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A review of the Miletini (Lepidoptera: Lycaenidae)

J. N. Eliot
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A review of the Miletini (Lepidoptera: Lycaenidae)

J. N. Eliot
Upcott House, Bishop’s Hull, Taunton, Somerset TA4 1AQ

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Synopsis

This review of the Miletini is based mainly on characters of the male genitalia. Keys to, and descriptions of, the genera, subgenera, species and subspecies are provided. One genus, one subgenus, eight species and seven subspecies are newly described. One species is relegated to subspecies, and three subspecies are raised to species; 41 new synonyms are established.

Introduction

The butterflies which are here considered to comprise the Oriental section of the tribe Miletini Reuter, 1897 (see Corbet, 1939b) were originally given family-group status (as the Gerydinae) by Doherty (1886), mainly on the basis of their distinctive eggs. Reuter (1897: 263) included the African genus Megalopalpus Röber, 1886, in the group, treating the latter as a tribe, the Miletidi, which is distinguished from all other Lycaenidae by the peculiar labial palpi bearing long hairs on the inner surface of the basal segment (Basalfleck). Corbet (1939b) used the family group name Miletinae in place of Gerydinae because Gerythus Boisduval, 1836, is an objective synonym of Miletus Hübner, 1819; his action is valid under Article 40b of the International Code of Zoological Nomenclature (1985). Eliot (1973) used Miletinae in a wider sense than previous authors, placing the Miletini (Miletinae sensu Corbet) as one of four tribes which he included in the subfamily.

Only two complete analyses of the Oriental Miletini (sensu Eliot) have so far been attempted, both by Fruhstorfer who based his studies in part on a number of genitalia preparations made by Reverdin. In the first (Fruhstorfer, 1913–14) it is evident that the new taxa he described had three separate origins. Many descriptions are based on specimens in his own collection, some of which bear type and/or determination labels attached either at that time or at some later date. Others relate to specimens in the collections of the British Museum (Natural History) and Walter Rothschild at Tring, to which no type or determination labels were attached; these collections were studied by Fruhstorfer during a visit to England. Finally, a few descriptions are based on records and figures by other authors of specimens which he had not seen; in Fruhstorfer’s first analysis such taxa were, in most cases, based on a work by Semper (1889), so those specimens listed by Semper may be considered to comprise Fruhstorfer’s type-series. In certain cases, however, it is clear that Fruhstorfer applied a name to a single specimen figured by
Semper, and in such cases the original of the figure is automatically the holotype; in other cases, however, it has been necessary to designate a lectotype. In his second analysis (Fruhstorfer, 1916) it is evident that he had in the meantime examined Semper’s collection, and he described further material to which type and determination labels were attached. There is some evidence to suggest that during this examination some of Semper’s original labels were inadvertently transferred from one specimen to another. Such instances are mentioned later under the relevant taxon.

As Fruhstorfer seldom selected types, I have designated lectotypes when it is not clear that a taxon was described from a single specimen. I have also designated lectotypes for some taxa named by other authors when I have been able to recognise primary type-material in the British Museum (Natural History). When the original type-series are in museums which I have not visited, I have generally left the selection of lectotypes to future workers, except in a few cases where, to avoid confusion, I have designated figured specimens.

The following abbreviations have been used for the actual or supposed location of type-material.

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<td>Carnegie Museum, Pittsburgh</td>
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<td>MNHU</td>
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Here it may be noted that there are in the BMNH collection a number of specimens bearing red type labels as well as, in some cases, labels in Corbet’s handwriting identifying them as holotypes or allotypes which were not cited as such in the original descriptions. Where it is reasonable to assume that these were part of the original type-series I have normally designated them as lectotypes in preference to any other syntypes. In some cases, however, it is quite clear that the specimens cannot possibly be part of the original type-series; such specimens I have rejected as syntypic material and labelled them accordingly. These ‘types’ are listed, however, in the section dealing with species and subspecies since it is possible that they may have misled authors in the past or might do so in the future.

**Acknowledgements**

This revision is based mainly on material in the BMNH, and I am grateful to the Trustees for access to the collections and library, to Mr R. J. Vane-Wright and Mr P. R. Ackery for their help and encouragement, and to the Photographic Unit for providing the photographs for Figs 55–104. I thank especially Mr Vane-Wright and Mrs S. M. North for undertaking a review of the African genus *Megalopalpus*, of which I have no practical knowledge in the field, and for preparing the draft incorporated in this paper. I am also very grateful to Dr Heinz Schröder for the loan of important material from the Semper collection in the Senckenberg Museum, without which it would have been impossible to carry out a satisfactory review. I thank Dr R. de Jong, RNH, and Professor S. Murayama, who sent material for examination. Mr G. C. Treadaway placed the whole of his extensive Philippine material at my disposal and sent me the photographs for Figs 105–108. I also received valuable Philippine material through the generosity of Mr Yusuke Takanami and Dr A. Ballantine, including new taxa which I have named in their honour. Major A. Bedford Russell lent me material from Vietnam and Sulawesi, and presented the holotype of *Allotinus samarensis russelli* to the BMNH, and Dr E. Diehl sent me material from Simeulue. In addition the collections of the late Mr W. A. Fleming (kindly placed at my disposal by his widow), Lt-Col C. F. Cowan, Dr T. Norman and my own have been examined.
Genus *ALLETONUS* C. & R. Felder, [1865]

**Subgenus** *ALLETONUS* C. & R. Felder, [1865]

*fallax* C. & R. Felder, [1865]

*fallax fallax* C. & R. Felder, [1865]

*sabazus* Fruhstorfer, 1913 syn. n.

*zaradus* Fruhstorfer, 1916

*fallax aphacus* Fruhstorfer, 1913

*ancius* Fruhstorfer, 1913 syn. n.

*artinus* Fruhstorfer, 1916

*fallax erximachus* Fruhstorfer, 1913

*fallax dotion* Fruhstorfer, 1913

*fallax tymphrestus* Fruhstorfer, 1916

*fallax audax* H. H. Druce, 1895

*fallax apus* de Nicéville, 1895

*michaelis* Eliot, 1959

*albifasciatus* Eliot, 1980

*subviolaceus* C. & R. Felder, [1865]

*subviolaceus subviolaceus* C. & R. Felder, [1865]

*alkamah* Distant, 1886 syn. n.

*manychus* Fruhstorfer, 1913 syn. n.

*kallikrates* Fruhstorfer, 1913 syn. n.

*silarus* Fruhstorfer, 1916 syn. n.

*subviolaceus mirus* Van Eecke, 1914

*tronola* ssp. n.

*nicholsi* Moulton, 1911

*nicholsi nicholsi* Moulton, 1911

*nicholsi battakanus* Fruhstorfer, 1913

*major* C. & R. Felder, [1865]

*depictus* Fruhstorfer, 1913 syn. n.

*kalawarus* Ribbe, 1926

*maximus* Staudinger, 1888 stat. n.

**Subgenus** *FABITARAS* subgen. n.

*fabius* (Distant & Pryer, 1887)

*fabius fabius* (Distant & Pryer, 1887)

*caudatus* Grose-Smith, 1893 syn. n.

*pamisus* Fruhstorfer, 1914 syn. n.

*fabius arrius* Fruhstorfer, 1914

*boreensis* Moulton, 1911

*elioti* Corbet, 1939 syn. n.

*punctatus* (Semper, 1889)

*anaxandridas* Fruhstorfer, 1916 syn. n.

*caesium* Fruhstorfer, 1916 syn. n.

*nigrum* (Semper, 1889)

*eretria* Fruhstorfer, 1916

*strigatus* Moulton, 1911

*strigatus strigatus* Moulton, 1911

*strigatus malayensis* Corbet, 1939

*denalus* Corbet, 1939 syn. n.

*brooksi* ssp. n.

*bidens* ssp. n.

*taras* (Doherty, 1889)

*panormis* (Elwes, 1893) syn. n.

*sarrastes* Fruhstorfer, 1913 stat. n.

*mendava* Riley, 1944 syn. n.

*porriginosus* Toxopeus, 1932 syn. n.

*portunus* (de Nicéville, 1894)

*portunus portunus* (de Nicéville, 1894)

*narsares* Fruhstorfer, 1913 syn. n.

*portunus maus* Fruhstorfer, 1914

*fruhstorferi* Corbet, 1939 syn. n.

*portunus pyxus* (de Nicéville, 1894)

*waterstradii* H. H. Druce, 1895

**Subgenus** *PARAGERYDUS* Distant, 1884

*Miletographa* Röber, 1892

*horsfieldi* (Moore, 1857)

*horsfieldi* *horsfieldi* (Moore, 1857)

*horsfieldi* permagnus Fruhstorfer, 1913

*infumata* Fruhstorfer, 1913

*nessus* Corbet, 1939

*horsfieldi* siporanus Riley, 1944

*horsfieldi* satelliticus Fruhstorfer, 1913

*leogon* Fruhstorfer, 1916

*leogon* *leogon* Fruhstorfer, 1916

*intricata* Fruhstorfer, 1913 (unavailable name)

*vadosus* Corbet, 1939

*lindus* Corbet, 1939

*leogon* normani Eliot, 1967

*leogon* batuensis Eliot, 1967

*leogon* plessis Eliot, 1967

*melos* (H. H. Druce, 1896) sp. rev.

*reverdini* Fruhstorfer, 1916 syn. n.

*talu* Eliot, 1967 syn. n.

*samarasensis* sp. n.

*samarasensis* samarics subsp. n.

*samarasensis* russellii subsp. n.

*macassarensis* (Holland, 1891)

*macassarensis* macassarensis (Holland, 1891)

*damodar* Fruhstorfer, 1913

*macassarensis* menadensis Eliot, 1967


*albatus* C. & R. Felder, [1865]

*albatus* albatus C. & R. Felder, [1865]

*albatus mendax* subsp. n.

*apries* Fruhstorfer, 1913

*apries* apries Fruhstorfer, 1913

*eupalion* Fruhstorfer, 1914 syn. n.

*apries* dosithaus Fruhstorfer, 1914

*apries* ristus subsp. n.

*corbeti* Eliot, 1956

*unicolor* C. & R. Felder, [1865]

*unicolor* unicolor C. & R. Felder, [1865]

*eurytyanus* Fruhstorfer, 1913 syn. n.

*dilatus* Corbet, 1939 syn. n.

*unicolor* continentalis Fruhstorfer, 1913

*atatcicus* Fruhstorfer, 1916

*unicolor* rekka Riley & Godfrey, 1920

*unicolor moorei* H. H. Druce, 1895

*motiones* Fruhstorfer, 1913 syn. n.

*unicolor* aphoca Heil, 1884

*myriandus* Fruhstorfer, 1913 syn. n.

*unicolor* posidion Fruhstorfer, 1913

*motiones* Fruhstorfer, 1913 syn. n.
niceratus Fruhstorfer, 1913 syn. n.
bajanus Fruhstorfer, 1913 syn. n.
enatheus Fruhstorfer, 1913
suka Piepers & Snellen, 1918
enganicus Fruhstorfer, 1913 syn. n.

unicolor georgius Fruhstorfer, 1913
leitus Fruhstorfer, 1916
unicolor zitema Fruhstorfer, 1916
paetus (de Nicéville, 1895)
parapus Fruhstorfer, 1913
nivalis (H. Druce, 1873)
nivalis nivalis (H. Druce, 1873)
nivalis felderii Semper, 1889
substrigosus (Moore, 1884)
substrigosus substrigosus (Moore, 1884)
magaris Fruhstorfer, 1913
substrigosus lenaia Fruhstorfer, 1913
substrigosus sibyllinus Riley, 1944
substrigosus ballantinei subsp. n.
substrigosus Yusukei subsp. n.
davidis Eliot, 1959
drumila (Moore, [1866])
drumila drumila (Moore, [1866])
multistrigatus de Nicéville, 1886
insignis (Staudinger, 1888)
drumila aphthonius Fruhstorfer, 1913
grisea Riley & Godfrey, 1920

Genus LOGANIA Distant, 1884
Malais Doherty, 1889
malayica Distant, 1884
malayica malayica Distant, 1884
malayica subura Fruhstorfer, 1914
nehabalema Fruhstorfer, 1914 stat. rev.
wattraudae sp. n.
regina (H. Druce, 1873)
regina regina (H. Druce, 1873)
evera Fruhstorfer, 1916 syn. n.
regina sriva Distant, 1886
paluana sp. n.
marmorata Moore, 1884
marmorata marmorata Moore, 1884
marmorata damis Fruhstorfer, 1914
marmorata hilairea Fruhstorfer, 1914
obscura Distant & Pryer, 1887 (nom. preocc.)
nada Fruhstorfer, 1914
stenosa Fruhstorfer, 1916 syn. n.
cineraria Fruhstorfer, 1916 syn. n.
sora Fruhstorfer, 1916 syn. n.
marmorata lahomi (Keile, 1884)
marmorata diehi subsp. n.
marmorata munichya Fruhstorfer, 1914
marmorata javanica Fruhstorfer, 1914
glypha Fruhstorfer, 1914
marmorata palawana Fruhstorfer, 1914
distanti Staudinger, 1889 (nom. preocc.)
marmorata samosata Fruhstorfer, 1914
marmorata faustina Fruhstorfer, 1914

obscura Röber, 1886
martinus (Fruhstorfer, 1913) syn. n.
donussa Fruhstorfer, 1916 syn. n.
distanti Semper, 1889
distanti distantii Semper, 1889
apsines Fruhstorfer, 1914
turdefa Fruhstorfer, 1916 syn. n.
distanti massalia Doherty, 1891 stat. n.
luka de Nicéville, 1894 syn. n.
distanti drucei Moulton, 1911
distanti staudingeri H. H. Druce, 1895
hampsonii Fruhstorfer, 1914
meeki Rothchild, 1915 syn. n.
masana Fruhstorfer, 1916 syn. n.
watsoniana de Nicéville, 1898
subfasciata Tyler, 1915

Genus LONTALIUS gen. n.
eltus sp. n.
eltus eltus subsp. n.
eltus treadawayi subsp. n.

Genus MILETUS Hübner, 1819
Symeta Horsfield, 1828
Gerydus Boisduval, 1836
Archaeogydus Fruhstorfer, 1916
chinensis C. Felder, 1862
chinensis chinensis C. Felder, 1862
chinensis learchus C. & R. Felder, [1865]
irroratus H. Druce, 1874
kelantanus Corbet, 1938
chinensis assamensis (Doherty, 1891)
milvius (Fruhstorfer, 1913)
chinensis longeana (de Nicéville, 1898)
croton (Doherty, 1889)
croton croton (Doherty, 1889)
tavoyana (Evans, 1932)
croton corus Eliot, 1961
croton karennius (Evans, 1932)
mallus (Fruhstorfer, 1913)
mallus mallus (Fruhstorfer, 1913)
mallus gethusus (Fruhstorfer, 1913)
mallus shanius (Evans, 1932)
gaesa (de Nicéville, 1895)
gaesa gaesa (de Nicéville, 1895)
gaesa carrinas (Fruhstorfer, 1916)
nymphis (Fruhstorfer, 1913)
nymphis nymphis (Fruhstorfer, 1913)
nymphis porus Eliot, 1961
nymphis fiuctus Corbet, 1939
nymphis unus Eliot, 1961
zinckenii C. & R. Felder, [1865]
zinckenii zinckenii C. & R. Felder, [1865]
zinckenii improbus (H. H. Druce, 1895)
gopara (de Nicéville, 1890)
gopara gopara (de Nicéville, 1890)
denticulata (Fruhstorfer, 1913)
gopara pardinus Eliot, 1961
gopara eustatus (Fruhstorfer, 1913)
**THE MILETINI**

**gopara artaxatus** (Fruhstorfer, 1913)

**oichalia** (Fruhstorfer, 1913)

**valeus** (Fruhstorfer, 1913)

**pallaxopas** (Fruhstorfer, 1913)

**gaetulus** (de Nicéville, 1894)

**gaetulus gaetulus** (de Nicéville, 1894)

**gaetulus innocens** (H. H. Druce, 1895)

**gaetulus aphytis** (Fruhstorfer, 1913)

**boisduvali** Moore, 1857

**boisduvali boisduvali** Moore, 1857

**vincula** (H. H. Druce, 1895)

**heraeon** (Fruhstorfer, 1916)

**courvoisieri** (Fruhstorfer, 1915)

**oxylus** (Fruhstorfer, 1916)

**lombokianus** (Fruhstorfer, 1913)

**acrages** (Doherty, 1891)

**burrinus** (Holland, 1900)

**ceramensis** Ribbe, 1889

**dossemus** (Fruhstorfer, 1913)

**stygianus** Butler, 1884

**adeus** (Fruhstorfer, 1913)

**boisduvali diotrophes** (Fruhstorfer, 1913)

**boisduvali avitus** (Fruhstorfer, 1916)

**drucei** (Semper, 1889)

**drucei drucei** (Semper, 1889)

**philippus** (Staudinger, 1889)

**jacchus** (Fruhstorfer, 1913)

**paianius** (Fruhstorfer, 1913)

**epidurus** (Fruhstorfer, 1913)

**drucei metrovius** (Fruhstorfer, 1913)

**phradimon** (Fruhstorfer, 1915)

**bigssii** (Distant, 1884)

**bigssii bigssii** (Distant, 1884)

**atomaria** (Fruhstorfer, 1913)

**xeragis** (Fruhstorfer, 1916)

**hyllus** (Fruhstorfer, 1916)

**sebethus** (Fruhstorfer, 1916)

**extraneus** (Toxopeus, 1929)

**bigssii natunensis** (Fruhstorfer, 1916)

**bigssii niassicus** (Fruhstorfer, 1913)

**batunensis** (Fruhstorfer, 1913)

**bigssii albotignula** (Van Eecke, 1914)

**simalurensis** (Toxopeus, 1928)

**cellarius** (Fruhstorfer, 1913)

**symethus** (Cramer, 1779)

**symethus symethus** (Cramer, 1779)

**pandu** (Horsfield, 1828)

**symethus petronius** (Distant & Pryer, 1887)

**diopeithes** (Fruhstorfer, 1913)

**bangkanus** (Fruhstorfer, 1914)

**hieropus** (Fruhstorfer, 1916)

**symethus solitarius** Okubo, 1983

**symethus acampsis** (Fruhstorfer, 1913)

**symethus nucius** Eliot, 1961

**symethus perclucidus** (Fruhstorfer, 1913)

**megaris** (Fruhstorfer, 1913)

**symethus vespesianus** (Fruhstorfer, 1913)

**symethus batuensis** (Fruhstorfer, 1914)

**symethus edonus** (Fruhstorfer, 1913)

**symethus philopator** (Fruhstorfer, 1914)

**symethus hierophantes** (Fruhstorfer, 1916)

**symethus phantus subsp. n.**

**gallus** (de Nicéville, 1894)

**gallus gallus** (de Nicéville, 1894)

**gallus leucocyon** (Toxopeus, 1940)

**heracleion** (Doherty, 1891)

**heracleion heracleion** (Doherty, 1891)

**heracleion arion** Eliot, 1961

**ancon** (Doherty, 1889)

**ancon ancon** (Doherty, 1889)

**ancon gigas** (H. H. Druce, 1895)

**anconides** (Fruhstorfer, 1913)

**archilochus** (Fruhstorfer, 1913)

**archilochus archilochus** (Fruhstorfer, 1913)

**archilochus siamensis** (Godfrey, 1916)

**gigantes** (de Nicéville, 1894)

**atimonicus** Murayama & Okamura, 1973

**celinus** Eliot, 1961

**takanamii sp. n.**

**leos** (Guérin-Méneville, 1830)

**leos teos** (Doherty, 1891)

**leos florensis** (Fruhstorfer, 1913)

**eulus** (Fruhstorfer, 1913)

**leos tellus** (Fruhstorfer, 1913)

**leos catoleucus** (Fruhstorfer, 1913)

**leos maximus** (Holland, 1891)

**divisa** (Fruhstorfer, 1913)

**saros** (Fruhstorfer, 1913)

**leos vaneecki** (Toxopeus, 1930)

**leos mangolicus** (Fruhstorfer, 1913)

**leos leos** (Guérin-Méneville, 1830)

**boisduvalii** (Butler, 1884)

**meronus** (Fruhstorfer, 1913)

**amphiarus** (Fruhstorfer, 1913)

**gardineri** (Fruhstorfer, 1914)

**leos virtus** (Fruhstorfer, 1913)

**pentheus** (Fruhstorfer, 1913)

**leos aronicus** (Fruhstorfer, 1914)

**nineyanaus** (Fruhstorfer, 1914)

**acrisius** (Fruhstorfer, 1914)

**melanion** C. & R. Felder, [1865]

**melanion melanion** C. & R. Felder, [1865]

**albiguttatus n.** (infrasubspecific name)

**melanion euphranor** (Fruhstorfer, 1914)

**batizanus** (Fruhstorfer, 1913) stat. n.

**vitelanus** (Fruhstorfer, 1913) syn. n.

Genus **MEGALOPALPUS** Röber, 1886

**angulosus** Grünberg, 1910

**metaleucus** Karsch, 1893

**simplex** Röber, 1886

**bicoloria** (Capronnier, 1889)

**similis** (Kirby, 1890)

**gigas** Bethune-Baker, 1914

**zymna** (Westwood, 1851)

**pallida** Aurivillius, 1922
Tribal characters

The characters of Miletini (sensu Eliot, 1973) are as follows. Eyes smooth. Antennae with narrow, gradually incrassate club and with the nudum extending down the shaft to the base or very nearly so. Labial palpi asymmetrical, but there is no constancy in which palpus is the longer. In most species the palpi are unusually long and thin, more so in females than in males, and protrude well beyond the head; they are also unusual in that the ‘Basalfleck’ of Reuter is clothed with hairs of unknown function. Proboscis long, bearing many sensilla throughout its length. Legs more or less abnormal, with the tarsi very long, flattened and blade-like in Miletus and Megalopalpus, cylindrical but very long and thin in Allotinus and with the tibiae outwardly swollen or incrassate in Logania and Lontalius. The mid- and hind-tibiae lack the usual pair of terminal spurs. The male fore-tarsus is reduced to a single segment ending abruptly but with a small pointed process directed downwards, except in the typical species of Logania in which the tarsus tapers to a down-curved point. The claws on the mid- and hind-tarsi of both sexes are small, and minute on the fore-tarsi of females. The abdomens of males are long and protrude well beyond the hindwings, except in Allotinus major. There is a double hair tuft, sometimes inconspicuous but sometimes large and erectile, on the sternum of the eighth segment; it is not known whether it plays any part in courtship. The tergum of the eighth segment is unusually long to accommodate the peculiar genitalia, and bears a long apophysis at its proximo-ventral edge. The wing venation shows a high degree of individual variation, and does not often provide good characters for separating genera and species. The forewing always has 11 veins (vein R₄ missing), and veins Sc and R₁ are separate throughout their lengths. In the males of most species the basal portion of vein M₃ is slightly swollen and devoid of normal cover scales, but bears small to very small specialised (?)scent) scales. The hindwing has a well-developed humeral vein in Megalopalpus and Lontalius, but in the other genera it is only weakly developed or absent. The male genitalia are highly characteristic. The uncus and tegumen are in the form of enormous paired plates, which are attached to the vinculum only narrowly in the dorsal region, so that they are capable of considerable freedom of movement. Articulating brachia are always present. The vinculum bears on either side two more or less triangular processes, one directed proximad and the other distad. The latter process is comparatively weakly sclerotised and overlies the sides of the tegumen. The valvae are small, with the outer dorsal portion (sometimes referred to as the ampulla) bearing a dense hair fringe. The juxta is present as a furca whose arms are united by a band above the phallus just distad of the ductus. Eliot (1973: 386) incorrectly called this band a form of transtilla. The female genitalia have not been investigated.

