Keffer's observations with *Curicta* and other nepid genera are affirmed in the genus *Nepa.* Male genitalia do separate the *cinerea* and *apiculata* species groups (Keffer et al. 1990). However, within the *cinerea* complex phallic structures, with one exception, are either invariant, or they vary randomly, across all taxa. For example, parameres appear to vary randomly and are therefore of no value in making species and subspecies determinations. Taminini (1973, figs. 61-78) figured parameres for *N. cinerea cinerea, N. cinerea poissoni, N. cinerea seurati*, and *N. sardiniensis*. We have observed *N. cinerea cinerea* specimens from Finland with paramere shapes similar to those figured by Taminini for *N. cinerea poissoni* and we have observed *N. sardiniensis* parameres that are similar to those figured by Taminini for *N. cinerea cinerea*. Further, Décu et al. (in press) have shown that *N. anophthalma* has parameres similar to those of *N. cinerea poissoni*.

Only one genitalic character, the shape of the secondary struts, appears to be of value for separating some *cinerea* group taxa. During copulation, the male's secondary struts and ventral diverticulum lodge in the female bursa copulatrix (Larsen 1938, fig. 26; secondary struts = 'gr, Griffel', bursa = 'vt, Vaginaltasche'; Keffer 1991, p.3) where they may have a holdfast and/or stimulatory function. If, in fact, the struts are stimulating the female during copulation, and thus subject to sexual selection, they could exhibit species specificity. Taminini (1973: 233) noted that, in ventral view, the secondary struts ('processi a spatola della coniunctiva') of *N. cinerea cinerea* specimens from Sicily and continental Italy converge toward the midline distally, whereas *N. sardiniensis* secondary struts are nearly straight. We would add to Taminini's description two of our own observations. First, converging secondary struts, as in *cinerea cinerea*, are also found in the cave dwelling *cinerea* group taxon, *N. anophthalma* and in *apiculata* group taxa. Second, in both *N. cinerea cinerea* and *N. sardiniensis* the secondary struts are dorsoventrally flattened whereas in *N. anophthalma* and in the *apiculata* group taxa the struts are tubular in shape. In sum, it appears that secondary struts can be used to separate *N. sardiniensis* (secondary struts nearly straight, not converging distally) and *N. anophthalma* (secondary struts tubular, not dorsoventrally flattened) from other *cinerea* group taxa.

The status of four species group taxa must be decided; they are *N. cinerea, N. dollfusi, N. sardiniensis* and *N. seurati*. The first question to be settled is the proposed synonymy of *dollfusi* and *N. sardiniensis*, by Seidenstücker (1963). This synonymy seems to rest on the strength of the similarity of the antennae of the two taxa. If this synonymy is accepted, and the modal antennal form is accepted as a valid discriminating character, then the range of *N. dollfusi*, the senior synonym, is Morocco, Tunisia, Corsica and Sardinia. Tamanini (1973) rejected this synonymy, however, and also rejected the citation of *N. sardiniensis* for Israel by Linnavuori (1960) and for Turkey, Transcaspica and Turkestan by various authors, as being narrowly based on antennal form only. In this contention he is supported by Mazza (1971, 1978), thus current opinion supports the recognition of *N. sardiniensis* as a valid species endemic to Corsica and Sardinia, with *N. dollfusi* relegated to synonymy under *N. cinerea*.

Tamanini (1973) contends that *N. cinerea cinerea* occurs only as far south as northern Italy, and that *N. cinerea seurati* is distributed from southern Italy through Sicily to Libyia and Tunisia (we would possibly add Morocco in part). He shows a gradation of characters on a latitudinal cline through Italy, which suggests a single species rather than subspecies. If the subspecies status of *seurati* were to be accepted, then *dollfusi* should be considered as a synonym with aberrent antennae. This would leave *N. cinerea cinerea* as a variable subspecies with a range throughout northern Europe and as far south as Morocco nearest Spain, across the Balkans, through the Middle East, and as far east as Siberia.

We here reject the subspecies concept for *seurati*, however, as based on insufficient evidence and unreliable characters, and synonymize it under *cinerea*.

Mayr & Ashlock (1991:43) give the following definition of the subspecies: 'A subspecies is an aggregate of phenotypically similar populations of a species inhabiting a geographic subdivision of the range of that species and differing taxonomically from other populations of that species'. We accept this definition, and all of the species group taxa of the *N. cinerea* complex that fail to conform to this definition are placed in synonymy of *N. cinerea* below. We have seen no convincing evidence that the characters upon which these taxa were founded are anything more than individual variations within and between populations, scattered more or less randomly, and without significant separation as required for subspecies characterization. It is indeed possible that sufficient evidence may be presented in the future to reestablish one or more of the synonymized taxa as valid subspecies, but for the present such clear evidence is lacking. We therefore recognize only three species, without subspecies, in the *cinerea* complex; *Nepa anophthalma* (endemic to the Movile Cave system of Romania), *N. sardiniensis* (endemic to Corsica and Sardinia), and the widespread *N. cinerea*.The results of our investigations are summarized as follows:

Nepa anophthalma Décu, Gruia, Keffer & Sarbu, in press.