The early stages are very imperfectly known. According to Doherty (1889) the eggs of Miletus and Allotinus are much flattened and disc-like, but in Logania are stouter and scarcely more than twice as wide as high. They bear between two and five lateral carinae which are either simple or broken into short teeth placed one above the other, giving the appearance of a cogged wheel. The larvae, so far as known, are wholly aphytophagous, feeding on Homoptera. They are more or less cylindrical and have a particularly thick cuticle, and apparently lack the ‘honey gland’ on the seventh and paired eversible tubercles on the eighth abdominal segments which are present in the majority of Lycaenidae. Their relationship with the ants attending the Homoptera appears to be one of neutrality, and from this it appears at least possible that the larvae may be furnished with small glands on a number of segments, as in many other Lycaenidae (Cottrell, 1984), and that these secrete some substance which inhibits ant aggression. In one species, Miletus boisduvali, the larva pupates inside ants’ nests and the pupa has attractant glands and is attended by ants; the emerging adult is clothed with fugitive scales, as in Liphyra brassolis, which confuse attacking ants (Roepke, 1918). However, in M. chinensis, the larva pupates in the open and is attached by the cremaster with or without a weak girdle (Kershaw, 1905), and in this species, as well as in Allotinus subviolaceus, there is no evidence to suggest that fugitive scales are present in the adult (Piepers & Snellen, 1918). The adults feed on the excretions of Homoptera and do not visit flowers.

The tribe comprises four Oriental genera and one African genus (the latter erroneously described from Borneo). The Oriental genera, totalling 69 mainly Sundanian species, have been
subjected to a full taxonomic revision. No comparable attempt has been made to revise the four species of *Megalopalpus*, but a review of the genus, based on a draft kindly prepared by Mr R. I. Vane-Wright and Mrs S. M. North, is included.

In the keys and descriptions which follow, the system of veins and spaces is as in Fig. 49 (p. 74).

**Key to the genera of Miletini**

1. Tarsi with first segment more or less cylindrical ........................................ 2
   - Tarsi with first segment flattened and blade-like ........................................ 4
2. Tibiae swollen or incassate ................................................................................. 3
   - Tibiae not swollen; legs long, thin, cylindrical .................................. *ALLOTINUS* (p. 7)
3. Hindwing without a humeral vein. Legs comparatively short ................................... *LOGANIA* (p. 57)
   - Hindwing with a humeral vein. Legs long and thin ...................................... *LONTALIUS* (p. 74)
4. Hindwing without a humeral vein. Oriental .................................................. *MILETUS* (p. 75)
   - Hindwing with a humeral vein. African ..................................................... *MEGALOPALPUS* (p. 84)

**Genus *ALLOTINUS* C. & R. Felder**


Legs long, thin, cylindrical. Labial palpus with third segment longer than half second segment. The wing venation shows a high degree of infra-specific individual variation. Hindwing cilia elongated into short tufts at vein endings in the male, the margin more or less crenulate and tufted in the female. Underside characteristic, white to pale buff, densely striated with small striae or spots, with heavier spots arranged in the usual lycaenid pattern. Forewing usually with very small white costal flecks at ends of veins Sc, R₁, R₂, R₃ and, in one species-group, R₃ also.

The genus ranges from north India to Sundaland, the Philippines and Sulawesi.

Fruhstorfer (1913-15; 1916) divided the genus into two subgenera: *Allotinus* for species allegedly without a sex stripe in the male and *Paragerydus* for species with a sex stripe. I maintain these subgenera, though not in the arrangement adopted by Fruhstorfer, and add a third subgenus.

**Key to the subgenera of Allotinus**

1. ♀ valva ending in an apical point; abdominal hair tufts poorly developed, not protruding except when genitalia are extruded. Hindwing usually with a weak humeral vein ........................................ 2
   - ♀ valva with costa abruptly truncate (except in *A. davidis*), but ending in a ventral, more or less pointed process; abdominal hair tufts prominent. Hindwing without a humeral vein ................................................................. *PARAGERYDUS* (p. 30)
2. Antenna barely longer than half the forewing costa, with less than 50 segments. ♀ forewing with vein M₃ not, or only very briefly, swollen .......................................................... *ALLOTINUS* (p. 7)
   - Antenna nearly two-thirds length of forewing costa, with 60 or more segments. ♀ forewing vein M₃ prominently swollen, clothed with specialised scales for one-third of its length or longer ................................................................. *FABITARAS* (p. 20)

**Subgenus *ALLOTINUS* C. & R. Felder**

The principal characters of the subgenus are as given in the key.

Nineteenth century authors separated *Allotinus* from *Paragerydus* by the former's possession of a short upper discocellular vein, but this character does not occur in *A. (A.) agnolia*, wherein veins R₃ and M₁ have a short common stalk. Typical species, in which the males have vein M₃ unswollen, have vein R₃ long, arising closer to the cell apex than to the wing apex; but in the two species in which the males have vein M₃ weakly swollen, vein R₃ is shorter, arising close to or opposite the end of vein R₂.

On the basis of the male structure the subgenus can be divided into two species-groups: the *fallax*-group in which the abdomen is of normal length for the tribe and the uncus/tegumen plates are long and narrow; and the *major*-group in which the abdomen is much shorter and the uncus/tegumen plates are more rounded.

The subgenus has a restricted distribution in Sundaland, the Philippines and Sulawesi, and comprises seven species.
Key to the species of subgenus *Allotinus*

1. **♂** abdomen longer than hindwing dorsum. Underside of hindwing with postdiscal spot in space 6 more or less below the spot in space 7 and remote from the spot in space 5 (*fallax*-group) ...... 2
   - **♂** abdomen same length as hindwing dorsum. Underside of hindwing with postdiscal spot in space 6 more or less equidistant from the spots in spaces 7 and 5 (*major*-group) .................. 6
2. Upperside with white or grey-blue areas .................................................. 3
3. Upperside with white areas ............................................................................ 4
4. Upperside with greyish-blue areas .................................................................. 5
   - **♂** upperside of hindwing brown or diffusely sullied with white scales .......... 5
   - **♂** upperside of hindwing with a clearly defined white band ......................... *albifasciatus* (p. 13)
5. Forewing with veins *R*$_1$ and *M*$_1$ just separate at their origins. **♂** forewing vein *M*$_3$ not swollen nor clothed with specialised scales. Underside with postdiscal series of spots clearly marked
   - Forewing with veins *R*$_1$ and *M*$_1$ stalked. **♂** forewing vein *M*$_3$ briefly swollen and clothed with specialised scales. Underside with postdiscal series not apparent on forewing and barely discernible on hindwing .......................................................... *agnolia* (p. 15)
6. Smaller, forewing 13.5–19.0 mm. **♂** upperside of forewing all brown or with a small white or whitish spot comprising at most a small sullied area at base of space 2 and a larger white area up to 3.0 mm wide in space *lb*. **♀** with a larger white area filling basal third of space 2 and about half of space *lb*, but not reaching vein *Cu*$_1$ nor entering the cell; white patch may be reduced, sullied or absent .......................................................... *maximus* (p. 17)
   - Larger, forewing 20.0–21.0 mm. **♂** upperside of forewing with a white patch filling basal third of space 2 and about half of space *lb* which is basally grey. **♀** with white patch larger, extending above vein *Cu*$_1$ and into lower edge of cell .......................................................... *major* (p. 17)

*Allotinus* (*Allotinus*) *fallax* C. & R. Felder

(Figs 1–3, **♂** genitalia)


The Felders confused two distinct species under this name. In pl. 35, fig. 24 they figured as a male what is currently treated as the female of *A. fallax*, and at figs 25, 26 as the female a different species which I describe later as the female of *A. (Paragerydus) albatis mendax*. Semper (1889: 163) correctly pointed out that the Felders' ‘male’ was in fact a female. However, he incorrectly identified their female as a male.
variety of fallax, having a white area on the upperside of the hindwing such as he had seen only in a few examples from Luzon; these may have been either males or females of mendax. Apart from these supposed variants from Luzon he correctly stated that the male of fallax has a plain brown hindwing in the Philippines.

The species is distinguished by lacking a swelling of vein $M_3$ in the male and by the presence of a white patch on the upperside of the dark brown forewing. The hindwing of the male is brown, except in Borneo where it is usually dusted with white scales. Except in Sumatra and the Malay Peninsula, where the hindwing is brown, the female has a white discal area (rarely vestigial or absent) which shows a high degree of individual variation, so that it is an unreliable character by which to distinguish subspecies.

On the basis of the male genitalia A. fallax can be divided into three subspecies-groups.

Type (a) (Fig. 1): valva with short apical hook and ventro-distal edge not strongly exaricate; phallus comparatively short, broad and abruptly tapered at distal end; Philippine.

Type (b) (Fig. 2): valva with short apical hook and ventro-distal edge strongly exaricate; phallus comparatively long and thin and gradually tapered at distal end; Philippine.

![Fig. 2 Allotinus (Allotinus) fallax aphacus Fruhstorfer; Mindanao. Male genitalia.](image)

Type (c) (Fig. 3): valva with long apical hook; phallus like type (c), but still slimmer; Sundanian.

So far as my experience goes type (a) occurs exclusively in Luzon, Masbate, Bohol, Samar and Leyte, and type (b) exclusively in Mindanao and Bazilan. Both occur in Mindoro, each type having a distinctive phenotype. I have not been able to dissect males from Cebu, Panaon, Camiguin de Mindanao and the Sulu Is., whence Fruhstorfer named subspecies, but I think it certain that type (a) will be found in Cebu and type (b) in Camiguin de Mindanao and Sulu Is., whilst in Panaon either might occur. The occurrence of type (a) in Bohol, Samar and Leyte is rather unexpected; usually butterflies from these islands are associated with Mindanao rather than with Luzon. The dichotomy in Mindoro can be paralleled in the lycaenopsid Acytolepis puspa which occurs in Mindoro in subsp. cagaya and the very different-looking subsp. bazilana in equality and without evidence of intergradation (Eliot & Kawazoe, 1983: 183). Conceivably types (a) and (b) may represent distinct species which evolved in the northern and southern groups of islands respectively and which may now have a wider overlap in distribution than is at present known; otherwise it is difficult to see how type (b) could have reached Mindoro without also becoming established in the intervening islands.

A. fallax flies at low to moderate elevations, and is common and widespread in the Philippines, but rare in Sundaland. It has not been found in Palawan, but is likely to occur there.

**Key to the subspecies of A. (A.) fallax**

1  ♂ genitalia of type (c). Sundanian ................................................................. 6
  ♂ genitalia of types (a) or (b). Philippine ...................................................... 2
2  ♂ genitalia of type (b). ♀ upperside of hindwing with white area normally confined to basal two-thirds of spaces 4 and 5, but may be vestigial or obsolete .......................... 3
- ♀ genitalia of type (a). ♂ upper side of hindwing with white area normally extending below vein $M_3$, often as far as vein $A_1$.

3 ♂ upper side of forewing with white patch reaching vein $Cu_1$.

- ♂ upper side of forewing with white patch usually not above mid-space 2; if reaching vein $Cu_1$, upper part narrow and sullied.

4 ♂ white patch comparatively large, reaching into space 2. Underside of forewing with central area above dorsum sparsely striated.

- ♂ sullied white patch smaller, usually confined to space 1b. Underside of forewing with central area above dorsum as densely striated as rest of wing.

5 Underside ground colour pale buff. ♂ upper side of hindwing with a small white patch.

- Underside ground colour whitish buff, with pale markings. ♂ hindwing white patch obsolete.

6 Upperside of hindwing with a dusting of white scales usually present in ♂ and always present in ♀.

- Upperside of hindwing plain brown.

Allotinus (Allotinus) fallax fallax C. & R. Felder

(Fig. 1, ♂ genitalia)

Allotinus fallax C. & R. Felder, [1865]: 285, partim ♂, recte ♀ [nec ♀, pl. 35, fig. 24 '♂']; Semper, 1889: 163, partim, pl. 31, figs 23♂, 26♀. LECTOTYPE ♀, PHILIPPINES: Luzon (BMNH), here designated [examined].

Allotinus fallax fallax Felder; Fruhstorfer, 1913: 343; 1916: 809.


In the male the white patch on the forewing almost always extends across vein $Cu_1$ into space 3. In the female the white patch on the hindwing is variable in extent, but almost always extends dorsad into space 3 and often as far as space 1b. The ground colour of the underside is pale buff, richer in the male than in the female.

The Felders did not specify a type. Their 'male', as pointed out by Semper (1889: 163), is a female, while their female belongs to another species described later as A. (Paragerydus) albatis mendax. In BMNH there is a male ex Felder coll. bearing a BMNH red type label, but as the original figure and description does not apply to this sex it seems better to reject this unpublished type selection and to designate as lectotype a female in BMNH labelled /79/Luzon Lorquin [round blue]/Felder Coll./Rothschild Bequest 1939-1/.

When naming sabazus, Fruhstorfer, evidently referring to the male, stated that the white patch on the forewing was reduced compared with subsp. fallax and that the underside was darker and more closely striated. The male from Bohol figured by Semper has the white patch entirely below vein $Cu_1$, as in occasional Luzon examples, but in a series of both sexes from Bohol in coll. Treadaway the males have the white patch extending above vein $Cu_1$ and in neither sex can I detect any consistent differences from Luzon fallax. I therefore consider that sabazus cannot be maintained as a valid subspecies. There is in SM a female labelled /Bohol/Coll. C. Semper/211/Typus [red]/, but in my view it cannot be accepted as the type of sabazus since Fruhstorfer's description did not apply to this sex. I therefore designate as lectotype the male figured by Semper (pl. 31, fig. 23), which unfortunately has not been recognised in SM.

Semper recorded fallax from Cebu, but did not figure it. It is not clear whether Fruhstorfer (1916) was merely attaching a name to Semper's record or actually saw specimens from Cebu. No examples from Cebu can now be found in SM, but according to Treadaway (pers. comm.) it is thought that some may possibly exist but be temporarily mislaid. The only specimen that I have seen from Cebu is a female in coll. Treadaway. This has the underside ground colour somewhat whiter than usual, but the difference from Luzon females seems too slight to justify retaining zaradrus as a valid subspecies, and I therefore provisionally synonymise it with fallax.

Examples from Mindoro and Sibuyan Is. do not differ from normal fallax, but two males from Masbate in coll. Treadaway have a more whitish underside, and a female from Panay is almost pure white and relatively weakly striated below and has an exceptionally large white patch on the upper side of the hindwing. I provisionally place these under fallax.

Males from Samar and Leyte seem never to have the forewing white patch extending above vein $Cu_1$ and...
in both sexes the underside ground colour is darker buff than in examples from Luzon and Bohol. These possibly constitute a distinct subspecies to which Fruhstorfer's name *artinus*, given by him to the population in Panaon, may apply. Unfortunately I have seen no males from Panaon and Semper's figure of a Panaon male (pl. 31, fig. 24) shows only the underside, from which it is not possible to establish whether or not it resembles Samar and Leyte examples. The single female from Panaon which I have seen does not differ from Mindanao females, and I therefore provisionally synonymise *artinus* with *aphacus*.

**Distribution.** Luzon, Mindoro, Sibuyan, Cebu, Bohol. In slightly different forms also in Masbate, Panay, Samar and Leyte. I have seen no examples from Negros, but it must occur there as well as in other islands.

*Allotinus (Allotinus) fallax aphacus* Fruhstorfer

(Fig. 2, ♂ genitalia)

*Allotinus fallax* C. & R. Felder; Semper, 1889: 163, partim, pl. 31, figs 24 ♂, 25 ♀.

*Allotinus fallax aphacus* Fruhstorfer, 1913: 343; 1916: 809. Holotype ♀, PHILIPPINES: Camiguin de Mindanao [not located].

*Allotinus fallax ancius* Fruhstorfer, 1913: 343; 1916: 809. LECTOTYPE ♂, PHILIPPINES: Mindanao (BMNH), here designated [examined]. **Syn. n.**

*Allotinus fallax ancius* Fruhstorfer, 1913: 343; 1916: 809. LECTOTYPE ♀, PHILIPPINES: Panaon (SM), here designated [examined].

On the upperside the forewing white patch of the male is barely half as large as in subsp. *fallax*, seldom fully crossing space 2, and when it does so the upper part is sullied with brown scales. The female has the white patch on the hindwing almost always restricted to the basal two-thirds of spaces 4 and 5, and often it is almost obsolete. On the underside of the forewing there is an almost unstriated central area above the dorsum. The male genitalia are type (b).

Fruhstorfer named *aphacus* from Semper's record and figure 25 of a female from Camiguin de Mindanao. The original of this figure, which I have not been able to locate, is therefore automatically the holotype. I have seen a single male labelled /Cam. de Mind./211/Coll. C. Semper/ which does not differ from Mindanao males.

I designate as lectotype of *ancius* a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/ Mindanao/Mindanao Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/Allotinus fallax ancius [in Corbet's hand]/. A female labelled /Type [red]/Type [Fruhstorfer orange]/Mindanao/Mindanao Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/fallax ancius Fruhst. [in Fruhstorfer's hand] becomes a paralecotyope.

I designate as lectotype of *artinus* a female in SM labelled /Coll. C. Semper/Panaon/211/Typus [red]/, which does not differ from Mindanao examples.

**Distribution.** Mindanao, Camiguin de Mindanao, Panaon. I also provisionally place under this subspecies a female in BMNH from Talaud I.

*Allotinus (Allotinus) fallax eryximachus* Fruhstorfer

*Allotinus fallax eryximachus* Fruhstorfer, 1913: 343; 1916: 809. LECTOTYPE ♂, PHILIPPINES: Mindoro (BMNH), here designated [examined].

This is the darkest subspecies. As pointed out by Fruhstorfer in his original description, the forewing white patch in the male is even more insignificant (unbedeutenderen) than in subsp. *aphacus*, being always more or less sullied with brown scales and sometimes restricted to a mere streak below vein *Cu*₂. On the underside the central area above the forewing dorsum, which is not, or is comparatively weakly, striated in the other subspecies, is striated all over. The male genitalia are type (b).

Fruhstorfer stated that the type was in BMNH. However, there are no males agreeing with his description labelled as types, but a pair of subsp. *fallax* have been placed in the type drawer above the name *eryximachus*. The male, with a large white forewing patch, is labelled /Mindoro Philippine Is. Dr. Platen/Godman-Salvin Coll. 1908-168/A. fallax 107 Var. 7/, and the female is labelled like the male but with an additional label /Allotinus ♂" fallax Felder/.. Agrees with figure of type F. A. H. 8. x. 09/. Neither specimen bears a BMNH red type label, presumably because they cannot be reconciled with Fruhstorfer's description of *eryximachus*. Although Fruhstorfer may have seen this pair in BMNH they are not to be considered as types, and I designate as lectotype a male from a series which Fruhstorfer may have seen at Tring and which he may have confused with what he saw in BMNH; it is labelled /Mindoro Platen/ Rothschild Bequest 1939-1/. It is interesting that Platen should have caught both subspecies in Mindoro.

**Distribution.** Mindoro, where it appears to outnumber sympatric subsp. *fallax*. 
**Allotinus (Allotinus) fallax dotion** Fruhstorfer

*Allotinus fallax dotion* Fruhstorfer, 1913: 343; 1916: 809, pl. 141h ♂ ♀ as 'dotion'. LECTOTYPE ♂, PHILIPPINES: Bazilan (BMNH), here designated [examined].

On the upperside both sexes resemble subsp. *fallax*, with the white patch on the forewing of the male unsullied and reaching vein Cu₂ broadly. On the underside the ground colour is a paler, more whitish buff than in subsp. *sabazus* and *aphacus*. The male genitalia are type b.

I designate as lectotype a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Philippinen Bazilan II–III. 98 Doherty ex coll. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/fallax dotion Fruhst. [in Fruhstorfer’s hand]/. A female labelled similarly, except that the final label reads /dotion [in Fruhstorfer’s hand]/, is labelled paralectotype.

**DISTRIBUTION.** Bazilan.

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**Allotinus (Allotinus) fallax tymphrestus** Fruhstorfer

*Allotinus fallax tymphrestus* Fruhstorfer, 1916: 809. LECTOTYPE ♂, PHILIPPINES: Sulu Is. (SM), here designated [examined].

I have seen only the original pair from which Fruhstorfer described the subspecies. The male exactly resembles subsp. *dotion* on the upperside, but on the underside the ground colour is slightly more whitish and the markings less well-defined. The female lacks the usual white patch on the upperside of the hindwing, but it may be that a white patch is sometimes present. The subspecies is doubtfully separate from subsp. *dotion*.

I designate as lectotype the male in SM labelled /Coll. C. Semper/Sulu Inseln Meyerink/211/Typus [red]/. The female is labelled paralectotype.

**DISTRIBUTION.** Sulu Is.

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**Allotinus (Allotinus) fallax audax** H. H. Druce

*Allotinus audax* H. H. Druce, 1895: 564, pl. 31, figs 11 ♂, 12 ♀. LECTOTYPE ♂, BORNEO: Mt Kina Balu (BMNH), here designated [examined].

*Allotinus fallax audax* Druce; Fruhstorfer, 1913: 343; 1916: 809; Corbet, 1939b: 66.

In both sexes the forewing white patch is more extensive than in the Philippine subspecies, almost reaching the wing base in space 1b where it is dusted with grey scales. The hindwing is more or less lightly dusted with white scales in the male, but heavily dusted over most of the wing in females.

The subspecies was described from an unspecified number of specimens in coll. H. H. Druce and Staudinger. I designate as lectotype a male in BMNH labelled /Kina Balu Waterstr. A. audax co-type H. H. Druce/ex coll. Hamilton Druce 1919/Type PT [green]/Joicey Bequest Brit. Mus. 1934-120/. A female labelled ♀ co-type, but otherwise as the male, is a paralectotype.

**DISTRIBUTION.** Borneo; apparently only known from Mt Kina Balu.

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**Allotinus (Allotinus) fallax apus** de Nicéville

(Fig. 3, ♂ genitalia)

*Allotinus apus* de Nicéville, 1895: 27, pl. S, fig. 17 ♀; Fruhstorfer; 1913: 343; 1916: 809. Syntypes ♀, SUMATRA (? ZSI).


Diffsers from subsp. *audax* in the plain brown hindwing in both sexes.

*A. apus* was described from two females from north-east Sumatra, which should be in ZSI. There is in BMNH a female labelled /Type [red]/Battak Mts. N.E. Sum. 11. 94 Dr Martin/Allotinus apus de Nicéville and, [on reverse], Collect Dr. Martin/Rothschild Bequest B.M. 1939-1/. As there is no evidence to suggest that this female was one of de Nicéville’s original two I reject it as a type.

**DISTRIBUTION.** Sumatra and West Malaysia, at elevations of about 500 m upwards.
Fig. 3 *Allotinus (Allotinus) fallax* apus de Nicéville; Malay Peninsula. Male genitalia.

*Allotinus (Allotinus) albifasciatus* Eliot

(Fig. 4, ♂ genitalia)


*Allotinus albifasciatus* Eliot, 1980: 143, figs 5 ♂, 6 ♀, 14 ♂ genitalia. Holotype ♂, Sumatra (BMNH) [examined].

The species is distinctive in possessing a clear white band crossing the hindwing in both sexes. On the underside the ground colour is off-white, with the postdiscal markings larger and more blotchy than in *A. fallax*.

**DISTRIBUTION.** The species is extremely rare, and has so far only been found in the Malay Peninsula and Sumatra at elevations of about 1000 m.

Fig. 4 *Allotinus (Allotinus) albifasciatus* Eliot; Sumatra. Male genitalia.
**Allotinus (Allotinus) subviolaceus** C. & R. Felder

(Fig. 5, ♂ genitalia)

*Allotinus subviolaceus* C. & R. Felder, [1865]: 286.

The greyish blue areas on the upperside render this species unmistakable. As in the white areas of *A. fallax* these blue areas are individually variable in extent, especially on the hindwing where they may be absent or cover almost the whole wing. On average they are more extensive on both wings in the female.

The species has the widest distribution in the subgenus, occurring from Assam to Java and the Philippines.

**Key to the subspecies of *A. subviolaceus***

1 Upperside greyish blue. Upperside of forewing in ♂ with space 3 all or almost all black
   *subviolaceus subviolaceus* (p. 14)
   - Upperside pale grey, with only a slight blue tint, becoming whitish in lower half of forewing disc.
   Upperside of forewing in ♂ with basal half of space 3 and base of space 4 bluish grey
   *subviolaceus mirus* (p. 15)

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**Allotinus (Allotinus) subviolaceus subviolaceus** C. & R. Felder

(Fig. 5 ♂ genitalia)

*Allotinus subviolaceus* C. & R. Felder, [1865]: 286, pl. 35, figs 27, 28 ♂; Piepers & Snellen, 1918: 17, pl. 20, figs 20a ♂, 20b ♀, 20c larva. LECTOTYPE ♂, JAVA (BMNH), here designated [examined].

*Allotinus alkamah* Distant, 1886a: 452, pl. 44, ‘♂’ recte ♀. Holotype ♀, WEST MALAYSIA (not located).

**Syn. n.**

*Allotinus subviolascens* [sic] Felder; Swinhoe, 1910: 196, pl. 616, figs 1, 1a ♀, 1b ♂.


*Allotinus subviolaceus manychus* Fruhstorfer, 1913: 342; 1916: 808; Evans, 1932: 212; Cantlie, 1967: 28. LECTOTYPE ♀, BURMA (BMNH), here designated [examined]. **Syn. n.**

*Allotinus subviolaceus callikrates* Fruhstorfer, 1913: 342; 1916: 808. LECTOTYPE ♂, PHILIPPINES: Mindanao (BMNH), here designated [examined]. **Syn. n.**

*Allotinus subviolaceus silarus* Fruhstorfer, 1916: 808. LECTOTYPE ♂, BORNEO (BMNH), here designated [examined]. **Syn. n.**

Males have a broad black border on the forewing which often fills the whole of space 3 and the cell, but in some examples the blue may enter the lower half of space 3 and fill the lower two-thirds of the cell. Usually the hindwing has only a few blue scales.

In the female the forewing border is much narrower, and the hindwing varies individually from wholly fuscous to nearly all blue.

In Palawan the greyish blue colour tends to be paler in both sexes than in other areas, and this does not appear to be due to season, as in the still paler examples flying in Burma and Thailand during the dry season. In addition the forewing border tends to be wider in females, measuring an average of 2.5 mm at vein Cu2 compared with an average of 2.0 mm in normal examples. These differences seem hardly sufficient to justify erecting another subspecies. Females from Borneo and Bangka also have, on average, the forewing border similar to Palawan examples.

The Felders described *subviolaceus* only from the male, but did not designate a type. I therefore designate as lectotype a male in BMNH labelled /Type [red]/Java Coll. . . [illegible]/[circular blue]/*Allotinus subviolaceae Felder./Felder COLN./subviolaceus n./Rothschild Bequest B.M. 1939-1/.

The holotype of *alkamah* is the ‘male’ (recte female) figured by Distant, which has a fuscous hindwing. In BMNH there is a Sumatran female labelled /Type [red]/alkamah Dist./Sumatra Forbes/Rothschild Bequest B.M. 1939-1/alkamah Dist. ♀ Allotype [in script believed to be by Corbet]/. As the holotype is a female the allotype cannot be another female, and I reject it as such. Fortunately Corbet does not appear to have published this type selection.

Fruhstorfer did not designate a type of *manychus*. He had no examples from Burma in his collection, but said that he had examined examples in BMNH from Pegu and Rangoon. There is a female in BMNH labelled /Type [red]/Moore Coll. 1908-208 Pegu Magaree/May be taken as type of Allotinus subviolaceus.
manychus Frh. [in script believed to be by Corbet]/. As it is likely that Fruhstorfer saw this specimen during his visit to BMNH I designate it as lectotype.

I designate as lectotype of *kallikrates* a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Mindanao Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/subviolaceus kallikrates Fr. [in Fruhstorfer's hand]/. A female labelled /Type [red]/Type [Fruhstorfer orange]/Mindanao/Mindanao Fruhstorfer/ Fruhstorfer Coll. B.M. 1933-131/Allotinus subviolaceus kallikrates Fruh. [in Corbet’s hand]/ is a paralectotype.

I designate as lectotype of *silarus* a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Nordborneo Brunei Waterstradt 1890/Fruhstorfer Coll. B.M. 1933-131/Allotinus subviolaceus silarus Frh. [in Corbet’s hand]/. A female in BMNH labelled /Type [red]/W. Borneo Sintang 16. III. 10/ Fruhstorfer Coll. B.M. 1933-131/subviolaceus silarus Fr. [in Fruhstorfer’s hand]/ is labelled paralectotype.

**Distribution.** Manipur; Burma; Thailand; West Malaysia; Singapore; Sumatra; Bangka I.; Java; Borneo; Palawan; Mindanao.

*Allotinus (Allotinus) subviolaceus mirus* van Eecke

*Allotinus subviolaceus mirus* van Eecke, 1914: 247; Fruhstorfer, 1916, 808. LECTOTYPE ♂, Simeulü I. (Simalur) (RNH), here designated [examined].

The subspecies is much paler than the palest dry season examples from Burma.

Above, both sexes are pale bluish grey, becoming whitish on the forewing in the middle of space 1b and basal half of space 2. In the male the forewing border is inwardly rather irregular and narrow, leaving the basal half of space 3, the base of space 4 and the lower three-quarters of the cell grey; it is narrowest at vein *Cu₂*, where it is just over 2-0 mm wide. The hindwing is mostly grey, with the discocellular veins darkened and with an inwardly diffuse fuscous marginal and costal border 2-3 mm wide. The female differs as usual in having more extensive bluish grey areas on both wings.

I designate as lectotype a male in RNH labelled /60. 49/E. Jacobson Sinabang. Sim. Sum. 7. 1913/ Museum Leiden Allotinus subviolaceus mirus Det. R. v. Eecke/Type/. A further male and a female labelled /60. 50/ and /60. 51/ respectively, but otherwise as the lectotype, are paralectotypes.

**Distribution.** Simeulü I. (Simalur).

*Allotinus (Allotinus) agnolia* sp. n.

(Figs 6 ♂ genitalia and scales; 55 ♀)

♂ forewing length 12-5 mm. Forewing with apex rounded, as in females of the genus; veins *M₁* and *R₃* with a short common stalk and vein *R₃* shorter than in the three preceding species, arising only a little before end
of vein $R_2$. Upperside dark brown, with basal quarter of forewing a paler grey brown. Forewing with a rhomboidal white patch about 3-5 mm broad resting on vein $A_1$ and reaching into lower angle of cell and base of space 3. Basal quarter of vein $M_3$ rather weakly swollen and clothed with very pale buff specialised scales about one-sixth size of white cover scales. Underside with a whitish area above mid-dorsum of forewing, but rest of both wings pale buff very densely striated with buff-brown striae; usual postdiscal and submarginal markings of the genus small and only made out with difficulty.

♀. Apart from lacking the swelling of vein $M_3$ of forewing, similar in all respects to male.

Material examined

Holotype ♂, Sumatra: ‘Battak Mts., N.E. Sum., II. 94 (Dr. Martin)’ (BMNH).

The specific name is an anagram of *Logania*, given because the holotype was found in BMNH among a series of *Logania distanti massalia* bearing a manuscript label (in an unknown hand) reading *Logania massalia* Doherty.

**Allotinus (Allotinus) nicholsi** Moulton

(Figs 7, ♂ genitalia; 56 ♂; 57 ♀)

*Allotinus nicholsi* Moulton, 1911: 83.

The species differs from all the preceding in being reddish brown without white or blue areas. On the forewing vein $R_3$ is as short as in *Paragerydus*, arising opposite the end of vein $R_2$. On the hindwing a weak humeral vein is present. In the male, vein $M_3$ of the forewing is weakly swollen in its basal quarter (a fact not noticed by Moulton and Corbet), and the specialised scales are slightly smaller than those of *A. agnolia*. The male genitalia possess a feature unique in the tribe, viz. a prominent cornutus in the phallus, consisting of a longer central and shorter outer bundles of minute spicules.

The species is known only from Borneo and Sumatra, and appears to be very rare. Provisionally I recognise two subspecies, but more material may show that no subdivision is necessary.

**Key to the subspecies of A. (A.) nicholsi**

1. Underside markings faint and comparatively broad ....................... *nicholsi nicholsi* (p. 17)
   - Underside markings narrow, darker and sharply defined ................... *nicholsi battakanus* (p. 17)
Allotinus (Allotinus) nicholsi battakanus Fruhstorfer; Sumatra. Male genitalia.

Allotinus (Allotinus) nicholsi nicholsi Moulton

Allotinus nicholsi Moulton, 1911: 83; Fruhstorfer, 1913: 343; 1916: 809; Corbet, 1939b: 66, fig. 11 ♂ genitalia. Holotype ♂, BORNEO: Sarawak (BMNH) [examined].

Allotinus nicholsi nicholsi Moulton; Eliot, 1967: 71.

The subspecies is known only from the male holotype, which is in worn condition. On the forewing veins M₅ and R₅ are just separate. On the underside the markings are rather faint and comparatively wide, and resemble those of A. subviolaceus, as pointed out by Moulton.

Allotinus (Allotinus) nicholsi battakanus Fruhstorfer

(Figs 7 ♂ genitalia; 56 ♂; 57 ♀)

Allotinus taras battakanus Fruhstorfer, 1913: 370 (partim); 1916: 813, ♀ pl. 141g ♀ (partim). LECTOTYPE ♂. SUMATRA (BMNH), here designated [examined].


The short series of one male and four females in BMNH have veins M₁ and R₅ of the forewing connate, and on the underside the markings are narrower, darker and more sharply defined than in subsp. nicholsi.

Although Fruhstorfer drew attention to the absence of the usual forewing brand of the male, part of his type-series, including two female syntypes in BMNH, comprise A. (Fabitaras) sarrastes, which is a common species in Sumatra. No doubt it was on this account that Fruhstorfer stated that the species was taken in great numbers by Dr Martin. It is not possible to say whether the figure of a female in Seitz represents battakanus or sarrastes.

I designate as lectotype the male in BMNH, unfortunately lacking its head, which is labelled /Type [red]/Type [Fruhstorfer orange]/CMB II. 95/Fruhstorfer Coll. B.M. 1933-131/Allotinus battakanus Frhst. [in Fruhstorfer’s hand]/.

DISTRIBUTION. Known only from the Battak Mts.

Allotinus (Allotinus) major C. & R. Felder sp. rev.

(Fig. 8, ♂ genitalia)

Allotinus major C. & R. Felder, [1865]: 286, partim ♂ nec ♀, pl. 35, fig. 29 ♂ LECTOTYPE ♂. SULAWESI (BMNH), here designated [examined].
Allothinus fallax major Felder; Fruhstorfer, 1913: 343; 1916: 809.  
Allothinus fallax depictus Fruhstorfer, 1913: 343; 1916: 809 [misspelled depista], pl. 141h ♀ [as major].  
LECTOTYPE ♂, SULAWESI (BMNH), here designated [examined]. Syn. n.  

The most remarkable feature of this species and A. maximus is the short abdomen, which in the male does not protrude beyond the hindwings; this is due to all the abdominal segments being relatively short compared with those of the other species of the genus. Both species can also be recognised by the arrangement of the postdiscal series on the underside of the hindwing, wherein the spot in space 6 is midway between those in spaces 7 and 5.  

A. major shows much individual variation in size and pattern. The male is typically of medium size (forewing 17-0 mm) with a small, sullied, white patch on the forewing astride the base of vein Cu₂. Occasionally the white area below vein Cu₂ is unsullied and up to 3-0 mm wide; but in more than half of the examples examined the white patch is entirely absent, and such examples from east and south Sulawesi were treated as a distinct subspecies, depictus, by Fruhstorfer. However, similar males occur throughout Sulawesi, so that depictus can only be used as a varietal name. Females have, on average, a larger white patch than males. In the commonest form the ovate white patch is about 4-0 mm wide and fills the centre of space 1b, the basal half of space 2 and may enter space 3. Unmarked brown females appear to be very rare, as there is only one example in BMNH, from west central Sulawesi, without a trace of white. Other females from the same area and also from east Sulawesi form a complete connecting series leading up to the normal white-patched form.  

I have not seen Ribbe’s type-series of A. kalawarus, so cannot be positive that the name is applicable to A. major. Ribbe described his species from at least four examples which he did not sex. He wrote that the upperside agreed with the figure of major (Fruhstorfer, 1916: pl. 141h) which is ♂-var depictus and that the underside was nearest to the figure of pyxus [A. portanus pyxus] (Fruhstorfer, 1916: pl. 141i), but differed in having a light whitish ground colour and heavier marginal flecks and other markings. He queried whether kalawarus might not be the same as damodar (= A. macassarensis macassarensis), but said that the only specimen which he had as damodar was a female with a crenulate hindwing termen (which is indeed a character of macassarensis female), whilst in kalawarus the termen was not crenulate. A non-crenulate hindwing is a feature of both sexes of A. major, so that if any of Ribbe’s specimens were females this would confirm that they were major. If they were males the absence of any mention of a brand (conspicuous in A. macassarensis) also suggests that they were major. I therefore feel reasonably confident that kalawarus is a synonym of major.

Fig. 8 Allotinus (Allotinus) major C. & R. Felder; south-west Sulawesi. Male genitalia. Lower left, uncus, tegumen and brachium of an example from north-east Sulawesi: Minahassa.
In the male genitalia the uncus/tegumen blades are shorter and more rounded than in any other Oriental species of Miletin. Judging by the few preparations I have made they are roundest in south Sulawesi and most elongated in Minahassa, those from east-central Sulawesi being intermediate.

I designate as lectotype of major a male in BMNH labelled /Celeb Lorquin type [blue circular]/Allotinus major $^{\star}$ Fd./Type [red]/FELDER COLLN./Rothschild Bequest 1939-1/. The female figured by the Felders is an example of the next species.

I designate as lectotype of depictus a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Süd-Celebes Dr. Martin Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/major fa depicta Fr. [in Fruhstorfer's hand]. A female labelled /Type [red]/Type [Fruhstorfer orange]/O. Celeb. Fruhstorfer/depictus Fruh. [in Corbet's hand] is a paralectotype; it is a typical example with a white patch on the forewing.

**DISTRIBUTION.** The species occurs at low levels throughout Sulawesi and in Banggai I. and Sangihe I.

**Allotinus (Allotinus) maximus** Staudinger stat. n.

(Fig. 9, $^{\star}$ genitalia)

[Allotinus major C. & R. Felder, [1865]: 286, partim $^{\star}$ nec $^{\star}$, pl. 35, figs 30, 31 $^{\star}$. Misidentification.]

Allotinus albatus Felder var. maximus Staudinger, 1888: 269, pl. 94. Holotype $^{\star}$, SULAWESI (coll. Staudinger, probably in MNHU).

Allotinus fallax major Felder $^{\star}$-f. albatus Felder [= maximus]; Fruhstorfer, 1913: 343; 1916: 809 [misspelled albadus and magnimus].

Both Fruhstorfer and Staudinger confused this species with Allotinus albatus, a distinct species in subgenus Paragerydus (p. 30). The former recognised its kinship with A. major, regarding it as a montane variety from Minahassa. I think it is more likely that major and maximus are distinct sibling species. The latter may well be wholly montane, since four of six males in BMNH the only two with complete data came from the Peak of Bonthain, 1000-2000 m. These examples from the extreme south-west of Sulawesi do not appear to differ from Staudinger's holotype male from Minahassa, so that it is probable that the species occurs unchanged throughout the mountains of Sulawesi.

A. maximus is larger than A. major, and in the male there is a clear white patch on the forewing filling the basal half of space 2 and the central half of space 1b, which is grey at the wing base. The only female I have seen is the misidentified female syntype of major figured by the Felders, which has a large white patch on the forewing extending into the base of space 4 and the lower edge of the cell. It is labelled /Type [red]/Celebes Lorquin type [blue circular]/Allotinus major $^{\star}$ Fd./major n/FELDER COLLN./Rothschild Bequest 1939-1/.

The male genitalia (Fig. 9) of the single example dissected differ slightly from those of A. major in having a narrower, more pointed phallus and longer, more rectangular uncus blades.

**DISTRIBUTION.** Confined to Sulawesi.

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**Fig. 9** Allotinus (Allotinus) maximus Staudinger; Sulawesi (no further data). Male genitalia.
**FABITARAS** subgen. n.

Type-species: *Paragerydus fabius* Distant & Pryer, 1887: 266. Gender masculine.

Antenna nearly two-thirds length of forewing costa, with about 62–66 segments. In males, abdominal hair tufts short, not protruding except when genitalia are everted. Forewing venation particularly subject to individual variation, with apical angle of cell sometimes sharply acute, sometimes almost a right angle. Veins *M₁* and *R₅* usually stalked, but sometimes connate from cell apex, most often in *A. tarsas* and *A. strigatus*, while in *A. bidiensis* they may be just separate. Vein *R₅* also very variable, usually arising from about middle of vein *R₅*, but sometimes as short as in subgen. *Paragerydus*, sometimes as long as in typical species of subgen. *Allotinus*. In males vein *M₃* always basally swollen and clothed with small specialised scales. Hindwing usually with a weakly developed humeral vein extending less than half-way across space 8, but sometimes absent or vestigial, most often in females. Underside characterised by a series of submarginal blackish dots which, on the forewing, are outwardly white-edged in females but not, or more indistinctly so, in males; indeed, even the blackish dots may be absent in males of *A. strigatus* and *A. portunus*. Male genitalia not unlike those of subgen. *Allotinus*, with valva ending in an apical hook but edges folded forwards more strongly in the form of a trough.

The species included in *Fabitaras* were placed in *Paragerydus* by earlier authors up to and including Fruhstorfer (1916) because of the swollen vein *M₃* of males and the common origin of veins *M₁* and *R₅* in both sexes; but on the basis of the male genitalia and the frequent presence of a humeral vein it is certain that *Fabitaras* is more closely allied to *Allotinus* than to *Paragerydus*.

The subgenus is found from central Burma to Sundaland and the Philippines, and comprises ten species.

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### Key to the species of subgenus *Fabitaras*

1. Underside of hindwing with postdiscal spot in space 6 placed below, or just inside, that in space 7. Female with hindwing produced at vein *M₃* (*fabius*-group) .......................................................... 2
   - Underside of hindwing with postdiscal spot in space 6 placed well outside spot in space 7. Female hindwing rounded (*tarsas*-group) .......................................................... 4
2. Underside of forewing with postdiscal series more or less parallel to termen except that spot in space 5 is moved a little outwards. Postdiscal spots above vein *M₃* on forewing and vein *M₁* on hindwing not enlarged or blotchy ........................................ 3
   - Underside of forewing with postdiscal series inclined towards apex; spots in spaces 4 and 5 moved out of line, the latter very close to termen. Postdiscal spots above vein *M₃* on forewing and vein *M₁* on hindwing enlarged and blotchy ........................................... *fabius* (p. 21)
3. ♂'s underside of forewing with vein *M₃* swollen for three-quarters of its length; visual brand prominent. Underside of forewing with apical region shaded reddish brown; hindwing with submarginal black spot in space 6 at most barely larger than other submarginal spots
   - ♂'s underside of forewing with vein *M₃* swollen for half its length; visual brand narrow and obscure. Underside of forewing with apical region not shaded reddish brown; hindwing with submarginal black spot in space 6 triangular and larger than other submarginal spots
4. ♂ ♀'s underside of hindwing with tornal area brown .......................................................... 5
   - ♂ ♀'s underside of hindwing with tornal quarter white .............................................. *brooksi* (p. 26)
5. Underside of hindwing with submarginal black spot in space 6 at most barely larger than other submarginal spots. ♂'s underside of forewing with at least indications of a visual brand astride swollen portion of vein *M₃* .......................................................... 6
   - Underside of hindwing with submarginal black spot in space 6 triangular and larger than other submarginal spots. ♂'s underside of forewing without a visual brand. ♀'s underside of hindwing may have a brownish cream border .............................................. *nigritus* (p. 24)
6. Underside of hindwing with postdiscal spot in space 6 placed roughly midway between the spots in spaces 7 and 5 .......................................................... 7
   - Underside of hindwing with postdiscal spot in space 6 placed much further from spot in space 7 so that it is almost on an even arc with the spots in spaces 2 to 5 .......................................................... 8
7. Underside ground colour white. ♂ forewing with vein *M₃* swollen for only one-third its length; visual brand ill-defined and less than 1-0 mm wide ....................................... *bidiensis* (p. 26)
   - Underside ground colour pale buff. ♂ forewing with swollen portion of vein *M₃* about half its length; visual brand about 2-0 mm wide ....................................... *strigatus* (p. 24)
8. ♂ forewing with vein *M₃* swollen for more than half its length; visual brand at least 1-0 mm wide
   - Underside ground colour pale buff. ♂ forewing with swollen portion of vein *M₃* about half its length; visual brand about 2-0 mm wide ....................................... *strigatus* (p. 24)
Underside ground colour greyish white; forewing apex shaded reddish brown .......... tara (p. 27)
9 Underside ground colour greyish white, not darkened towards forewing apex; black submarginal spots outwardly white-edged; postdiscal series slightly closer to termen at dorsum than at costa. ♂ upperside of forewing with vein $M_3$ swollen for two-thirds its length; visual brand up to 2.0 mm wide, comparatively well defined ........................................... sarrastes (p. 28)

Allotinus (Fabitaras) fabius (Distant & Pryer)  

(Fig. 10, ♂ genitalia)

Paragerydus fabius Distant & Pryer, 1887: 266.

The species is readily recognised by the underside markings. On the forewing the postdiscal spots in spaces 4 and especially 5 are shifted towards the termen, whilst the spots in spaces 6 and 7 are placed much further basad; in addition the spots above vein $M_3$ are more or less enlarged and blotchy. On the hindwing the postdiscal spots in spaces 6 and 7 are placed one above the other and are large and blotchy. The female has the hindwing weakly caudate at vein $M_3$. The male has vein $M_3$ of the forewing swollen for about three-quarters of its length and the visual brand is about 1.5 mm wide.