Nepa anophthalma Décu, Gruia, Keffer & Sarbu, in press. Holotype: ♂, Movile Cave, Romania. (ERSI) [examined].

Distribution. – Europe, Romania, nr. Mangalia, Movile Cave. Endemic.

Nepa cinerea Linnaeus, 1758

Nepa cinerea Linnaeus 1758: 440. Syntypes, ♂, ♀, Sweden (type locality restricted to Sweden by Tamanini 1973: 226). (UZIU) [not examined].

Nepa rubra Linnaeus 1758: 440. Holotype, ♀, locality unknown. (UZIU) [not examined]. (syn. of *Nepa cinerea* Linnaeus 1758; see Opinion 1335/1985).

Nepa scorpioaquaticus De Geer 1773: 361. Syntypes, 5, sex unknown, type locality unknown. (coll De Geer, NHRS) [not examined]. Unneccessary new name for N. *cinerea* L. (see Retzius 1783: 90).

Nepa cinerarea P. L. S. Müller 1774: 472. Incorrect subsequent spelling.

Nepa cinerea var. *minor* Puton 1886: 8. Syntypes, sex unknown, Tunisia, Oued Tessa, 'Sidi-Mohamed-ben-Ali', Oued Bateha, Oued Eddedj, Gafsa, Gabés. (Depository unknown) [not examined] (syn. Jaczewski 1934, suspected). **Syn. n.**.

Nepa seurati Bergevin 1926: 290. Holotype, ♂, Tunisia, Kebili. (MNHN) [not examined]. **Syn. n.**

Nepa cinerea var. *major* Bergevin 1926: 294. Holotype, ♂, Morocco, Taza. (Depository unknown; coll. Bergevin; MNHN?) [not examined]. **Syn. n.**

Nepa dollfusi Esaki 1928: 434 (April). Holotype, ♀, Morocco, Oued Djenanimès près Khénifra. (MNHN) [not examined]. (syn. Lindberg 1929: 9; restored by Seidenstücker 1963: 315, and named senior synonym of *Nepa sardiniensis*; synonymy with *sardiniensis* rejected by inference by Nieser 1978: 283). **Syn. n.**

Nepa cinerea var. *orientalis* Esaki 1928: 436. Syntypes, 3♀, Russia, Amur (BMNH) [not examined]. **Syn. n.**

Nepa rubra meridionalis Poisson 1961: 635. Syntypes, ♂, ♀, France, Tunisia, 'Iberian Peninsula'. (coll. Poisson, USNM) [examined]. **Syn. n.**

Nepa remyi Poisson 1961: 636. Syntypes, 1♂, 2♀, Morocco, region d'Ifrane, Tagbaloute. (coll. Poisson, USNM) [examined]. **Syn. n.**

Nepa cinerea poissoni Tamanini 1973: 239. Holotype, ♂, France, Pyrenées-Orientales, Collioure. (LTRC) [not examined]. (syn. Nieser & Montes 1984: 38).

Distribution. – Europe, North Africa, Middle East, northern Asia.

Note. – *Nepa annulipes* (non Laporte 1833): Kolenati 1857: 481 is a misidentification referring to a *Laccotrephes* species, not collected in the Caucasus; see Kiritshenko 1918: 171; see also Esaki 1928: 434.

Nepa sardiniensis Hungerford, 1928

Nepa sardiniensis Hungerford, 1928: 120 (June). Syntypes, 1♂, 1♀, Italy, Sardinia. (SEMC) [examined]. (syn. with *dollfusi* by Seidenstücker 1963: 322; considered as valid species by Mazza 1971: 539, 1978: 85, Tamanini 1973: 241).

Distribution. – Europe (Corsica, Sardinia)

Depositories

Abbreviations (codens) for depositories follow Arnett, Samuelson & Nishida (1993), with the addition of: ERSI (Emil Racovitâ Speleological Institute, Bucharest); LTRC (Livio Tamanini Collection, Rovereto, Italy).

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The 'Tijdschrift voor Entomologie' (Netherlands Journal of Entomology) has a long tradition in the publication of original papers on insect taxonomy and systematics. The editors particularly invite papers on the insect fauna of the Palaearctic and Indo-Australian regions, especially those including evolutionary aspects e.g. phylogeny and biogeography, or ethology and ecology as far as meaningful for insect taxonomy. Authors wishing to submit papers on disciplines related to taxonomy, e.g. descriptive aspects of morphology, ethology, ecology and applied entomology, are requested to contact the editorial board before submitting. Usually, such papers will only be published when space allows.

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INSTRUCTIONS TO AUTHORS

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A cover page should provide the names of the authors and a proposal for a running title. The second page starts with author names (in all capitals), use & for 'and', on a new line the name of institute (as short as possible), with multiple authors using superscript ^{1} ^{2} etc. The title is brief and informative, typed in all capitals, with order and family of the taxon treated in parentheses.

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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:

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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.

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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].

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