The species has a restricted distribution in Sundaland, and has not been found in Java, Palawan or the islands off the west coast of Sumatra. There are two subspecies.

Key to the subspecies of A. (F.) fabius

1 ♂ upperside of hindwing outwardly white .................................................. fabius fabius (p. 21)
- ♂ upperside of hindwing brown .................................................. fabius arrius (p. 21)

Allotinus (Fabitaras) fabius fabius (Distant & Pryer)  

Paragerydus fabius Distant & Pryer, 1887: 266; Cowan, 1966: 5. Holotype ♂. BORNEO: Sandakan (BMNH) [examined].

Allotinus caudatus Grose-Smith, 1893: 34. Holotype ‘♂’ recte ♂. BORNEO: Mt Kina Balu (BMNH) [examined]. Syn. ♂.

Paragerydus caudatus (Grose-Smith); H. H. Druce, 1895: 563, pl. 31, figs 7, 8 ♂.

Allotinus fabius fabius (Distant & Pryer); Fruhstorfer, 1914: 22; 1916: 814; Corbet, 1939b: 74.

Allotinus fabius caudatus Smith; Fruhstorfer, 1914: 22; 1916: 814; Corbet, 1939b: 74. [misspelt pamisus]. Holotype ♂. BORNEO: south-east (BMNH) [examined]. Syn. ♂.

Fruhstorfer (1915) perpetuated Grose-Smith's mistake over the sex of caudatus by incorrectly stating that both sexes of the race from Kina Balu have the outer part of the hindwing white. In fact it is only females which have the hindwing partly white, and examples from Kina Balu do not differ significantly from those from the rest of Borneo nor from examples from south-west Sumatra.

DISTRIBUTION. Borneo, including Pulo Laut; south Sumatra (1 ♂, 3 ♂, Lebong Tandai (C. J. Brooks)).

Allotinus (Fabitaras) fabius arrius Fruhstorfer  

(Fig. 10, ♂ genitalia)

[Paragerydus panormis Elwes, 1893: 619 (partim), pl. 43, fig. 9 ♂; Misidentification.]

Allotinus fabius arrius Fruhstorfer, 1914: 22; 1916: 814, pl. 141i, ♂; Corbet, 1939b: 74, fig. 4 ♂ genitalia; Fleming, 1975: 21, pl. 58, fig. L45 ♂; Elliot, 1978: 240. LECTOTYPE ♂. SUMATRA (BMNH), here designated [examined].

[Allotinus fabius panormis (Elwes); Fruhstorfer, 1916: 814. Misidentification.]
Fig. 10 Allotinus (Fabitaras) fabius arrius (Fruhstorfer); Malay Peninsula. Male genitalia.

Differs from the nominate subspecies only in the all brown female.
I designate as lectotype of arrius a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/CMB II. 94/Sumatra Montes Battak ex coll. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/fabius arrius Frhst. [in Fruhstorfer’s hand]/. A similarly labelled female is a paralectotype.

DISTRIBUTION. Malay Peninsula; north Sumatra.

Allotinus (Fabitaras) borneensis Moulton
(Figs 11 ♂ genitalia; 58 ♂)

Allotinus borneensis Moulton, 1911: 81; Fruhstorfer, 1913: 371; 1916: 814. Holotype ♂, BORNEO: Sarawak (BMNH) [examined].
Allotinus borneensis borneensis Moulton; Corbet, 1939b: 76, fig. 3, ♂ genitalia.

On the upperside both sexes resemble A. fabius arrius, but are more reddish brown and, in the male, the
swollen portion of vein $M_3$ is very slightly longer and the visual brand is very slightly wider. The underside is greyish white to pale buff-white, with the apical area of the forewing shaded with reddish brown. On the forewing the postdiscal series is parallel to the termen except that the spot in space 5 is shifted outwards, but not nearly as much as in $A. fabius$. On the hindwing the spot in space 6 is usually placed just inside that in space 7.

**Distribution.** Borneo; Malay Peninsula; Sumatra; Bangka.

**Allotinus (Fabitaras) punctatus** (Semper)

(Figs 12, ♂ genitalia; 59 ♀)

*Paragerydus punctatus* Semper, 1889: 165, pl. 31, figs 16 ♂, 17 ♀. LECTOTYPE ♂, PHILIPPINES: Mindanao (SM), here designated [examined].

*Allotinus punctatus* (Semper); Fruhstorfer, 1913: 371; 1916: 814; Corbet, 1939b: 74, fig. 1, ♂ genitalia.

*Allotinus anaxandridas* Fruhstorfer, 1916: 814. Holotype ♀, PHILIPPINES: Mindanao (SM) [examined].

[♀-morph.] Syn. n.


On the upperside the male has vein $M_3$ swollen for half its length and the visual brand is rather narrow and ill-defined. The underside is pale buff with the postdiscal markings showing great individual variation in width, in some examples being as much as 2.0 mm wide. In females the ground colour is greyish white, and the postdiscal markings are much narrower, seldom as much as 1.0 mm in width. The white-edged black submarginal spots are well marked, that in space 6 of the hindwing being triangular and larger than the others. As in *A. fabius* and *A. borneensis* the postdiscal spots in spaces 7 and 6 of the hindwing are placed more or less one above the other, and the female has the hindwing weakly caudate at vein $M_3$.

The species is chiefly remarkable for the polymorphism of the female, which was recognised by Semper who described three morphs. Fruhstorfer, however, considered that the three morphs were distinct species—a view for which there is no supporting evidence. The typical female is plain brown on both wings. In ♀-f. *caesemius* Fruhstorfer the forewing has a large white patch while the hindwing is brown; it seems to be the commonest morph. In ♀-f. *anaxandridas* Fruhstorfer the forewing resembles that of *caesemius* but the hindwing also has a large white patch; it appears to be much the rarest morph. Another ♀-morph was described by Fruhstorfer as ♀-f. *eretria*, but I think that the butterfly in question was a female of *A. nigritus* (see p. 24).

Semper did not designate a type of punctatus, whilst Fruhstorfer named *caesemius* from two females and *anaxandridas* from a single female in Semper coll., which Semper had designated merely as varieties of punctatus. I now designate as lectotype of punctatus one of two males ex Semper coll. in SM labelled /Coll. C. Semper/Sibulan/215/Parag. punctatus typ. Semper/297c/Typus [red]/. A second male labelled /215/Coll. C. Semper/ is a paralectotype. I designate as lectotype of caesemius a female ex Semper coll. in SM labelled /Sibulan/297a/215/. The single female of anaxandridas is automatically the holotype and has been so labelled.

---

**Fig. 12** *Allotinus (Fabitaras) punctatus* (Semper); Mindanao. Male genitalia.
DISTRIBUTION. The species has hitherto been recorded only from Mindanao. There is a single female in coll. Treadaway from Leyte (Catmon 450 m, 10.v.1977) which differs from f. caesiumius in having the white forewing patch reduced, with the dusky scaling at the wing base and above the dorsum almost as dark brown as the marginal and costal borders, whilst the underside is yellowish white with the markings heavier and more reddish than in females from Mindanao. It is probable that a distinct subspecies flies in Leyte, but I hesitate to name one on the basis of a single female.

_Allotinus (Fabitaras) nigritus_ (Semper)
(Figs 13, ♂ genitalia, 60 ♀)

*Paragerydus nigritus* Semper, 1889: 164, pl. 31, fig. 15 ♂. LECTOTYPE ♂, PHILIPPINES: Mindanao (SM), here designated [examined].

_Allotinus nigritus_ (Semper); Fruhstorfer, 1914: 22; 1916: 814.


In the male vein _M_3 is swollen for a little under half its length and there is no visual brand. The underside is pale brownish ochreous with darker brown markings. The black submarginal spots resemble those of _A. punctatus_, from which _A. nigritus_ can be separated by the postdiscal spot in space 6 of the hindwing being placed midway between the spots in spaces 7 and 5, or a little closer to the latter, as well as by its richer, more ochreous appearance.

The only female I have seen (Mindanao, Mt Apo, 15.ii.1983, (A. Ballantine)) is dark brown above with an inwardly diffuse, sullied whitish border 2-0 mm wide on the hindwing from the tornus to vein _R_s. The hindwing termen is barely dentate at the end of vein _M_3, as in all species of the subgenus dealt with subsequently.

Fruhstorfer named as _A. punctatus_ ♀-f. _eretria_ a female with the underside bright ochreous bearing thick brown markings and black marginal spots. The underside of females of _A. punctatus_ is greyish white, so that I suspect that _eretria_ really applies to _A. nigritus_. Fruhstorfer did not mention the upperside of _eretria_, which was presumably unmarked brown, as in the typical female morph of _A. punctatus_, and if my supposition of the true identity of _eretria_ is correct it would appear that the female of _A. nigritus_ is dimorphic – with or without a whitish border on the hindwing.

I designate as lectotype of _nigritus_ a male in SM labelled /Coll. C.Semper/Ost Mind./214/297b/15/Parag. nigritus typ. Semper/Typus [red]/. A second male labelled /Ost Mind./214/Typus [red]/is a paralectotype.

DISTRIBUTION. Mindanao.

Fig. 13 _Allotinus (Fabitaras) nigritus_ (Semper); Mindanao. Male genitalia.

_Allotinus (Fabitaras) strigatus_ Moulton
(Figs 14, ♂ genitalia; 61 ♂)

_Allotinus strigatus_ Moulton, 1911: 80.

The species can be recognised by the fact that on the underside of the hindwing the postdiscal spot in space
6 is placed midway between those in spaces 7 and 5, while on the forewing the postdiscal series is much closer to the termen near the tornus than near the costa. The underside ground colour is a uniform pale buff. On the upperside the male has vein $M_3$ swollen for half its length, and the visual brand is quadrate, about 2 mm wide and not sharply outlined.

The species is strictly Sundanian, and has not yet been found in Java, Palawan or the islands off the west coast of Sumatra. There are two subspecies.

**Key to the subspecies of A. (F.) strigatus**

1. On the underside of the forewing the blackish submarginal dots are inconspicuous and not outwardly white-edged.............................................................. *strigatus strigatus* (p. 25)
   
   – On the underside of the forewing the blackish submarginal dots are outwardly white-edged in ♀ and in the apical half of the wing in ♂ ........................................... *strigatus malayanus* (p. 25)

**Allotinus (Fabitaras) strigatus strigatus** Moulton

(Fig. 61 ♂)

*Allotinus strigatus* Moulton, 1911: 80. Holotype ♂, BORNEO: Pulo Laut (BMNH) [examined].

*Allotinus strigatus strigatus* Moulton; Fruhstorfer, 1914: 22; 1916: 813; Corbet, 1939b: 75, fig. 5, ♂ genitalia.

On the underside the submarginal blackish dots are not white-edged, and the usual markings are comparatively broad and well defined.

**DISTRIBUTION.** Borneo, including Pulo Laut.

**Allotinus (Fabitaras) strigatus malayanus** Corbet

(Fig. 14, ♂ genitalia)

*Allotinus strigatus malayanus* Corbet, 1939b: 75; Fleming, 1975: 22, pl. 58, fig. L48 ♂; Eliot, 1978: 240. Holotype ♂, WEST MALAYSIA (BMNH) [examined].

*Allotinus strigatus denalus* Corbet, 1939b: 75. Holotype ♂, SUMATRA: Battak Mts (BMNH) [examined].

**Syn. n.**

On the underside of the forewing the blackish submarginal dots are outwardly edged with whitish in the female, but in the male less distinctly and only in the apical half of the wing. The markings are narrower and less well defined than in the nominate subspecies. In the male the swelling of vein $M_3$ is slightly shorter, being just under half its length, and the visual brand is usually a little narrower.

**DISTRIBUTION.** Malay Peninsula, including Singapore; Sumatra.

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Fig. 14 *Allotinus (Fabitaras) strigatus malayanus* Corbet; Malay Peninsula. Male genitalia.
**Allotinus (Fabitaras) brooksi** sp. n.
(Figs 15, ♂ genitalia; 63 ♂)

♂ forewing length 15.0 mm. Venation normal for the subgenus, with veins $M_1$ and $R_5$ of forewing having a moderately long common stalk. Upperside brown, with tornal quarter of hindwing white, very sparsely dusted with brown scales and with adjoining cilia white chequered with dark brown at vein endings. Forewing with vein $M_3$ swollen for slightly less than one-third of its length; visual brand very narrow, obscure. Underside very pale greyish white, sparsely striated; postdiscal spots small, more or less parallel to termen; hindwing with postdiscal spot in space 6 a little closer to that in space 7 than to that in space 5; cell-end bars unusually heavy, especially on hindwing; forewing with submarginal blackish dots outwardly white-edged. Genitalia similar to those of *A. strigatus*, *A. taras* and *A. sarrastes*, but apical process of valva slightly larger.

♀ forewing length 15.0 mm. Differs from male in that inwardly diffuse white area on hindwing a little larger, occupying one-third of wing. At first sight this sex might be mistaken for *A. fabius fabius*, but the rounded hindwing termen separates it readily.

**Material examined**


![Fig. 15 Allotinus (Fabitaras) brooksi sp. n.; Borneo. Male genitalia.](image)

**Allotinus (Fabitaras) bidiensis** sp. n.
(Figs 16, ♂ genitalia; 62 ♂)

♂ forewing length 15.0–16.0 mm. In the two examples examined forewing venation differs from rest of subgenus in that veins $M_1$ and $R_5$ are just separate at their origins; vein $R_3$ rather short, arising just before end of vein $R_2$. Upperside brown, with basal third of vein $M_3$ swollen; visual brand narrow, obscure. Underside with markings generally arranged as in sympatric *A. strigatus*, but differing in the pale greyish white ground colour, the smaller, more rounded postdiscal spots and the prominently white-edged blackish submarginal dots on the forewing. Male genitalia distinguished by valva, in which the lower process extends beyond the short apical hook, and comparatively short, stout phallus.

♀ forewing length 14.0 mm in the single example seen, wherein veins $M_1$ and $R_5$ of forewing connate from cell apex. Upperside brown. Underside similar to male.

**Material examined**


Fig. 16  *Allotinus (Fabitaras) bidiensis* sp. n.; Borneo. Male genitalia.

*Allotinus (Fabitaras) taras* (Doherty)

(Fig. 17, ♂ genitalia)

*Paragerydus taras* Doherty, 1889: 437, pl. 23, fig. 10 ♂. Syntypes, Burma: Tenasserim (not located).

*Paragerydus panormis* Elwes, 1893: 619, partim ‘♂’ recte ♀, nec ♀, pl. 43, fig 8 ‘♂’. Holotype ‘♂’ recte ♀, Burma: East Pegu (BMNH) [examined]. **Syn. n.**

*Allotinus taras* (Doherty) Bingham, 1907: 300; Swinhoe, 1910: 199, pl. 617, figs 2, 2b ♂, 2a, 2c ♀; Evans, 1932: 212; Cantlie, 1963: 27.

*Allotinus panormis* (Elwes) Bingham, 1907: 301; Swinhoe, 1910: 197 partim, pl. 616, figs 3, 3b ‘♂’ recte ♀, nec ♀.

*Allotinus taras taras* (Doherty); Fruhstorfer, 1913: 370; 1916: 813; Corbet, 1939b: 74, partim.

*Allotinus fabius panormis* (Elwes); Fruhstorfer, 1916: 814, partim; Evans, 1932: 212.

*Allotinus panormis panormis* (Elwes); Corbet, 1939b: 74; Cantlie, 1963: 27.

On the upper surface of the forewing the male has vein M₃ swollen for half its length, and the visual brand is very narrow and inconspicuous; indeed Doherty, in his original description, gave absence of the brand as

Fig. 17  *Allotinus (Fabitaras) taras* (Doherty); Burma. Male genitalia.
one of the characters of the species. The underside of both sexes is greyish white turning to reddish brown towards the forewing apex and, occasionally, at the hindwing apex also. The postdiscal series of spots is rather lightly marked, and though these spots were mentioned by Doherty they are wanting in the example chosen for his figure. Such examples cannot be regarded as typical, only two out of 28 males in BMNH being similar to Doherty's figure.

The ‘male’ (recte female) of Paragerydus panormis is a quite typical female of A. taras, and I am at a loss to understand why Corbet regarded it as a different species conspecific with A. portunus.

The male genitalia of A. taras and A. sarrastes are similar, so there are grounds for regarding these two taxa as conspecific. However, they overlap in south Burma between Tavoy and Mergui over a distance of some 160 km without any evidence of intergradation, so that it seems highly probable that their period of isolation, when there was a sea barrier in the region of the Isthmus of Kra, was sufficiently prolonged for interbreeding to be impossible when they again met.

I have seen none of Doherty's type-series and as the figured male is atypical I do not designate it as lectotype.

**DISTRIBUTION.** Burma, from the Karen Hills to Mergui.

*Allotinus (Fabitaras) sarrastes* Fruhstorfer stat. n.

(Fig. 18, ♂ genitalia)


[Allotinus taras battakanus Fruhstorfer, 1913: 370, partim; 1916: 813 partim, ? pl. 141g ♀. Misidentification.]


[Allotinus taras taras (Doherty); Corbet, 1939b: 74, fig. 2, ♂ genitalia. Misidentification.]

Allotinus taras mendava Riley, 1944: 253, pl. 2, fig. 30 ♂, 31 ♀. Holotype ♂, MENTAWAI Is.: Sipora (BMNH) [examined]. Syn. n.

This Sundanian species is obviously very closely related to A. taras, but it is best regarded as specifically distinct. It differs from A. taras on the underside by the absence of reddish brown shading towards the forewing apex. In addition, on the upperside of the male forewing the swelling of vein $M_3$ extends over about two-thirds of its length and the visual brand is prominent and usually about 1.5 mm wide. On the underside the white edges to the blackish submarginal spots are particularly well marked, especially in the female.

I designate as lectotype a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Kina Balu ex coll. H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/sarrastes Frhst. [in Fruhstorfer's hand]/. A female labelled /Type [red]/Type [Fruhstorfer orange]/Nord-Borneo Brunei Waterstradt 1890/Fruhstorfer Coll. B.M. 1933-131/sarrastes Frhst. [in Fruhstorfer's hand]/ is a paralectotype.

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**Fig. 18** *Allotinus (Fabitaras) sarrastes* Fruhstorfer; Malay Peninsula. Male genitalia.
DISTRIBUTION. Burma, from Tavoy southwards; Malay Peninsula; Sumatra; Mentawai Is.; Borneo; Java; Mindanao (SM, 1 $\sigma$ labelled /Ost Mind./298a/213/Coll. C. Semper/reverdini/; this specimen has the visual brand obscure and ill-defined, but this may be due partly to its rubbed condition.)

**Allotinus (Fabitaras) portunus** (de Nicéville)

(Fig. 19, $\sigma$ genitalia)

*Paragerydus portunus* de Nicéville, 1894: 27.

Males are easily recognised by the long swelling of vein $M_3$ of the forewing, extending over nearly four-fifths of its length, and the rather diffuse and narrow visual brand, as well as by the buff or pale rufous underside on which the usual blackish submarginal spots are absent or, if present, are not outwardly white-edged. Females most nearly resemble that sex of *A. taras* on the underside, but the subapical darkening on the forewing is less developed and brownish ochreous without the red tinge of *taras*. In both sexes the postdiscal series of spots on the forewing is more exactly parallel to the termen than in the other species of the subgenus.

As already pointed out (p. 28) Corbet (1939b) subordinated *A. portunus* and its subspecies under *A. panormis*, which is a synonym of the Burmese species *A. taras* (Doherty).

The species is purely Sundanian, not extending to Palawan or the islands off the west coast of Sumatra, and, at least in the Malay Peninsula, flies at higher average elevations than the other species of the subgenus, being seldom found below 800 m.

I recognise three weak subspecies based on a mean of differences.

**Key to the subspecies of *A. (F.) portunus***

1. $\sigma$ underside of forewing with blackish submarginal spots normally absent.......................... 2
2. $\sigma$ underside of forewing with blackish submarginal spots normally present... *portunus pyxus* (p. 30)

Allotinus (Fabitaras) portunus maitus (de Nicéville)

*Paragerydus portunus* de Nicéville, 1894: 27, pl. 5, fig. 14 $\sigma$. Syntypes, Java (?ZSI). *Allotinus taras narsares* Fruhstorfer, 1913: 370; 1916: 813; Corbet, 1939b: 74, partim. LECTOTYPE $\varphi$, Java (BMNH), here designated [examined]. Syn. n.

*Allotinus portunus portunus* (de Nicéville) Fruhstorfer, 1914: 22; 1916: 813. [Allotinus strigatus dositheus Fruhstorfer, 1914: 22 partim, $\varphi$ nec $\sigma$.] [Allotinus taras (Doherty); Piepers & Snellen, 1918: 14, pl. 19, fig. 16 $\varphi$. Misidentification.] *Allotinus portunus* (de Nicéville); Piepers & Snellen, 1918: 15, pl. 20, figs 18a $\sigma$, 18b $\varphi$.

*Allotinus panormis portunus* (de Nicéville); Corbet, 1939b: 75.

On the underside the ground colour is variable in both sexes. In the male it varies from pale buff to rufous buff, and generally the postdiscal markings are ill-defined and may be absent as in the example figured by de Nicéville. In the female the ground colour may be as buff as in the male, but in some examples, as in the lectotype of *narsares*, which apparently was the model for the figure of *A. taras* in Piepers & Snellen (1918), it is pale greyish. The blackish submarginal spots on the underside of the forewing are usually missing in the male but present in the female and at most only weakly edged with white.

I designate as lectotype of *narsares* a female in BMNH labelled /Type [red]/Java occident. Sukabumi 2000 ex coll. H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/narsares Frhst. [in Fruhstorfer's hand]/.

DISTRIBUTION. Java.

**Allotinus (Fabitaras) portunus maitus** Fruhstorfer

(Fig. 19, $\sigma$ genitalia)

*Allotinus portunus maitus* Fruhstorfer, 1914: 21; 1916: 813. LECTOTYPE $\sigma$, SUMATRA (BMNH), here designated [examined].
Fig. 19  *Allotinus* (Fabitaras) *portunus maitus* Fruhstorfer; Malay Peninsula. Male genitalia.

*Allotinus panormis frrhorferi* Corbet, 1939b: 74, fig. 7, ♂ genitalia; Fleming, 1975: 22, pl. 58, fig. L47 ♂; Eliot, 1978: 240. Holotype ♂, West MALAYSIA (BMNH) [examined]. Syn. n.

*Allotinus panormis maitus* Fruhstorfer; Corbet, 1939b: 74.

In the male the postdiscal markings on the underside are usually more clearly defined than in subsp. *portunus* and the submarginal blackish spots are missing; in the female the ground colour is more greyish white.

I designate as lectotype of *maitus* a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/CMB 111. 94/Fruhstorfer Coll. B.M. 1933-131/portunus maitus Frhst. [in Fruhstorfer's hand]/. A female labelled /Type [red]/Type [Fruhstorfer orange]/Sumatra Montes Battak ex coll. H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/allotype *Allotinus portunus maitus* Fruh. [in Corbet's hand]/ is a paralectotype.

DISTRIBUTION. Sumatra; West Malaysia.

*Allotinus* (Fabitaras) *portunus pyxus* (de Nicéville)

*Paragerydus pyxus* de Nicéville, 1894: 27, pl. 5, fig. 2 ♂. Holotype ♂, BORNEO: Kina Balu (? ZSI).

*Paragerydus waterstradii* H. H. Druce, 1895: 562, pl. 31, figs 1 ♂, 2 ♀. LECTOTYPE ♂, BORNEO (BMNH), here designated [examined]. [Synonymised by Fruhstorfer, 1914: 22.]


*Allotinus portunus pyxus* (de Nicéville); Fruhstorfer, 1914: 22; 1916: 813, pl. 141i, ♂ ♀. *Allotinus panormis pyxus* (de Nicéville); Corbet, 1939b: 75.

Females appear to be inseparable from the nominate subspecies but in males the blackish submarginal spots on the underside of the forewing are more often present.

De Nicéville, who named the subspecies from a single male, differentiated it from subsp. *portunus* by the more rufous tone of the upperside and the pale rufous instead of pale ochreous colour of the underside. However, the ground colour is very variable in all three subspecies and is not a reliable character. De Nicéville's figure is misleading, as it does not show the visual brand which is mentioned in his description.

H. H. Druce described *waterstradii* from syntypes in coll. Staudinger and in his own collection. I designate as lectotype a male in BMNH labelled /Kina Balu Waterstr./P. waterstradii co-type H. H. Druce/ex coll. Hamilton Druce/Joicey Bequest Brit. Mus. 1934-120/. As there is no specimen in BMNH of ab. *absens* H. H. Druce, it is likely that the name applies to a specimen in coll. Staudinger.

DISTRIBUTION. Borneo, apparently only known from Mt Kina Balu.

Subgenus **PARAGERYDUS** Distant

*Paragerydus* Distant, 1884: 207. Type-species: *Miletus horsefieldi* Moore, 1857: 19, pl. 1a, fig. 1, by designation of Kirby, [1885]: 191.

*Miletographa* Röber, 1892: 277. Type-species: *Miletus drumila* Moore, [1866]: 777, pl. 41, fig. 12, by monotypy. [Synonymised by Fruhstorfer, 1913: 371.]
Antenna a little over half length of costa, slightly longer than in subgen. *Allotinus* and shorter than in subgen. *Fabitaras*. Antennal segments number about 40 to 60. Shaft segments of the smaller species relatively longer, consequently fewer in number; thus in the *nivalis*-group and in *A. corbeti* there are about 40 segments, whereas in the larger species, such as *A. horsfieldi* and *A. apries*, there are about 58 segments. Species of intermediate size have an intermediate number of segments, for example in *A. unicolor* there are usually about 45. In dwarf individuals, occurring most frequently in *A. horsfieldi* and *A. unicolor*, there is no diminution in the number of segments. Venation shows less individual variation than in *Fabitaras*. Hindwing without humeral vein. Forewing veins *M*₁ and *R₅* usually connate or briefly stalked, but in the *nivalis*-group they may be just separate at their origins. In males, vein *M*₃ of forewing basally swollen, clothed with small specialised scales, those of the *nivalis*-group being relatively large. In males, abdominal hair tufts prominent, permanently extruded and, in the genitalia, the valva has a truncate apex, except in *A. davidis*, and its ventral edge prolonged into a more or less pointed process. With only a few exceptions, the interspecific differences in the valva are very slight and perhaps inconstant; in general the genitalia give little assistance in identification.

Early authors, up to Fruhstorfer (1913; 1916), used *Paragerydus* in a wider sense, either as a genus or subgenus (Artengruppe) to include the species here placed in *Fabitaras*.

The subgenus ranges from north India to Sundaland, the Lesser Sunda Is., Philippines and Sulawesi (including Sula Is.). It comprises 16 species.

### Key to the species of subgenus *Paragerydus*

<table>
<thead>
<tr>
<th>Key</th>
<th>Description</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Underside mottled with brown specks and striae; postdiscal series not outlined by darker lines nor catenulate. Smaller, forewing 9·0–23·0 mm</td>
<td><em>drumila</em> (p. 56)</td>
</tr>
<tr>
<td>-</td>
<td>Underside mottled with brown spots ringed with pale buff; postdiscal series catenulate and outlined by darker lines. Larger, forewing usually over 23·0 mm</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>Underside of forewing without a white fleck at end of vein <em>R₅</em> (<em>horsfieldi</em>-group)</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>Underside of forewing with a white fleck at end of vein <em>R₅</em> (<em>nivalis</em>-group)</td>
<td><em>p. 51</em></td>
</tr>
<tr>
<td>3</td>
<td>Underside with postdiscal series more or less the same size throughout. Upperside of hindwing unmarked brown</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>Underside with postdiscal spots below vein <em>M₃</em> on forewing much larger than those above, and spots above vein <em>M₁</em> on hindwing much larger than those below. Upperside of hindwing partly white in ♀ ♀ or in ♀ alone</td>
<td><em>paupertus</em> (p. 51)</td>
</tr>
<tr>
<td>4</td>
<td>Upperside of forewing brown; white patch or streak present in ♀ of two species. Hindwing brown, of same shade as forewing; termen crenulate (except in <em>A. apries</em>)</td>
<td></td>
</tr>
<tr>
<td>-</td>
<td>Upperside of forewing white to wing base, with dark brown margin and costa. Hindwing uniform pale buff-brown; termen not crenulate</td>
<td><em>samarsensis</em> (p. 37)</td>
</tr>
<tr>
<td>5</td>
<td>♀ underside brown. ♂ with visual brand, if present, not extending into cell basad of origin of vein <em>Cu₁</em></td>
<td></td>
</tr>
</tbody>
</table>
| - | ♀ underside of forewing with white patch or streak. ♂ (where known) with visual brand extending obscurely into cell basad of origin of vein *Cu₂* | *
| 6 | Underside of forewing with postdiscal spots in spaces 4, 5 and 6 more or less in line and equidistant, or with the spot in space 5 nearer to, and often touching, the spot in space 6 | *macassaren*s (p. 39) |
| - | Underside of forewing with postdiscal spots in spaces 4, 5 and 6 on an uneven curve, that in space 5 overlapping that in space 4 and well separated from that in space 6 | |
| 7 | Forewing veins *M₁* and *R₅* connate or with a common stalk not more than 1·0 mm long. Underside of forewing with postdiscal spot in space 2 nearer termen than the spots in spaces 3 and 1b (if present). ♂ ♀ with hindwing cilia elongated into tufts at vein endings, termen crenulate in ♀ | |
| - | Forewing veins *M₁* and *R₅* with a stalk more than 1·0 mm long. Underside of forewing with postdiscal spots in spaces 3, 2 and 1b (if present) in line and parallel to termen. ♂ ♀ with hindwing cilia barely longer at vein endings and termen not crenulate in ♀ | *apries* (p. 42) |
| 8 | ♂ underside of forewing with a visual brand, vein *M₃* swollen for about half its length or longer | |
| - | ♂ underside of forewing without a visual brand, vein *M₃* swollen for only one-quarter of its length | *corbeti* (p. 44) |
| 9 | Forewing veins *M₁* and *R₅* usually with a very short common stalk. ♂ valva with terminal process not rising above costa; tip of uncus not, or only a little, produced | |
| - | Forewing veins *M₁* and *R₅* usually connate. ♂ valva with terminal process curved upwards, ending just above costa; tip of uncus produced, rostriform | *horsfieldi* (p. 32) |
10 **♂** forewing with vein $M_3$ swollen for at least three-fifths of its length; visual brand comparatively wide ................................................................. 11
   - **♂** forewing with vein $M_3$ swollen for only half its length or slightly over; visual brand comparatively narrow, less than 1.5 mm wide (except in subspp. *continentalis*, and *moorei* sometimes, of *A. unicolor*) ................................................................. 12

11 **♂** valva with terminal process comparatively long and narrow (Fig. 21). Underside of sympatric taxa greyish white; on hindwing postdiscal spot in space 6 usually more or less below that in space 7. ................................................................. *leogoron* (p. 34)
   - **♂** valva with terminal process short and broad (Fig. 22). Underside ground colour very pale buff; on hindwing postdiscal spot in space 6 nearly always inside the spot in space 7 and sometimes nearly mid-way to the end-cell bar ................................................................. *melos* (p. 36)

12 Underside ground colour greyish white to pale buff. Comparatively small, with forewing 10.5-18.0 mm. **♂** valva (Figs 29, 30) comparatively broad, with terminal process in centre line ................................................................. *unicolor* (p. 45)
   - Underside chalky white. Larger, forewing 18.0-20.0 mm. **♂** valva narrower (Fig. 31), with terminal process nearly in line with ventral edge ................................................................. *paetus* (p. 50)

13 **♂** upperside greyish brown. **♀** with a whitish discal patch on forewing and an obscure whitish streak in space 5 on hindwing. **♂** **♀** discocellular veins on hindwing not darkened
   - **♂** **♀** upperside partly white on both wings. Discocellular veins blackened ........... *luzonensis* (p. 40)

14 Underside of hindwing with central spot in space 7 at least partly blackened. Smaller, forewing 9.0-14.5 mm ................................................................. 15
   - Underside of hindwing with central spot in space 7 not blackened (may be darker brown than other spots). Larger, forewing 12.5-15.5 mm ................................................................. *nivalis* (p. 51)

15 **♂** valva with costa incised shortly before apex (as in all preceding species). Underside of hindwing with postdiscal spot in space 7 not blackened on its inner edge, except sometimes in the dry season form in Burma; ground colour greyish white, except in Philippines where it is pale buff ................................................................. *substrigusosus* (p. 53)
   - **♂** valva with costa entire. Underside of hindwing with postdiscal spot in space 7 blackened on its inner edge; ground colour pale buff. Not found in Burma or Philippines ........... *davidis* (p. 55)

**Allothinus (Paragerydus) horsfieldi** (Moore)

(Fig. 20, **♂** genitalia)


This and three succeeding species, *leogoron*, *melos* and *macassarensis*, form a confusing group difficult to separate by superficial characters. In the males of all four species the swelling of vein $M_3$ and the visual brand on the forewing vary according to locality. Venation is individually variable, but in *A. horsfieldi* veins $M_1$ and $R_5$ of the forewing are nearly always connate, whereas in the other three species they usually share a very short common stalk. In both sexes the hindwing cilia are elongated into short tufts at the vein endings and females have the hindwing termen crenulate. In the female of *A. horsfieldi* the hindwing is particularly strongly crenulate. In *A. leogoron* the crenulations are much less pronounced, while in *A. melos* and *A. macassarensis* they are intermediate. On the underside the markings show much individual variability in their density and in the position of the postdiscal series. On the forewing this series is dislocated at vein $M_3$, with the stria in space 3 moved basad and often forming with the stria in space 2 an irregular, oblique stripe; but the degree of dislocation is variable and usually slight in *A. macassarensis*. In addition the stria in space 1b, if present, is moved basad in relation to that in space 2.

Males of *A. horsfieldi* can always be identified with certainty by the genitalia (Fig. 20), wherein the ventral tip of the uncus is much produced and the terminal process of the valva is long and curled up above the costa.

In both sexes *A. horsfieldi* shows great variability in size. The smaller males, with forewing length as little as 14 mm, have the forewing apex and termen more rounded and the visual brand relatively narrow, but they are connected by a complete range of intermediates to the largest males, with forewing length up to 23 mm, which have the forewing apex more pointed and the termen straighter.

*A. horsfieldi* has a restricted distribution confined to Sundaland excluding Palawan. Where it occurs it is usually the commonest species of the subgenus apart from *A. unicolor*. 


Key to the subspecies of *A. (P.) horsfieldi*

1. Underside pale buff, postdiscal series not quadrate
   - Underside greyish white, postdiscal series comprising large, dark, quadrate spots
     \[\text{**horsfieldi siporanus** (p. 34)}\]

2. Upperside brown without a reddish tinge. Underside usually lightly marked
   - Upperside brown with a reddish tinge, especially strong in ♀ and in basal half of forewing in ♂.
     \[\text{**horsfieldi permagnus** (p. 33)}\]

3. ♀ with visual brand broad, for about half its length contiguous with vein Cu₁. ♀ with forewing disc not conspicuously paler
   - ♀ with visual brand narrower, only its basal quarter touching vein Cu₁. ♀ with forewing disc conspicuously paler
     \[\text{**horsfieldi satelliticus** (p. 34)}\]

\[\text{**Allotinus (Paragerydus) horsfieldi horsfieldi** (Moore)}\]

*Miletus horsfieldi* Moore, 1857: 19, pl. 1a, fig. 2 ♂. LECTOTYPE ♂, JAVA (BMNH), here designated [examined].


*Allotinus horsfieldii* [sic] (Moore); Piepers & Snellen, 1918: 12, pl. 19, figs 12a ♂, 12b ♀, 14a ♂, 14b ♀.

In the male the visual brand is broad, and touches vein Cu₁ for about half its length. The female is dull brown without a reddish tinge, and the forewing disc is only a little paler. On the underside, especially in females, the usual lycaenid markings are generally light and may be faded out, as in the extremes shown in Piepers & Snellen (1918: pl. 19, figs 14a, 14b), and on the hindwing the postdiscal spot in space 6 is usually placed well inside the spot in space 7.

I designate as lectotype a male in BMNH labelled /Type [red]/60-15 E.E.C./Miletus horsfieldi ♂ M/GENITALIA Slide No ASC 23 Allotinus/. A female labelled /Type [red]/60-15 E.E.C./ is a paralectotype.

**Distribution.** Java.

*Allotinus (Paragerydus) horsfieldi permagnus* Fruhstorfer

(Fig. 20, ♂ genitalia)

*Paragerydus horsfieldi* (Moore); Distant, 1884: 207, pl. 20, fig. 7 ‘♀’ recte ♂.

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*Fig. 20 Allotinus (Paragerydus) horsfieldi permagnus* Fruhstorfer; Rhio Archipelago: Great Karimon I. Male genitalia.
**Allotinus horsfieldi permagnus** Fruhstorfer, 1913: 366; 1916: 812. LECTOTYPE ♂, SUMATRA (BMNH), here designated [examined].

**Allotinus horsfieldi nessus** Corbet, 1939b: 72, fig. 15, ♂ genitalia; Eliot, 1978: 240. Holotype ♂, WEST MALAYSIA (BMNH) [examined]. [Synonymised by Eliot, 1967: 66.]

[**Allotinus leogoron lindus** Corbet, 1939b: 73, partim ♀ nec ♂. Misidentification.]

**Allotinus horsfieldi permagnus** Fruhstorfer; Eliot, 1967: 66, fig. 1, ♂ genitalia; Fleming, 1975: 21, pl. 58, fig. L43 ♂.

The subspecies is best distinguished by the female which is reddish brown with the forewing disc only very slightly paler. The female named by Fruhstorfer as f. *infumata* is within the normal range of individual variation. In the male the visual brand is comparatively narrow, only touching vein Cu₁ at its base, and the wing base of the forewing has a more reddish tinge than the darker apical region.

I designate as lectotype of *permagnus* a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/W. Sumatra H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/horsfieldi permagnus Fruhst. [in Fruhstorfer’s hand]/. The specimen, which is rather more lightly marked on the underside than usual, has lost its abdomen. A female labelled /Type [red]/Sumatra Montes Battak ex coll. H. Fruhstorfer/♀ horsfieldi Selesseh 19. xii. 94/Fruhstorfer Coll. B.M. 1933-131/horsfieldi permagnus Fruhst. [in Fruhstorfer’s hand]/ is a paralectotype.

I designate as lectotype of *infumata* a female in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/N. Oekor viii. 94/Fruhstorfer Coll. B.M. 1933–131/infumata Fruhst. [in Fruhstorfer’s hand]/.

**DISTRIBUTION.** Malay Peninsula, including Singapore; Sumatra; Bangka; Borneo; Peninsular Thailand (Pinratana). Three females in BMNH from Batu Is. are provisionally included in this subspecies; they are small with the underside ground colour whiter and the postdiscal markings rather dark and heavy, showing an approach to subsp. *siporanus*. They are also rather similar to *A. leogoron battensis*, with which Eliot (1967) originally confused them and from which they can be distinguished by their more crenulate hindwing termen.

**Allotinus (Paragerydus) horsfieldi siporanus** Riley

**Allotinus horsfieldi siporana** Riley, 1944: 253. Holotype ♂. MENTAWAI IS.: Sipora (BMNH) [examined].

The subspecies was described from a single large female in extremely battered condition; the whole of the outer half of the left hindwing and the tornal quarter of the right hindwing below vein Cu₁ are missing. The greyish white ground colour of the underside and heavy dark brown markings suggest that it might pertain to *A. leogoron*, but such crenulations as remain on the termen of the right hindwing suggest *A. horsfieldi*, and it seems best to leave Riley’s combination unchanged pending the discovery of the male.

**DISTRIBUTION.** Mentawai Is.

**Allotinus (Paragerydus) horsfieldi satelliticus** Fruhstorfer


In the male the visual brand is like that of subsp. *permagnus*, but in other respects the subspecies more nearly resembles the nominate subspecies, especially in the female which is without a reddish tinge on the upperside. However, this sex differs from Javanese females by having a very prominent paler discal patch on the forewing.

I designate as lectotype a female in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Engano April-Juli Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/horsfieldi satelliticus Fruhst. [in Fruhstorfer’s hand]/.

**DISTRIBUTION.** Engano I.

**Allotinus (Paragerydus) leogoron** Fruhstorfer

(Fig. 21, ♂ genitalia)

**Allotinus leogoron** Fruhstorfer, 1916: 811.

This species has been much confused in the past with *A. horsfieldi*, from which the male is readily separated by the genitalia, wherein the ventral tip of the uncus is not produced and the terminal process of the valva is
fairly long and narrow but not upturned. Females are best distinguished by the hindwing termen, which is
less crenulate than in horsfieldi, but the cilia bear slightly longer and narrower tufts at the vein endings. On
the forewing veins $M_1$ and $R_5$ usually have a short common stalk and, except in Java, the ground colour of
the underside is whiter with darker, more contrasted markings than in horsfieldi.

A. leogoron has the same distribution as A. horsfieldi. I recognise four subspecies.

**Key to the subspecies of A. (P.) leogoron**

1. ♀ visual brand narrow, only its base touching vein $Cu_1$ .................................................. 2
2. ♀ visual brand wide, touching vein $Cu_1$ throughout half its length .................................. leogoron leogoron (p. 35)
3. Underside greyish white with dark markings .................................................................... leogoron plessis (p. 36)
4. ♀ visual brand with only its extreme base touching vein $Cu_1$. Underside of hindwing with
postdiscal spot in space 6 below that in space 7, as in the nominate subspecies
leogoron normani (p. 36)
5. ♀ visual brand a little wider, touching vein $Cu_1$ for a quarter of its length. Underside of hindwing
with postdiscal spot in space 6 placed inside that in space 7, sometimes almost half-way to
cell-end bar .......................................................... leogoron batuensis (p. 36)

**Allotinus (Paragerydus) leogoron leogoron** Fruhstorfer

(Fig. 21, ♀ genitalia)

*Allotinus horsfieldi* permagnus ♀-f. intricata Fruhstorfer, 1913: 366; 1916: 812. LECTOTYPE ♀, SUMATRA
(BMNH), here designated [examined]. [Unavailable name.] [Synonymised by Eliot, 1967: 68.]

*Allotinus leogoron* Fruhstorfer, 1916: 811. LECTOTYPE ♂, SUMATRA (BMNH), here designated
[examined].

*Allotinus continentalis* vadosus Corbet, 1939b: 72. Holotype ♂, WEST MALAYSIA (BMNH) [examined].
[Synonymised by Eliot, 1967: 69.]

*Allotinus leogoron leogoron* Fruhstorfer; Corbet, 1939b: 73; Eliot, 1967: 68, fig. 5, ♂ genitalia; 1978: 240;
Fleming, 1975: 21, pl. 58, fig. L44 ♂.

*Allotinus leogoron lindus* Corbet, 1939b: 73, partim ♂ nec ♀. Holotype ♂, WEST MALAYSIA (BMNH)
[examined]. [Synonymised by Eliot, 1967: 69.]

The male can be separated from that sex of sympatric *A. horsfieldi* by the wider, more sharply defined
visual brand which touches vein $Cu_1$ throughout its basal half, and the female by the less crenulate hindwing
termen. In addition, the underside is whiter and the markings are darker brown.

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**Fig. 21** *Allotinus (Paragerydus) leogoron leogoron* Fruhstorfer; Malay Peninsula. Male genitalia.
I designate as lectotype of _leogoron_ a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/CMB viii. 94/A. _leogoron_ Fr. [in Fruhstorfer’s hand] and of _intricata_ a female in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Sumatra Montes Battak ex coll. H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/♀ horsfieldi CMB viii. 94/intricata [in Fruhstorfer’s hand].

**Distribution.** Malay Peninsula; Sumatra; Bangka; Peninsular Thailand (Pinratana).

_Allotinus (Paragerydus) leogoron normani_ Eliot

*Allotinus leogoron normani* Eliot, 1967: 69. Holotype ♂, BORNEO (BMNH) [examined].

Differs from the nominate subspecies only in that the male has the visual brand much narrower, only touching vein _Cu_1 at its extreme base.

**Distribution.** Borneo.

_Allotinus (Paragerydus) leogoron batuensis_ Eliot

*Allotinus leogoron batuensis* Eliot, 1967: 69. Holotype ♂, BATU Is. (BMNH) [examined].

A small subspecies, with a slightly more reddish brown tinge than in the two preceding subspecies. In the male the visual brand is intermediate between that of _leogoron_ and that of _normani_, touching vein _Cu_1 along its basal quarter. It differs on the underside of the hindwing in that the postdiscal spot in space 6 is placed inside the spot in space 7.

**Distribution.** Batu Is.

_Allotinus (Paragerydus) leogoron plessis_ Eliot

*Allotinus leogoron plessis* Eliot, 1967: 69. Holotype ♂, JAVA (BMNH) [examined].

In the male the visual brand is narrow, as in _subsp. normani_, whereas the brand of sympatric _A. horsfieldi horsfieldi_ is as wide as in _subsp. leogoron_. The subspecies is further distinguished by the pale buff underside on which the markings are smaller and less contrasted.

**Distribution.** Java.

_Allotinus (Paragerydus) melos_ (H. H. Druce)

(Figs 22, ♂ genitalia; 64 ♂

[Paragerydus horsfieldi (Moore) sensu Semper, 1889: 164 partim, pl. 31, figs 19 ♂, 20 ♀. Misidentification.]

_Paragerydus melos_ H. H. Druce, 1896: 652. LECTOTYPE ♂, PHILIPPINES: Cagayan Sulu (BMNH), here designated [examined]

_Allotinus melos_ (Druce) Fruhstorfer, 1913: 369.

_Allotinus horsfieldi leos [sic]_ (Druce); Fruhstorfer, 1916: 812.

_Allotinus horsfieldi reverdini_ Fruhstorfer, 1916: 812. LECTOTYPE ♂, PHILIPPINES (SM), here designated [examined]. **Syn. n.**

_Allotinus macassariensis [sic] melos_ (H. H. Druce); Eliot, 1967: 68.

_Allotinus macassariensis [sic] reverdini_ Fruhstorfer; Eliot, 1967: 68.

_Allotinus macassariensis [sic] talu_ Eliot, 1967: 68. Holotype ♂, BORNEO: Pulo Laut (BMNH) [examined]. **Syn. n.**

This species replaces _A. horsfieldi_, with which it has been confused in the past, in the southern Philippines. Both species are found in Borneo, but _A. melos_ seems to be the commoner throughout most of the island. Sympatric examples of the two species are very difficult to separate by external characters, but males may be separated by the genitalia without difficulty; in _melos_ the terminal process of the valva is short and broad and the tip of the uncus is not produced. Females may be impossible to separate with certainty, but on the underside of the hindwing of _melos_ the postdiscal spot in space 6 is usually placed inside the spot in space 7, sometimes almost half-way to the end-cell bar, whereas in _horsfieldi_ these spots usually overlap. In addition the hindwing termen of _melos_ is very slightly less crenulate.

Eliot (1967) treated _melos_ as conspecific with the allopatric _A. macassariensis_, but in view of constant small differences in the male genitalia and in the arrangement of the postdiscal spots in spaces 4, 5 and 6 on the underside of the forewing (see p. 39), I no longer maintain this combination.
Fig. 22 Allotinus (Paragerydus) melos (H. H. Druce); Mindanao. Male genitalia.

Males have vein $M_3$ swollen for three-fifths of its length and the visual brand is clearly defined and about 1.75 mm wide. The underside shows very great individual variation in the intensity of the markings and in the placing of the postdiscal series. The postdiscal series is quite well separated from the wing margins in typical examples but, especially in north-east Borneo, examples occur in which this series is placed close to the termen, as in $A. \text{macassarensis}$. On the hindwing the postdiscal spot in space 6 is usually placed inside that in space 7, sometimes as much as mid-way to the end-cell bar, and this character may be of assistance in separating Bornean females from sympatric $A. \text{horsfieldi permagnus}$.

H. H. Druce stated that the types of $melos$ were in Mus. Cator and Druce. There is in coll. Cator (now in BMNH) a long series of both sexes, none of which has been labelled type, and in the main BMNH coll. a pair ex H. H. Druce coll. labelled as paratypes. Of the latter I designate the male as lectotype; it is labelled /Paratype [yellow]/Cagayan 3. 6. 94/Paragerydus melos $\sigma$ co-type H. H. Druce/ex coll. Hamilton Druce 1919/Joiccy Bequest Brit. Mus. 1934-120/. The female, labelled /Paratype [yellow]/Cagayan 2. 6. 94/P. melos $\varphi$ co-type H. H. Druce/ex Coll. Hamilton Druce 1919/Joiccy Bequest Brit. Mus. 1934-120/, as well as the series in coll. Cator, are paralectotypes.

When naming reverdini, Frühstorfer referred to large males in coll. Semper. I designate as lectotype a male in SM labelled /19/Bohol/298b/213/Coll. C. Semper/Original of Semper Pl. 31, fig. 19 from Mindanao. $? \text{loc. label changed. Det. as A. melos reverdini Fruh.} \text{\varphi}$ J. N. Elliot. ix. 1982/. The male figured by Semper on pl. 31, fig. 19 was said by him to have come from Mindanao. I think it more likely that the label ‘Bohol’ was inadvertently transferred from the male shown in fig. 18 (which is the holotype of $A. \text{posidon georgius}$ and which is without a locality label – see p. 49) than that Semper made a mistake in the legend to his plate 31.

DISTRIBUTION. Cagayan Sulu; Mindanao; Palawan; Balabac I.; Borneo (many localities, including Pulo Laut). There is a male in BMNH labelled /Sula Mangoli, Oct. '97, W. Doherty/, which I suspect may be wrongly labelled although Doherty certainly collected there at that date. Examples from Mindanao tend to be rather heavily marked on the underside. Males from Palawan and Balabac tend to have the visual brand slightly longer and narrower. Examples from Pulo Laut are slightly richer buff on the underside than typical examples from Cagayan Sulu, but the difference is hardly sufficient to justify maintaining $talut$ as a distinct subspecies. There is in coll. Cator a series of seven males and one female from Melikop and Sapagaya (small islands off the north coast of Sabah) which Cator had placed separately from his series of $melos$ as an unrecognised species; they are small, darker brown above and with a greyish white underside bearing darker markings. Superficially they resemble $A. \text{leogoron normani}$, but the male genitalia prove them to be $A. \text{melos}$, of which they could well be regarded as a microsubspecies.

Allotinus (Paragerydus) samarensis sp. n.

(Figs 23, $\sigma$ genitalia; 65, 66 $\varphi$, 105 $\sigma'$)

Upperside of both sexes blackish brown, almost as dark as the shade of $A. \text{macassarensis}$. Male, only known from the nominate subspecies, distinctive in that visual brand extends obscurely as a paler streak
into forewing cell basad of origin of vein \( Cu_2 \). Female distinguished by the possession of a white area on forewing. Underside marked like \( A.\ melos \).

Male genitalia hardly differ from those of \( A.\ leogoron \), of which it may conceivably be a subspecies; because of the unusual visual brand and shorter swelling of vein \( M_3 \) in the male, and the distinctive white-marked female, I think it is best regarded as a distinct species.

The species is only known from a very few examples from the southern Philippines and Sulawesi in slightly different subspecies.

**Key to the subspecies of \( A.\ (P.)\ samarensis \)**

1 Underside pale greyish white. ♀ upperside of forewing with white area extending into cell well basad of origin of vein \( Cu_2 \)............................... **samarensis samarensis** (p. 38)

   - Underside very pale buff. ♀ upperside of forewing with white area not, or only just, entering cell **samarensis russelli** (p. 38)

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**Allotinus (Paragerydus) samarensis samarensis subsp. n.**

(Figs 23, ♂ genitalia; 65 ♀, 105 ♂)

♂ upperside blackish brown, with vein \( M_3 \) swollen for just over half its length, visual brand about 1.25 mm wide; a pale streak above cubitus extending a little basad of origin of vein \( Cu_2 \) appears to be an extension of the brand. Underside marked as in sympatric \( A.\ melos \), but with ground colour more greyish white.

♀ upperside blackish brown. Forewing with a creamy white streak in spaces 4 and 3 ending 2.5 mm from termen and extending into cell along cubitus to beyond origin of vein \( Cu_2 \). Underside similar to male.

**Material Examined**


Paratypes. **Philippines**: 1 ♀ (allotype), west Samar, Hinabangan, 1000 m, 5.ii.1984 (coll. Treadaway); 2 ♂, data as holotype (coll. Treadaway).

Excluded from type-series. **Mindanao**: 1 ♀, Surigao Sur, Tandag, viii. 1981 (ex Takanami coll.) (BMNH), with the white streak wider and extending into space 2.

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**Allotinus (Paragerydus) samarensis russelli subsp. n.**

(Fig. 66 ♀)

♂ unknown.

♀ forewing 19.0–21.0 mm. Upperside dark brown with a white discal patch divided by dark veins on forewing, measuring 4.0 mm in space 2 and 8.0 mm in space 3, entering base of space 4 and lower angle of cell where it is sullied. In a second specimen the white patch is smaller, not extending above vein \( M_3 \) nor entering cell. Underside very pale buff with brown markings arranged as in nominate subspecies.
Material examined
Holotype ♀, Sulawesi: east-central, north-west of Morowali, Kabalo, 450 m, 10.iii.1980 (A. Bedford Russell) (BMNH).
Paratype. 1 ♀, data as holotype (coll. Bedford Russell).

*Allotinus (Paragerydus) macassarensis* (Holland)
(Figs 24 ♂, genitalia; 67 ♂, 68 ♀)

*Paragerydus macassarensis* Holland, 1891: 70.

The species name has been consistently misspelled *macassariensis* in subsequent literature.

Previously (Eliot, 1967) I united this species and *A. melos*, but in view of small but apparently constant differences in facies and male genitalia it seems best to treat them as separate allopatric species.

The upperside in both sexes is slightly blacker brown than in the other species of the subgenus. On the underside the postdiscal markings, which are usually heavy and dark chocolate brown on an off-white ground, are placed closer to the termen than in the preceding species. A distinguishing character is that on the forewing the postdiscal spots in spaces 4, 5 and 6 are on an irregular curve, with the spot in space 5 overlapping that in space 4 and well separated from that in space 6. In the male genitalia the valvae differ from those of *A. melos* in two respects; the terminal process is narrower and slightly longer from whichever angle it is viewed and, in lateral view, there is a distinct concavity (indicated in Fig. 24 by an arrow) about two-thirds from the base.

The species is confined to Sulawesi and its satellite islands and is represented by two subspecies.

Key to the subspecies of *A. (P.) macassarensis*

1 ♂ vein *M*₃ of forewing swollen for over two-thirds of its length, visual brand usually less than 1 mm wide ................................................................. *macassarensis macassarensis* (p. 39)
- ♂ vein *M*₃ of forewing swollen for only half its length, visual brand more than 1 mm wide *macassarensis menadensis* (p. 40)

*Allotinus (Paragerydus) macassarensis macassarensis* (Holland)
(Figs 24, ♂ genitalia; 67 ♂, 68 ♀)

*Paragerydus macassarensis* Holland, 1891: 70, pl. 4, fig. 5 ♀. Holotype ♀, Sulawesi (not located, probably in CM).

*Allotinus horsfieldi macassarensis* [sic] (Holland) Fruhstorfer, 1913: 368; 1916: 812, pl. 141h.

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Fig. 24  *Allotinus (Paragerydus) macassarensis macassarensis* (Holland); Sulawesi. Male genitalia. Lower left, right valva enlarged.

Allotinus macassariensis [sic] (Holland); Corbet, 1939b: 72, fig. 14 ♂ genitalia.

Allotinus macassariensis macassariensis [sic] (Holland); Eliot, 1967: 68.

In the male the swelling of vein $M_3$, extending just over two-thirds of its length, is the longest in the subgenus and the visual brand is typically very narrow. But in east-central Sulawesi there is a tendency for the brand to become wider and less well-defined; in one extreme example in coll. Bedford Russell (Fig. 64) there is a diffuse lighter patch which reaches across vein $Cu_1$ more than half-way to vein $Cu_2$. The female has the forewing disc at most only slightly paler.

I designate as lectotype of damodar a small but otherwise normal male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/S. Celebes Tonus 27.xi.06/Fruhstorfer Coll. B.M. 1933-131/unicolor damodar Frhst. [in Fruhstorfer’s hand]. A female labelled /Type [red]/S. Celebes Samangi 17.xi.06/ Fruhstorfer Coll. B.M. 1933-131/damodar Frhst. [in Fruhstorfer’s hand] is a paralectotype.

**DISTRIBUTION.** South to central Sulawesi; Banggai I.

**Allotinus (Paragerydus) macassarensis menadensis** Eliot


Differs from the nominate subspecies in that the swollen portion of vein $M_3$ in the male is only half its length and the visual brand is quite well-defined and from 1-25 to 2-0 mm wide. In both sexes the forewing disc may be lightened by a scattering of white scales, extreme examples showing an approach to *A. samarensis russelli*.

**DISTRIBUTION.** North Sulawesi as far south as Paloe Bay (Lat. 0° 35' S). A single male from Bangka I. (off the tip of the Minahassa Peninsula) is more lightly marked beneath and the ground colour has a buff tint.

**Allotinus (Paragerydus) luzonensis** Eliot stat. n.

*(Figs 25, ♂ genitalia; 69 ♂, 70 ♀)*

*Allotinus macassariensis [sic] luzonensis* Eliot, 1967: 68, fig. 3 ♂ genitalia. Holotype ♂, PHILIPPINES: Luzon (BMNH) [examined].

The male is greyish brown above; on the forewing vein $M_3$ is swollen for half its length and the visual brand is rather diffuse. The underside is buff, closely striated, and the postdiscal markings in spaces 2 and 3 on the

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**Fig. 25** *Allotinus (Paragerydus) luzonensis* Eliot; Luzon. Male genitalia.
forewing and 6 and 7 on the hindwing are broad and rather blotchy. The female has a small white patch on
the forewing disc and an obscure whitish streak in space 5 of the hindwing. In these white patches it shows
an approach to the female of *A. albatis mendax*, but they are less developed than in that species, and the
discocellular veins on the hindwing are not blackened.

The species must be closely related to *A. albatis* because of the same arrangement of the markings on the
underside. The male genitalia of the only example dissected are intermediate between those of *A. albatis*
and *A. melos*.

**Distribution.** Luzon.

```latex
Allotinus (Paragerydus) albatis C. & R. Felder
(Figs 26, σ* genitalia; 71 ♀, 72 ᵃ, 73 ♀)
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*Allotinus albatis* C. & R. Felder, [1865]: 287.

The species is readily recognised by the presence in both sexes of white areas on both wings and by the
heavily blackened discocellular veins on the hindwing. The underside is white marked more or less as in *A.
luzonensis*, and like this species veins *M₁* and *R₅* of the forewing usually have a very short common common
The male genitalia most nearly resemble those of *A. leogoron*, with the terminal process of the valva rather
long and slender.

The species appears to be very rare and to be confined to Wallacea.

**Key to the subspecies of *A. (P.) albatis***

1 ♀ upperside with larger white areas, on forewing extending from space 1b to base of space 5, on
hindwing from outer part of space 6 to dorsum ........................................... *albatis albatis* (p. 41)

- ᵃ ♀ upperside with smaller white areas, on forewing not below mid-space 1b and not entering
  spaces 4 and 5, on hindwing usually not below vein 4 ................................... *albatis mendax* (p. 41)

```latex
Allotinus (Paragerydus) albatis albatis C. & R. Felder
(Fig. 71 ♀)
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*Allotinus albatis* C. & R. Felder, [1865]: 267. Holotype ♀, *Sulawesi* (BMNH) [examined].

[*Allotinus fallax major* Felder f. *albatis* Felder (= *maximus* Staudinger) sensu Fruhstorfer, 1913: 343,
partim; 1916: 809, partim, as *albadus* [sic].]

The subspecies is known only from the female holotype, which the authors stated was from 'Celebes
Lorquin'. It was therefore surprising to find the holotype bearing labels reading /Halmaleira Lorquin
(round blue)/Allotinus albatis Feld./Type [red]/FELDER COLLn./albatis n./Rothschild Bequest B.M.
1939-1/. As no *Allotinus* species is known from east of Weber's Line I feel confident that the locality
'Halmaleira' is the result of a wrongly acquired label and that the specimen came from north Sulawesi,
where Lorquin is known to have collected.

The forewing is white dusted with brown basally and along the dorsum below vein *A₁*, and with an
irregular dark brown border narrowest at vein *Cu₂*, where it measures 2.5 mm; above vein *Cu₂* it curves to
the wing base through the upper third of the cell. The hindwing is white, becoming sullied towards the
dorsum, except for most of the cell and spaces 8, 7 and the basal half of space 6 which are brown; the
discocellular veins are heavily blackened. The underside is white with heavy brown markings.

Fruhstorfer confused *A. albatis* with large examples of *A. major* with extensive white areas on the
forewing which were named f. *maximus* by Staudinger.

**Distribution.** Sulawesi.

```latex
Allotinus (Paragerydus) albatis mendax subsp. n.
(Figs 26, σ* genitalia; 72 ᵃ, 73 ♀)
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[*Allotinus fallax* C. & R. Felder, 1865: 285, partim, pl. 35, figs 25, 26 ♀; Semper, 1889: 163, partim.
Misidentifications.]

σ* forewing length 20.0 mm. Upperside blackish brown. Forewing with a discal white patch 7.0 mm wide at
the bases of spaces 3, 2 and upper part of 1b and entering the lower angle of the cell; the inner and lower
part of the cell and lower part of space 1b paler brown than the marginal and costal border. Vein *M₃* swollen
Fig. 26 Allotinus (Paragerydus) albatus mendax subsp. n.; Luzon. Male genitalia. Lower left, internal view of left valva enlarged; lower centre, lateral view of phallus.

for just under three-fifths of its length. Hindwing with a white streak filling most of space 5, the upper basal part of space 4 and just entering the cell; discocellular veins heavily blackened. Underside white, with reddish brown markings arranged as in sympatric A. luzonensis.

♀ similar to the male, except that the white streak on the hindwing is wider and enters space 6.

**Material examined**


Excluded from type-series. **Marinduque**: 1 ♀, Nu Boac, xi.1980 (coll. Treadaway) with the white area on the hindwing more extensive and nearly reaching the dorsum and the discocellular veins less heavily blackened. **Samar**: 1 ♀, east, Borongan, 100', 10.vii.1979 (coll. Treadaway), resembling the allotype above, but beneath with the postdiscal markings diffuse and obscure.

Allotinus (Paragerydus) apries Fruhstorfer

(FIGS 27 ♂ genitalia; 74, 106 ♂)

Allotinus horsfieldi apries Fruhstorfer, 1913: 344, partim.

Fruhstorfer's type-series probably comprised more than one species; in addition he confused apries with A. strigatus. I use apries here for the species identified as such by Corbet (1939b).

The species has several characters which enable it to be recognised with comparative ease. On the forewing veins $M_1$ and $R_5$ share a long common stalk averaging 1-5 mm. On the underside of the forewing the postdiscal series is not, or only very slightly, dislocated at vein $M_1$ and the spots in spaces 4, 3, 2 and 1b (if present) are small, rounded and well separated from, and parallel to, the termen. In the female the hindwing termen is almost evenly rounded and the cilia are a little longer, but not tufted, at the vein endings. In the male genitalia the comparatively slender phallus is distinctive.

The species occurs throughout Sundaland.

**Key to the subspecies of A. (P.) apries**

1. Underside pale buff, tending to become darker towards forewing apex in ♂, with darker buff-brown markings. ♂ visual brand 2-0 mm wide, with half its lower edge touching vein $Cu_1$ 2

   - Underside greyish white, with darker greyish brown markings. ♂ visual brand 1-5 mm wide, with only basal fifth of its lower edge touching vein $Cu_1$ ........................................... **apries ristus** (p. 44)

2. Upperside reddish brown ........................................................... **apries apries** (p. 43)

   - Upperside brown without a reddish tint ................................................ **apries dosithes** (p. 44)
Allotinus (Paragerydus) apries apries Fruhstorfer
(Figs 27, ♂ genitalia; 74 ♀)

[Allotinus horsfieldi (Moore) sensu Swinhoe, 1910: 198, partim, pl. 617, fig. 1 ♂. Misidentification.]
Allotinus horsfieldi apries Fruhstorfer, 1913: 344, partim; 1916: 812, partim, pl. 141g ♂ nec ♀. LECTOTYPE ♂, BORNEO (BMNH), here designated [examined].
Allotinus strigatus eupalion Fruhstorfer, 1914: 22; 1916: 813. LECTOTYPE ♂, SUMATRA (BMNH), here designated [examined]. Syn. n.
Allotinus apries eupalion Fruhstorfer; Corbet, 1939b: 70.
Allotinus apries eupalion Fruhstorfer; Corbet, 1939b: 70; Fleming, 1975: 21, pl. 58, fig. L42 ♂; Eliot, 1978: 240.

In both sexes the underside is nearly always pale buff, with darker buff-brown markings, but occasionally it is more greyish white with only a slight buff tint. In the female the postdiscal series is lightly marked and may be obsolete on the forewing. The male has vein M₃ swollen for a little over three-fifths its length, and the visual brand is clearly defined and 2.0 mm wide. The female is more reddish brown above, with the forewing disc a little paler.

Fruhstorfer described A. horsfieldi apries from several males from Sintang (south-west Borneo) and 10 females from north Borneo. He wrote that the underside was bluish white speckled with pale brown in the male and thicker grey-brown in the female. This description does not accord well with the taxon here treated as apries. However, there is a male from Sintang in BMNH labelled apries by Fruhstorfer and with the underside paler and greyer than usual, which presumably formed part of the type-series. In addition there are seven males of A. horsfieldi permagnus from Sintang ex Fruhstorfer coll., and it seems likely that these also formed part of Fruhstorfer's type-series even though none had been labelled by him as apries. The only other males of apries ex coll. Fruhstorfer in BMNH are one labelled by Fruhstorfer as A. strigatus Moulton and one which was apparently regarded by Corbet as the holotype of apries and is labelled /Type [red]/Type [Fruhstorfer orange]/Kina Balu ex coll. H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/apries/. As it did not come from Sintang it cannot have formed part of the type-series, and I reject it as a type. In its place I designate as lectotype of apries the male from Sintang, which is labelled /Sintang Dr Martin H. Fruhstorfer/21.IV.10/Fruhstorfer Coll. B.M. 1933-131/apries Fr. [in Fruhstorfer's hand]/A. apries apries Det. by Dr. A. S. Corbet [in Corbet's hand]/.

There are also two females of apries in BMNH which have been treated as syntypes. One is labelled /Type [red]/Type [Fruhstorfer orange]/Kina Balu Borneo/Fruhstorfer Coll. B.M. 1933-131/horsfieldi apries Fhrst. [in Fruhstorfer's hand]/ and is a paralectotype. The other, labelled /Type [red]/Type [Fruhstorfer orange]/Sintang 10.IV.10/Fruhstorfer Coll. B.M. 1933-131/ is rejected as a paralectotype as it did not come from north Borneo and therefore cannot have formed part of the type-series.

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Fig. 27 Allotinus (Paragerydus) apries apries Fruhstorfer; Malay Peninsula. Male genitalia. Lower left, lateral view of phallus.
I designate as lectotype of eupalion a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/CMB II.94/Fruhstorfer Coll. B.M. 1933-131/strigatus eupalion Frhst. [in Fruhstorfer’s hand]/GENITALIA Slide No. ASC 9 Allotinus/.

Here it may be mentioned that the female figured by Fruhstorfer (1916: pl. 141g) as apries is a different species, either A. horsfieldi or A. melos, and also that the male and female figured by Swinhoe (1910: pl. 617, figs 1, 1a) as A. horsfieldi are in BMNH and are in fact Bornean specimens of A. apries and A. melos respectively.

**DISTRIBUTION.** Borneo, including Pulo Laut; Malay Peninsula; Sumatra.

*Allotinus (Paragerydus) apries dositheus* Fruhstorfer

*Allotinus strigatus dositheus* Fruhstorfer, 1914: 22; 1916: 813. LECTOTYPE ♂, JAVA (BMNH), here designated [examined].

[Allotinus strigatus Moulton sensu Piepers & Snellen, 1918: 22, pl. 20, fig. 17 ♂. Misidentification.]

*Allotinus apries dositheus* Fruhstorfer; Corbet, 1939b: 72.

The male does not differ from that sex of the nominate subspecies. The female differs in being brown without a reddish tint, in this respect showing parallel variation with the female of *A. horsfieldi*.

I designate as lectotype of dositheus a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Java occident. Sukabumi 2000’ ex coll. H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/strigatus dositheus Frhst. [in Fruhstorfer’s hand]/GENITALIA Slide No. ASC 8 Allotinus/. A female, similarly labelled, which has been treated as a syntype, is a misidentified example of *A. portunus portunus*.

**DISTRIBUTION.** Java.

*Allotinus (Paragerydus) apries ristus subsp. n.*

(Fig. 106 ♂)

♂ on the upperside differs from subsp. apries in having a narrower forewing visual brand 1-5 mm wide. The underside differs by its greyish white ground colour and darker greyish brown markings. The striations are fine and the postdiscal spots small.

**MATERIAL EXAMINED**

Holotype ♂, Philippines: central Palawan, Languan, i.1981 (Treadaway Coll.).

*Allotinus (Paragerydus) corbeti* Eliot

(Fig. 28, ♂ genitalia)

[Allotinus dilutus Corbet sensu Corbet, 1940b: pl. 1, figs 13 ♂, 14 ♀. Misidentification.]

*Allotinus corbeti* Eliot, 1956: 34; 1984: 100. Holotype ♂, WEST MALAYSIA (BMNH) [examined].

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*Fig. 28 Allotinus (Paragerydus) corbeti* Eliot; Borneo: Pulo Laut. Male genitalia.

*Allotinus felder corbeti* Eliot; Eliot, 1967: 70, fig. 2 ♀ genitalia; 1978: 240; Fleming, 1975: 21, pl. 21, fig. L41 ♂.

This very small species has an uniform reddish brown upperside in both sexes, and the underside marked as in *A. leogoron leogoron*. In the male the forewing apex is rounded, and the swelling of vein *M*₃ is confined to the basal quarter of the vein; there is no visual brand. The female has the hindwing termen more strongly crenulate than *A. leogoron*.

Although smaller, it is possible that *A. corbeti* might be confused with *A. nicholisi*, since the males of both species are similar on the upperside. Females are also a similar shade of uniform reddish brown, but those of *corbeti* are readily separated by their crenulate hindwing with the cilia elongated into tufts at the vein endings. In addition, *corbeti* has no humeral vein on the hindwing, this vein being present in all six examples of *nicholisi* which I have examined.

**DISTRIBUTION.** West Malaysia; Singapore; Sumatra; Pulo Laut; Mindanao; Peninsular Thailand (Pinratanap). The species appears to be extremely rare, but is perhaps often overlooked.

*Allotinus (Paragerydus) unicolor* C. & R. Felder

(Figs 29, 30, ♂ genitalia)

*Allotinus unicolor* C. & R. Felder, [1865]: 286.

This, the most wide-ranging species of the genus, shows great individual variation in size, wing shape and underside pattern. In general the smaller males, with forewing length as little as 11-0 mm, have a more rounded forewing apex and termen and a relatively shorter brand, whilst the bigger males have a more acute apex and straighter termen and a brand which is slightly longer and narrower in relation to wing span. Examples, such as the holotype of *unicolor*, in which the usual lycaenid markings on the underside are heavy, are comparatively sparsely striated. In examples in which the underside is more densely striated there is usually a reduction in the size and darkness of these markings. On the forewing the postdiscal series is typically on an almost even curve, but examples in which it is dislocated at vein *M*₃ to a greater or less extent are equally frequent.

The best characters for identifying the species are the male genitalia (Figs 29, 30) with a broad valva with the terminal process almost in the centre line, the short stalk of veins *M*₁ and *R*₅ of the forewing and the relatively short swelling of vein *M*₃ in the male.

Fruhstorfer grouped the complex into three sympatric 'species': *unicolor*, *aphocha* and *posidion*. Under *unicolor* he grouped comparatively small specimens with a whitish ground colour on the underside and heavy postdiscal markings, and under *aphocha* specimens of similar size and wing shape but with less pronounced markings. He reserved *posidion* for large specimens in which the male forewing was more produced. Corbet (1939b), though at first inclined to agree with Fruhstorfer's arrangement, finally decided that all three constituted a single, variable species, but at the same time erected a new 'species', *A. dilutus*,

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**Fig. 29** *Allotinus (Paragerydus) unicolor continentalis* Fruhstorfer; Burma. Male genitalia.
Fig. 30  *Allotinus* (Paragerydus) *unicolor zitema* Fruhstorfer; Sulawesi. Male genitalia.

which he later (1956) relegated to subspecies, for very small examples from the Malay Peninsula. The various sizes, wing shapes and patterns are connected by intermediates and, like Corbet, I can find no differences in the male genitalia of the largest and smallest specimens. Therefore I also consider that there is only one species, to which I now add the taxon *continentalis*, which has previously been treated as a subspecies of *A. horsfieldi* or as a distinct species.

It is extraordinarily difficult to decide what constitutes a valid subspecies because of the great range of phenetic variation. When large series are available for comparison, as in coll. BMNH, it is possible to detect differences between the average phenotype of different geographical areas, but because of the overlap of phenetic characters it may often be impossible to ascribe individual specimens, if deprived of their locality labels, to any particular country of origin. I have opted to retain as subspecies those groups of populations which can be distinguished by a mean of differences and which are contained within generally accepted faunal areas in preference to lumping together into just two or three polytypic subspecies the populations of widely separated geographical areas which in all probability differ genetically to a considerable degree. In using the key below this limitation should be borne in mind.

The species ranges from Assam to the Lesser Sunda Is., Philippines and Sulawesi (including the Sula Is.), and is most abundant in low level primary or secondary forest.

**Key to the subspecies of *A. (P.) unicolor***

1 Underside of hindwing with the postdiscal spot in space 6 well inside that in space 7 and often mid-way to the end-cell spot ................................................................. 2
   - Underside of hindwing with the postdiscal spot in space 6 much closer to the spot in space 7 than to the end-cell spot ........................................................................................................................................ 7
2 Underside ground colour greyish white. ♂ vein $M_3$ of forewing swollen for not more than half its length. ♀ upperside of forewing with disc not conspicuously paler ................................................................. 3
   - Underside ground colour pale buff. ♂ vein $M_3$ swollen for a little over half its length. ♀ forewing disc conspicuously paler and often sullied whitish ................................................................. *unicolor continentalis* (p. 47)
3 ♂ forewing brand 1-0 mm or more wide. Continental Asia and Borneo ........................................................................................................ 4
   - ♂ brand less than 1-0 mm wide. Philippines and Sulawesi ........................................................................................................ 6
4 ♀ upperside reddish brown .......................................................................................................................... 5
   - ♀ upperside brown without a reddish tint ......................................................................................... *unicolor rekkia* (p. 48)
5 ♂ forewing brand about 1-0 mm wide ........................................................................................................ *unicolor unicolor* (p. 47)
   - ♂ brand comparatively short and broad, about 1-75 mm wide in large specimens.
      Underside rather lightly marked ........................................................................................................ *unicolor moorei* (p. 48)
6 Underside with postdiscal markings usually heavy and sharply defined. ♂ vein $M_3$ swollen for just under half its length, brand sharply defined ......................... *unicolor georgius* (p. 49)
   - Underside with postdiscal markings usually rather light and tending to be blurred. ♂ vein $M_3$ swollen for half its length and brand usually rather inconspicuous ........................... *unicolor zitema* (p. 50)
7 Upperside hindwing with postdiscal spot in space 6 often below and conjoined to the spot in space 7. ♀ upperside brown without a reddish tint, forewing disc paler... *unicolor position* (p. 48)
- Underside hindwing with the postdiscal spot in space 6 nearly always inside the spot in space 7. ♀ upperside with a slight reddish tint, forewing disc only slightly paler... *unicolor aphocha* (p. 48)

*Allotinus (Paragerydus) unicolor unicolor* C. & R. Felder

*Allotinus unicolor* C. & R. Felder, [1865]: 286. Holotype ‘♂’ recte ♀, SINGAPORE (BMNH) [examined].
[**Allotinus posidion myriandus** Frühstorfer, 1913: 368 (partim); 1916: 811 (partim).]
*Allotinus posidion eurytanus* Frühstorfer, 1913: 368; 1916: 811. LECTOTYPE ♀, BORNEO (BMNH), here designated [examined]. **Syn. n.**

*Allotinus unicolor unicolor* Felder; Frühstorfer, 1913: 369; 1916: 809, pl. 141i; Corbet, 1939b: 68, pl. 1, figs 3 ♀ holotype, 4 ♀; 1956: 269, pl. 44, fig. 153 ♀; Eliot, 1978: 240, pl. 20, figs 5 ♀, 6 ♀.
[**Allotinus aphocha aphocha** (Kheil); Frühstorfer, 1913: 370 (partim); 1916: 810 (partim).]

*Allotinus unicolor eurytanus* Frühstorfer; Corbet, 1939b: 70, pl. 1, figs 9 ♀ ‘holotype of eurytanus’ (in error), 10 ♀ ‘holotype of eurytanus f. rebilus’ (in error).

*Allotinus dilutus* Corbet, 1939b: 70. Holotype ♀, WEST MALAYSIA (BMNH) [examined]. **Syn. n.**

*Allotinus unicolor dilutus* Corbet; Corbet, 1956: 269; Cantlie, 1967: 27; Fleming, 1975: 21, pl. 57, fig. L40 ♀.

The female holotype, figured by Corbet (1939b) and mistaken by the Felders for a male, is an atypical specimen with heavy markings and a whiter than usual ground colour. Such specimens occur most often in Singapore, where they are connected by intermediates to normal phenotypes. The male figured by Corbet (1939b), which matches the holotype fairly well but has a slightly greyer ground colour on the underside (as usual in males), would probably have been identified by Frühstorfer as *A. posidion myriandus* because of its size and wing shape.

In general Bornean examples have the lycaenid markings smaller than in those from continental Asia, but compensate by being slightly more densely striated. This tendency is most extreme in examples from south-west Borneo, named *eurytanus* by Frühstorfer, which are particularly densely striated but can be matched by occasional examples from other areas.

I designate as lectotype of *eurytanus* a male in BMNH labelled /Type [red]/Type [Frühstorfer orange]/Sintang 19.IV.10/Fruhstorfer Coll. B.M. 1933-131/posidion eurytanus Fr. [in Frühstorfer’s hand]/. It was figured by Corbet (1939b: fig. 10) in error as the holotype of *A. unicolor eurytanus f. rebilus*. The smaller specimen figured by Corbet at fig. 9 in error as the holotype of *eurytanus* is labelled /Type [red]/Type [Frühstorfer orange]/Sintang 26.IV.10/aphocha rebilus Frst. [in Frühstorfer’s hand]/GENITALIA Slide No. ASC 14 Allotinus/. Despite Frühstorfer’s identification label it cannot be accepted as lectotype of *rebilus*, since this taxon was described from North Borneo; it probably formed part of Frühstorfer’s original type-series of four males and one female of *A. posidion eurytanus*, and how it obtained its label as *rebilus* is a mystery.

**Distribution.** This very variable subspecies is found in south Burma, where it has a zone of intergradation with subs. *continentalis* between Rangoon and Tavoy, and in Peninsular Thailand, West Malaysia, Singapore, Lingga Is., Natuna Is. and throughout Borneo, except in the Kina Balu area where it merges into subs. *moorei*.

*Allotinus (Paragerydus) unicolor continentalis* Frühstorfer

(Fig. 29, ♀ genitalia)

[**Paragerydus horsfieldi** (Moore) sensu de Nicéville, 1890: 26, pl. 36, fig. 156 ♀. Misidentification.]

[**Allotinus horsfieldi** (Moore) sensu Bingham, 1907: 287, 299, fig. 73 ♀; sensu Swinhoe, 1910: 198 (partim, nec pl. 617, figs 1, 1a, 1b, 1c). Misidentifications.]

*Allotinus horsfieldi continentalis* Frühstorfer, 1913: 344; 1916: 812; Evans, 1932: 212; Cantlie, 1963: 27.
Holotype ♀, BURMA: Bhamo (probably in ZSI).

[**Allotinus posidion subsp.**; Frühstorfer, 1913: 368.]


*Allotinus unicolor atacinus* Frühstorfer; Corbet, 1939b: 68, pl. 1, fig. 2 ♀ holotype; Cantlie, 1963: 27.

*Allotinus continentalis continentalis* Frühstorfer; Corbet, 1939b: 72.

*Allotinus continentalis* Frühstorfer; Eliot, 1967: 70, fig. 4 ♀ genitalia.
This is the most distinctive and largest subspecies of *A. unicolor*, with the forewing length of the male usually 18–19 mm. On the underside both sexes are pale buff. On the upperside the male brand is longer and wider than in the other subspecies, usually 2-0 mm wide and touching vein Cu₁ at its origin, while the swelling of vein *M*₃ is a little over half its length. The female is distinguished by the prominently paler discal area on the upperside of the forewing, which may be sullied whitish in the dry season.

**Distribution.** Assam; Burma as far south as Tavoy; north-west Thailand. Around the latitude of Rangoon it intergrades with subs. *unicolor*.

**Allotinus (Paragerydus) unicolor rekkia** Riley & Godfrey

*Allotinus posidion rekkia* Riley & Godfrey, 1921: 180, pl. 6, figs 1 ♂, 2 ♀. Holotype ♂, THAILAND: east (BMNH) [examined].

*Allotinus unicolor rekkia* Riley & Godfrey; Eliot, 1967: 70.

Females are brown without the reddish tint of subs. *unicolor*, but otherwise the subspecies does not differ and is of doubtful validity.

**Distribution.** Only known from eastern Thailand, but probably also occurs in Cambodia, Laos and Vietnam.

**Allotinus (Paragerydus) unicolor moorei** (H. H. Druce)


*Allotinus paetus moorei* (Druce) Fruhstorfer, 1913: 369: 1916; 811.

*Allotinus aphocha rebilus* Fruhstorfer, 1913: 370; 1916: 810. LECTOTYPE ♀, BORNEO (BMNH), here designated [examined]. Syn. n.

*Allotinus moorei* (H. H. Druce); Corbet, 1939b: 68.

Druce’s figure of the male shows a comparatively large specimen weakly marked beneath and with the brand on the upperside of the forewing rather short, broad and diffuse. Judging by material in BMNH such males are rare, and are connected by intermediates to smaller males which differ little, if at all, from nominate *unicolor*. The subspecies is therefore of doubtful validity.

Fruhstorfer’s taxon *rebilus* is applicable to smaller examples. I designate as lectotype a female in BMNH labelled /Type [red]/Kina Balu/ex coll. H. Fruhstorfer/Allotinus aphocha rebilus Fr. [in Corbet’s hand]/.

**Distribution.** The subspecies flies on Mt Kina Balu, and might conceivably be a local modification occurring at higher elevations than normal examples referable to subs. *unicolor*.

**Allotinus (Paragerydus) unicolor aphocha** Kheil

*Allotinus aphocha* Kheil, 1884: 28, pl. 5, fig. 30 ♀. Holotype ♀, NIAS (probably in MNHU).


*Allotinus aphocha aphocha* Kheil; Fruhstorfer, 1913: 370 (partim); 1916: 810 (partim), pl. 141g ♂ ♀.

*Allotinus unicolor myriandus* Fruhstorfer; Corbet, 1939b: 68, pl. 1, figs 5 ♂ holotype, 6 ♀ allotype.

*Allotinus unicolor aphocha* Kheil; Corbet, 1939b: 70, pl. 1, fig. 11 ♀.

Differs from subs. *unicolor* only in that on the underside of the hindwing the postdiscal spot in space 6 is usually placed closer to the spot in space 7. Many specimens are inseparable from *unicolor*, so the subspecies is of doubtful validity.

Fruhstorfer did not designate a type of *myriandus*, but Corbet (1939b) figured its ‘holotype’ male and ‘allotype’ female, and this action constitutes a valid lectotype selection.

**Distribution.** Sumatra; Bangka Is.; Batu Is.; Mentawai Is; Nias I.

**Allotinus (Paragerydus) unicolor posidion** Fruhstorfer

*Allotinus posidion posidion* Fruhstorfer, 1913: 368; 1916: 811. Lectotype ♂, JAVA: west (BMNH), by designation (as holotype) of Corbet, 1939b: 68 [examined].

*Allotinus posidion molionides* Fruhstorfer, 1913: 368; 1916: 811. Lectotype ♂, BALI (BMNH), by designation (as holotype) of Corbet, 1939b: 70 [examined]. Syn. n.
Allotinus posidion niceratus Fruhstorfer, 1913: 368; 1916: 812. LECTOTYPE ♂, SUMBAWA (BMNH), here designated [examined]. Syn. n.

Allotinus unicolor enganicus Fruhstorfer, 1913: 369; 1916: 811. Lectotype ♂, ENGANO I. (BMNH), by designation (as holotype) of Corbet, 1939b: 70, pl. 1, fig.12 [examined]. Syn. n.

Allotinus unicolor bajanus Fruhstorfer, 1913: 369; 1916: 811; Corbet, 1939b: 70. LECTOTYPE ♂, LOMBOK (BMNH), here designated [examined]. Syn. n.

Allotinus aphocha enatheus Fruhstorfer, 1913: 370; 1916: 810. LECTOTYPE ♀, JAVA (BMNH), here designated [examined]. [Synonymised by Corbet, 1939b: 70.]

Allotinus horsfieldii [sic] f. posidion Fruhstorfer; Piepers & Snellen, 1918: 12, pl. 19, figs 14a ♂, 14b ♀.

Allotinus suka Piepers & Snellen, 1918: (partim), pl. 27, fig. 181 ♂. LECTOTYPE ♂, JAVA (probably in RNH), here designated. [Aberration reduced to infrasubspecific status by Corbet, 1939b: 70.]

Allotinus unicolor Felder; Piepers & Snellen, 1918: 14, pl. 19, figs 13a ♂, 13b ♀. [Allotinus aphocha Khel; Piepers & Snellen, 1918: 15, pl. 19, figs 15a ♂, 15b ♀.]

Allotinus unicolor posidion Fruhstorfer; Corbet, 1939b: 68, pl. 1, figs 7 ♂ holotype, 8 ♀ ‘allotype’ of enatheus.

Allotinus unicolor molionides Fruhstorfer; Corbet, 1939b: 70, pl. 1, fig. 13 ♂ holotype.

Allotinus unicolor bajanus Fruhstorfer; Corbet, 1939b: 70.

The female lacks the reddish tint of subsp. myriandus and usually the forewing disc is paler. On the underside of the hindwing the postdiscal spot in space 6 is more often directly below, and conjoined to, the spot in space 7; this character occurs most often in examples from the Lesser Sunda Is., which also have the postdiscal spots on average heavier than in Javanese examples.

Fruhstorfer did not designate types of his taxa, but Corbet (1939b) figured the ‘holotype’ males of posidion, molionides and enganicus, and this action constitutes valid lectotype selections. He also figured a female which he described as A. unicolor posidion f. enatheus Fruh. ♀ allotype. I now designate this female as lectotype of enatheus; it is labelled: /Type [red]/Type [Fruhstorfer orange]/Java occident. Sukabumi 2000' ex coll. H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/apochea enatheus Fr. [in Fruhstorfer's hand]/

I designate as lectotype of niceratus a male in BMNH labelled /Type [red]/Sumbawa/Allotinus posidion niceratus Fruh. Type [in Corbet's hand]/Adams Bequest B.M. 1912-399/. It is to be presumed that Fruhstorfer saw this specimen during his visit to BMNH prior to publication of his 1913 paper, as there are no specimens from Sumbawa from his collection in BMNH.

I designate as lectotype of bajanus a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Pringabaja April 1896 H. Fruhstorfer/unicolor bajanus Frst. [in Fruhstorfer’s hand]/.

Piepers & Snellen (1918) figured two different species as Allotinus suka: a female on pl. 19, fig. 12b to which they had previously referred as Allotinus horsfieldii and a male on pl. 27, fig. 181. When relegating suka to the status of a form of A. unicolor posidion, in which the usual striations of the underside are absent, Corbet (1939b: 70) referred only to the latter figure which he said, in error, represented a female. Corbet’s action could, perhaps, be taken to restrict the name suka to the species represented in fig. 181, but to make absolutely certain that there should be no confusion in the application of the name I now designate this male as lectotype. It should be in RNH.

Distribution. Java; Bali; Lombok; Sumbawa; Engano I.

Allotinus (Paragerydus) unicolor georgius Fruhstorfer

[Paragerydus horsfieldii (Moore) sensu Semper, 1889: 164, partim. pl. 31, fig. 18 ♂.]

Allotinus posidion georgius Fruhstorfer, 1913: 368, partim; 1916: 812. Holotype ♂, PHILIPPINES: Bohol (SM) [examined].


Fruhstorfer named georgius from Semper’s records and figures of ‘horsfieldii’ from Bohol and Mindanao, which he subsequently (1916) realised represented two species. Thereupon he restricted georgius to Bohol, so that this name applies to the male figured by Semper at fig. 18, which automatically becomes the holotype; it is labelled /18/213/Coll. C. Semper/reverdini/original of Semper Pl. 31, fig. 18 ♂ from Bohol. Holotype of Allotinus posidion georgius Fruh. det. J. N. Eliot ix.1982/. It is heavily marked below much as in the holotype of unicolor, but on the upperside the brand is a little shorter and narrower than in that subspecies.

Fruhstorfer named leitus from a single female with a yellowish discal area on the forewing and heavy
markings on the underside. The latter character suggests that it pertains to the same subspecies as *georgius*, but as I have seen no examples from Mindoro it is provisionally placed in synonymy.

**DISTRIBUTION.** *A unicolor* must be very rare in the Philippines, as it is not represented in coll. Treadaway, and in BMNH there are only two females, one of which is labelled ‘Philippines Pryer’. This appears to be an aberration; it is lightly striated on the underside, as in examples from north Borneo, and the postdiscal markings are elongated into longitudinal streaks. It may have come from the Sulu Is., which were visited by Pryer, or may be a mislabelled example from Borneo, where Pryer did nearly all his collecting.

**Allotinus (Paragerydus) unicolor zitema** Fruhstorfer

(Fig. 30, ♂ genitalia)

*Allotinus aphocha zitema* Fruhstorfer, 1916: 810. LECTOTYPE ♀, SULAWESI (BMNH), here designated [examined].

The subspecies is distinguished by the male brand, which is a little narrower and more obscure than in other subspecies.

I designate as lectotype a female in BMNH labelled: Type [red]/Type [Fruhstorfer orange]/Nord-Celebes Toli Toli Nov. – Dez. 1895 H. Fruhstorfer/aphocha zitema Fr. [in Fruhstorfer’s hand]/Fruhstorfer Coll. B.M. 1933-131/. I have seen no males ex Fruhstorfer coll.

**DISTRIBUTION.** Sulawesi and the Sula Is.

**Allotinus (Paragerydus) paetus** (de Nicéville)

(Fig. 31 ♂ genitalia)


*Allotinus paetus paetus* (de Nicéville) Fruhstorfer, 1913: 369; 1916: 811, pl. 141i ♀. *Allotinus paetus* (de Nicéville); Corbet, 1939b: 68, pl. 1, fig. 1 ♂.

This species bears a fairly close resemblance to examples of *A. unicolor* which are strongly marked beneath, as in the holotype of *unicolor*. But it is larger, with forewing length averaging 18–19 mm in males, the forewing brand and swelling of vein $M_3$ are slightly longer than in all *unicolor* subspecies apart from subsp. *continentalis*, being just over half the length of the vein, and on the underside the ground colour is more chalky whitish. The male genitalia are rather similar to those of *A. unicolor*, but the phallus is stouter and the distal portion of the valva narrower, with the terminal process not curved up so strongly towards the centre line.

**DISTRIBUTION.** The species is only known from Sumatra, where it appears to fly in the Barisan Range from the Battak mountains in the north to the extreme south, where it was taken in numbers by Doherty.

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Fig. 31 *Allotinus (Paragerydus) paetus* (de Nicéville); Sumatra. Male genitalia.
**Allotinus (Paragerydus) parapus** Fruhstorfer

(Fig. 32, ♀ genitalia)

*Allotinus parapus* Fruhstorfer, 1913: 343; 1916: 809, pl. 141h ♂; Corbet, 1939b: 66, fig. 8 ♂ genitalia.

LECTOTYPE ♂, BORNEO (BMNH), here designated [examined].

The sexes are alike in wing shape and in having a rounded hindwing termen with the cilia inconspicuously elongated at the vein endings. In the male vein \( M_3 \) is swollen for just under half its length and clothed with the usual specialised scales. The white forewing bordered with dark brown and the paler brown hindwing render the species unmistakable.

Both Fruhstorfer and Corbet, whose figure of the male valva is completely misleading, stated that vein \( M_3 \) was not swollen in the male, and on this account placed the species in the *fallax*-group (*Artengruppe Allotinus*). In fact the swelling is as well developed as in some other species of the subgenus, but because the surrounding area is white no visual brand is apparent.

I designate as lectotype a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Fruhstorfer Coll. B.M. 1933-131/Nord-Borneo/Allotinus parapus Frhst. [in Fruhstorfer's hand]/. A female, similarly labelled, is a paralectotype.

**DISTRIBUTION.** The species is montane and is known only from Mt Kinabalu in Sabah.

**Allotinus (Paragerydus) nivalis** (H. Druce)

(Figs 33, 34, ♂ genitalia; 75 ♂)

*Miletus nivalis* H. Druce, 1873: 348.

This and the next two taxa form a natural group of small species distinguished by the possession of a white fleck at the end of vein \( R_5 \) at the apex of the forewing in addition to the usual white flecks at the ends of veins \( Sc, R_1, R_2 \) and \( R_3 \). In males the swelling of vein \( M_3 \) is weak and short, and there is no visual brand.

In *A. nivalis* the forewing termen is almost regular in both sexes, and on the underside of the hindwing the central spot in space 7 is not, or only very little darkened. On average it is larger than the allied *A. substrigosus* and *A. davidis*.

The species is confined to Borneo and the Philippines.

**Key to the subspecies of *A. (P.) nivalis***

1 Underside of forewing with a more or less developed submarginal brownish blotch about 1·0–1·5 mm wide astride vein \( M_3 \); postdiscal series strongly dislocated at veins \( M_3 \) and \( Cu_2 \)

*nivalis nivalis* (p. 52)
Fig. 33 *Allotinus (Paragerydus) nivalis nivalis* (H. Druce); Borneo. Male genitalia.

- Underside without a brownish blotch astride vein $M_3$; postdiscal series placed nearer the termen and only a little dislocated at veins $M_3$ and $Cu_2$ ........................................... *nivalis felderi* (p. 52)

*Allotinus (Paragerydus) nivalis nivalis* (H. Druce)

(Fig. 33, ♂ genitalia)

*Miletus nivalis* H. Druce, 1873: 348, ‘♂’ recte ♀. Holotype ♀, BORNEO (BMNH) [examined].

*Allotinus nivalis nivalis* (Druce) Fruhstorfer, 1913: 370; 1916: 810, pl. 141g.

*Allotinus nivalis* (H. Druce); Eliot, 1967: 71.

The characters of the subspecies are given in the key. The figure by Fruhstorfer (1916: 141g) is very poor and shows an undersized specimen.

**DISTRIBUTION.** Throughout Borneo, including Pulo Laut.

*Allotinus (Paragerydus) nivalis felderi* Semper

(Fig. 34 ♂ genitalia; 75 ♂′)

*Allotinus felderi* Semper, 1889: 163, pl. 31, fig. 22 ♀; Fruhstorfer, 1913: 370; 1916: 810. LECTOTYPE ♂, PHILIPPINES (SM), here designated [examined].

Fig. 34 *Allotinus (Paragerydus) nivalis felderi* Semper; Mindanao. Male genitalia. Lower left, ventral view of valvae and phallus of another specimen.
Alotinus felder felder Semper; Eliot, 1967: 70, partim.
Alotinus nivalis felder felder Semper; Eliot, 1984: 100.

The differences from the nominate subspecies are given in the key.
Semper described the taxon from two males from Mindanao and two females from Luzon. I designate as lectotype one of the males in SM, labelled /Coll. C. Semper/Ost Mind./212/All. felder typ. Semper/. Eliot (1967) confused felder with A. corbeti from a pair of corbeti and one exceptionally small female of true felder from Mindanao, all of which had been placed under the latter name in coll. BMNH.

DISTRIBUTION. Throughout the Philippines. In addition to examples from Luzon, Sibuyan and Mindanao in BMNH I have examined examples in coll. Treadaway from Marinduque, Negros and Samar.

**Allotinus (Paragerydus) substrigosus** (Moore)

(Figs 35, ♂ genitalia; 76, 77 ♀)

*Logania substrigosa* Moore, 1884: 22.

Until separated by Eliot (1967) all authors treated this species as, or as a subspecies of, A. nivalis, from which it differs as follows. On average it is smaller, with forewing length occasionally as little as 9.0 mm. In both sexes the forewing termen is distinctly crenulate, becoming more exaggerated in the dry season form from Burma. On the underside of the hindwing the central spot in space 7 is at least partially blackened and there is often a black subbasal spot in space 1b, the corresponding spots in nivalis not being blackened. The male genitalia are very similar, but in substrigosus the phallus is narrower than in sympatic nivalis.

The species ranges from central Burma and Thailand to Sundaland and Mindanao. In Borneo it appears to be rarer than A. nivalis.

**Key to the subspecies of A. (P.) substrigosus**

1. Underside of hindwing with the spot mid-space 7 blackened only in upper half of space, and not more than 1.0 mm wide ................................. 2
   - Underside of hindwing with the spot mid-space 7 solidly black, nearly 2.0 mm wide and extending right across space .................................. *substrigosus ballantinie* (p. 55)
2. Underside greyish-white. Forewing crenulate .............................................. 3
   - Underside pale grey. Forewing only very weakly crenulate .................. *substrigosus yusukei* (p. 55)
3. On underside of forewing the white fleck at end of vein 7 barely enters space 6 ................................. 4
   - On underside of forewing the white fleck at the end of vein R₅ is continued as an oblique white streak half-way across space 6 ............................. *substrigosus substrigosus* (p. 53)
4. ♀ with vein M₃ swollen for only one-quarter of its length ..................... *substrigosus lenaia* (p. 54)
   - ♀ with vein M₃ swollen for one-third of its length, as in subspp. *substrigosus*

**Allotinus (Paragerydus) substrigosus substrigosus** (Moore)

(Fig. 35, ♂ genitalia)

*Logania substrigosa* Moore, 1884: 22; 1886; 39, pl. 3, fig. 8 ♂. Holotype ♂, **BURMA**: Mergui Archipelago (probably in ZS).
[Paragerydus nivalis] (H. Druce) sensu Distant, 1884: 207, pl. 22, fig. 11 ♂. Misidentification.
[Alotinus nivalis] (H. Druce) sensu de Nicéville, 1890: 30 partim, pl. 36, fig. 159 ♂ holotype of substrigosus; sensu Bingham, 1907: 301; sensu Swinhoe, 1910: 197, pl. 616, figs 2, 2b ♂, 2a ♀; sensu Piepers & Snellen, 1918: 16, pl. 20, fig. 19 ♂. Misidentifications.


*Allotinus substrigosus substrigosus* (Moore); Fleming, 1975: 21, pl. 57, fig. L38 ♂.

In the male the swelling of vein M₃ extends to one-third of its length. On the underside there is a prominent white streak at the forewing apex, and on the hindwing the central spot in space 7 is strongly blackened.

From central Burma as far south as Tavoy a distinct dry season form occurs. The forewing termen is more
Fig. 35 Allotinus (Paragerydus) substrigosus yusukei subsp. n.; Mindanao. Male genitalia. Lower left, A. substrigosus substrigosus (Moore), Malay Peninsula; right valva and phallus.

strongly crenulate; on the underside the ground colour becomes more greyish; on the forewing the apex and margin to a depth of 2-0–3-0 mm are shaded with brown, so that the oblique apical white streak stands out more conspicuously; and on the hindwing there is a similar brown area in spaces 3, 4 and 5, and the outer postdiscal spot in space 7, and sometimes that in space 6 also, may be blackened on their inner edges—a feature otherwise only found in A. davidis. This dry form, with its mottled appearance and crenulate wings, gives the impression of a Logania species.

I designate as lectotype of magaris a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Selesseh 15.VII.94/Fruhstorfer Coll. B.M. 1933-131/Sumatra Montes Battak ex coll. Fruhstorfer/nivalis magaris Frhst. [in Fruhstorfer's hand]/. The locality Selesseh lies a little above sea level in north-east Sumatra and is more likely to be the correct locality than the Battak Mts.

DISTRIBUTION. Burma, as far north as east Pegu; Thailand; West Malaysia; Sumatra; Borneo; Java (Piepers & Snellen, 1918).

Allotinus (Paragerydus) substrigosus lenaia Fruhstorfer

Allotinus nivalis lenaia Fruhstorfer, 1913: 370; 1916: 810. LECTOTYPE ♂, Nias (BMNH), here designated [examined].


In the single male which I have seen the swelling of vein $M_3$ is confined to the basal quarter of the vein. On the underside of the forewing the white streak at the end of vein $R_5$ at most barely enters space 6, and in females the markings are on average lighter than in the nominate subspecies.

I designate as lectotype a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Nias ex coll. Fruhstorfer/nivalis lenaia Frhst. [in Fruhstorfer's hand]/.

DISTRIBUTION. Nias I.

Allotinus (Paragerydus) substrigosus sibyllinus Riley

Allotinus nivalis sibyllina Riley, 1944: 254, pl. 2, fig. 27 ♂. Holotype ♂, MENTAWAI Is.: Sipora (BMNH) [examined].

The upperside agrees with the nominate subspecies. On the underside the white fleck at the forewing apex is as reduced as in subsp. lenaia. On the hindwing the central spot in space 7 may be heavily blackened, as in the nominate subspecies, or only lightly blackened. In his original description Riley wrote that this spot is not blackened, but in seven out of the eight specimens in the type-series it is blackened to a greater or less degree. The eighth specimen, a worn male, is so rubbed that it is possible some black scales were originally present.

The subspecies seems to be only doubtfully separable from subsp. lenaia.

DISTRIBUTION. Mentawai Is.
**Allotinus (Paragerydus) substrigosus ballantinei** subsp. n.

(Fig. 76 ♂)

♂ forewing 13-5 mm. Wing shape, as in subsp. *substrigosus*, with forewing termen crenulate and apex rather pointed. Swelling of vein *M₃* inconspicuous, extending a little under one-third of its length. Underside very pale buff, rather densely striated but with postdiscal spots small or evanescent, as in some individuals of subsp. *substrigosus*. Forewing with white speck at end of vein *R₅* not extending into space 6. Hindwing with spot in mid-space 7 exceptionally large, rather quadrilateral, nearly 2-0 mm wide and extending right across space.

**Material examined**

Holotype ♂, **Philippines**: Palawan, Port Barton, ix.1983 (A. Ballantine) (BMNH).

The subspecies is named after Dr Alistair Ballantine, who caught the unique holotype and presented it to BMNH.

**Allotinus (Paragerydus) substrigosus yusukei** subsp. n.

(Figs 35 ♂ genitalia; 77 ♂)

♂ forewing 11-5 mm. Termen more rounded and apex less pointed than in foregoing subspecies. Swelling of vein *M₃* short, extending over one-quarter of vein, overlying specialised scales pale so that it stands out prominently. Underside ground colour pale buff; forewing with white fleck at end of vein *R₅* extending as an oblique white streak half-way across space 6. Hindwing with central black spot in space 7 narrow but well-defined; a small subbasal black spot in space 1a.

**Material examined**

Holotype ♂, **Philippines**: Mindanao, Tandag, Sürigao, xii.1982 (ex Takanami coll.) (BMNH).

The subspecies is named after Mr Yusuke Takanami, who generously presented the holotype and many other rare Philippine lycaenids to BMNH.

**Allotinus (Paragerydus) davidis** Eliot

(Fig. 36, ♂ genitalia)

*Allotinus davidis* Eliot, 1959: 377, pl. 10, figs 6 ♂, 7 ♀, text-fig. ♂ valva; 1978: 240; Fleming, 1975: 21, pl. 57, fig. L39 ♀. Holotype ♂, SINGAPORE (BMNH) [examined].

The wing shape is that of *A. nivalis*, with the forewing termen barely perceptibly crenulate. On the underside both sexes are reddish brown. In the male vein *M₃* of the forewing is swollen only in its basal quarter. On the underside the ground colour is pale buff; on the forewing the white fleck at the apex does not cross vein *R₅*; on the hindwing the central spot in space 7 is blackened and the postdiscal spot is also narrowly blackened on its inner edge.

In the male genitalia the valva differs from all others in the subgenus by not having the costa truncate before the terminal process, which curves upwards in the manner of subgenus *Allotinus*. In all other

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**Fig. 36** *Allotinus (Paragerydus) davidis* Eliot; Singapore. Male genitalia.
respects the genitalia are typical of *Paragerydus*, and the absence of a humeral vein on the hindwing helps to confirm its position in this subgenus.

**Distribution.** West Malaysia; Singapore; Sumatra (coll. Diehl); Peninsular Thailand (Pinratana). The species appears to be extremely rare, but is perhaps sometimes overlooked because of its small size and resemblance to *A. substrigosus*.

**Allotinus (Paragerydus) drumila** (Moore)

(Fig. 37, ♂ genitalia)

*Miletus drumila* Moore, [1866]: 777.

This large species stands rather far apart from the remainder of the subgenus in its markings and in its pronounced seasonal variation. On the other hand the male genitalia, presence on the forewing of a swollen vein $M_3$ and absence of a humeral vein on the hindwing, are characteristic of *Paragerydus*, so that it seems unnecessary to retain for it the separate subgenus *Miletographa*.

On the underside the appearance is of a *Miletus* species, with the catenulate markings characteristic of that genus; the difference is that in *A. drumila* the ground between the usual lycænid markings is speckled with small, irregular pale-edged spots. The upperside and especially the seasonally dimorphic wing shape recall the smaller, sympatric *Miletus chinensis*. The wet season form is brown, with a similar curved series of postdiscal spots on the forewing, paler brown in the male, larger and sullied white in the female. In the dry season the forewing acquires a sharp point at the apex and prominent lobe at the tornus, and the mainly white female is broadly similar to the dry season *M. chinensis longeana*. The main point of dissimilarity is that in *A. drumila* the most extreme dry form occurs in the Himalayas and Assam, whereas in *M. chinensis* the most extreme dry form occurs in Burma.

The species is Indo-Burmese, submontane and apparently not rare where it occurs, but with a restricted distribution. There are two rather doubtfully valid subspecies.

**Key to the subspecies of A. (P.) drumila**

1 ♂ dry season form white with black costal and marginal border on the forewing and blackish costal area on the hindwing ........................................... *drumila drumila* (p. 56)
   - ♂ dry season form with the white areas sullied with buff scales ................ *drumila aphthonius* (p. 57)

**Allotinus (Paragerydus) drumila drumila** (Moore)

(Fig. 37, ♂ genitalia)


[Dry season form.]

*Gerydus drumila* (Moore) Moore, 1883: 521. [Wet season form.]

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**Fig. 37** *Allotinus (Paragerydus) drumila drumila* (Moore) wet season form *multistrigatus* de Nicéville; Sikkim. Male genitalia.
Allotinus multistrigatus de Nicéville, 1886: 253. pl. 11, figs 11 θ', 2 φ; de Nicéville, 1890: 29, pl. 26, figs 157 θ', 158 φ; Bingham, 1907: 298; Swinhoe, 1910: 195, pl. 615, figs 2, 2b θ', 2a, 2c φ; Fruhstorfer, 1913: 371; 1916: 815, pl. 141h θ' φ. LECTOTYPE θ', INDIA: Sikkim (BMNH), here designated [examined] [Wet season form.] [Synonymised by Cantlie, 1963: 26.]


Allotinus drumila (Moore) de Nicéville, 1890: 28; Bingham, 1907: 297; Swinhoe, 1910: 194, pl. 615, figs 1, 1b θ', 1a, 1c φ; Fruhstorfer, 1913: 371; 1916: 815, pl. 141i θ; Evans, 1932: 211.

Miletographa drumila (Moore) Röber, 1892: 277.

Allotinus multistrigatus multistrigatus de Nicéville; Evans, 1932: 242.

Allotinus drumila drumila (Moore) with wet season form multistrigatus de Nicéville; Cantlie, 1963: 26, pl. 26, fig. H.6.2.

Moore originally described the dry season female in error as the male. Later (1883) he realised his mistake and correctly described the male from the wet season form, which de Nicéville later redescribed as a separate species, A. multistrigatus.

Judging by material in BMNH, intermediate forms, with the wing shape of the dry form drumila, fly in the autumn and winter, while drumila, with its mostly white female, is really a spring form flying from February to May (one female ex Fruhstorfer coll. is labelled June, but I feel sure this is an error, as the type-series of multistrigatus was caught in this month).

Moore's type of drumila cannot be traced, but there are two wet season males in BMNH from Darjiling and the Khasi Hills from which Moore described the male, both of which bear BMNH type-labels. But as they did not form part of the original type-series they cannot be accepted as types.

The figures accompanying de Nicéville's original description of multistrigatus were taken from examples in coll. Möller, and I designate as lectotype a male in BMNH, presumably from the original type-series, labelled /Type [red]/Sikkim Möller/Allotinus multistrigatus de Nicéville θ TYPE/Rothschild Bequest B.M. 1939-1/.

DISTRIBUTION. Kumaon, in the central Himalayas, to Assam.

Allotinus (Paragerydus) drumila apthonius Fruhstorfer


Allotinus multistrigatus apthonius [sic] Fruhstorfer; Evans, 1932: 242

Allotinus drumila apthonius [sic] Fruhstorfer; Cantlie, 1963: 26; Pinratana, 1981: 31, pl. 4, fig. 19 θ', pl. 5, figs 10 θ', 11 φ.

The subspecies is doubtfully valid, differing only in that the most extreme dry form of female has the white areas always suffiled with buff scales, as in the holotype of grisea and as in Pinratana's figure of the female. The wet season and intermediate forms do not differ from the corresponding forms of subsp. drumila.

In BMNH there are one male and two females labelled as types of apthonius. I designate as lectotype the male labelled /Type [red]/Type [Fruhstorfer orange]/Tenasserim Tandong 4000' Mai Fruhstorfer leg./Fruhstorfer Coll. B.M. 1933-1/Allotinus apthonius Frhst. [in Fruhstorfer's hand]/. Two females, similarly labelled, except that one bears a final label /Allotinus apthonius Fruh. [in Corbet's hand]/ in place of the label in Fruhstorfer's hand, are paralectotypes. The male has a pointed forewing and rather dentate hindwing, and is marked as in the wet season form. Fruhstorfer stated that it was a dry season form, but in fact it is an intermediate form nearer to the wet than to the dry season form. Of the two females, one is intermediate, as in the male, and the other of the normal wet season form.

DISTRIBUTION. Throughout Burma, except in the extreme south of Tenasserim; Thailand.

Genus LOGANIA Distant

Logania Distant, 1884: 197, 208. Type-species: Logania malayica Distant, 1884: 208, pl. 22, fig. 21 φ, by monotypy. Gender feminine.

Malais Doherty, 1889: 414, 415, 436. Type-species: Logania sriwa Distant sensu Doherty, 1889 [ = Logania marmorata Moore, 1884], by designation of Corbet, 1940a: 111. Gender feminine. [Synonymised by de Nicéville, 1890: 32.]

Eyes smooth. Antennae half the length of the forewing costa, with about 36 segments in the type-species;
shorter, with under 30 segments in *L. waltraudae*; rather longer, with 40–45 segments in the *marmorata*-group (= *Malais*). Nudum extending widely to the base of the shaft. Legs much shorter than in *Allotinus*, with the tibiae outwardly swollen and the fore-tarsi, except in *L. waltraudae*, gradually incrasate. In *L. malayica* and *L. waltraudae* the male fore-tarsus ends in a rather long, tapered, down-curved point, but in the *marmorata*-group the fore-tarsus ends abruptly in a rounded pad from which a minute point is directed downwards, as in *Allotinus*. Labial palpi shorter than in *Allotinus*, with the third segment usually shorter than one-half of the second segment in males, but may be slightly longer than half in females. Males of all species have a small double hair tuft on the sternum of the eighth abdominal segment. The type-species has the forewing apex produced to a sharp point and veins $M_1$ and $R_3$ have a long common stalk; all the remaining species have a rounded or square apex and, except in *L. nehalemia*, the stalk of veins $M_1$ and $R_3$ is absent or short. There is no trace of a humeral vein on the hindwing. Males of the *malayica*-group have vein $M_3$ of the forewing unswollen; in the *marmorata*-group the basal portion of vein $M_3$ is briefly swollen and clothed with small, specialised scales which are about the same size as those of the *nivalis*-group of *Paragerydus*. In *L. regina*, and probably also in *L. palauna*, the swelling is inconspicuous and partly hidden by normal cover scales. The underside pattern is generally similar to that of *Allotinus*, but the ground colour is seldom uniform, being mottled in shades of black, brown and white, for which reason Evans coined the popular name 'Mottles' for the genus. On the forewing the usual lycanid markings may be difficult to make out, but on the hindwing they are usually apparent and the postdiscal series may be catenulate. In some species there is very great individual variation in the extent of whitish scaling on the upperside of the hindwing, which may be absent or cover almost the whole of the wing. The male genitalia are of the usual miletine type and are rather constant in appearance, except that *L. waltraudae* shows some characters suggestive of *Allotinus*.

Doherty (1889: 414, 415) erected the generic name *Malais* and wrote that 'it will include *L. marmorata* and *L. sriwa* (probably the same species) and one or two rare kinds undescribed'. He had before him only a single female from Mergui which he treated with some doubt as the same as the taxon named *Logania sriwa* Distant, 1886. De Nicéville (1890: 33), who had custody of the type of *L. marmorata* Moore, 1884, stated that he had examined Doherty's female of 'sriwa' and found that 'it appears to differ from *L. marmorata* only by the greater prominence of all the markings of the underside'. As the females of *L. sriwa* and *L. marmorata* differ so strongly that it is inconceivable that Doherty's female was really *sriwa*, and highly probable that de Nicéville was correct in assuming that it was *L. marmorata*. I can find no convincing evidence that *L. sriwa* has ever been taken in Burma, although it was recorded by Evans (1932) and Cantlie (1963) from Mergui, probably on the basis of Doherty's misidentified female.

Soon afterwards Doherty (1891a: 29) doubted if *Malais* was distinct from *Logania*; and though he did not formally synonymise the two he thereafter used *Logania* for species which would fall naturally into *Malais*. Bingham (1907: 302), Swinhoe (1910: 200), Evans (1932: 199) and Cantlie (1963: 2) all treated *Malais* as a subjective synonym of *Logania*, as did Corbet (1940a: 111) who stated that *L. sriwa* was its type-species. However, as Doherty's 'sriwa' was misidentified, Corbet's statement cannot, under Article 70 of the *Code*, be held to constitute a valid type selection. Fruhstorfer (1914; 1915), whilst using *Logania* as the generic name, employed *Malais* in a subgeneric sense for the 'Artengruppe' with banded legs and rounded forewing apex which includes *L. marmorata* and *L. sriwa*. Hemming (1960: 11), apparently unaware of Corbet's action, designated *Logania malayica* Distant, 1884, as type-species of *Malais*. His action is invalid, since *malayica* was not one of the species originally included in *Malais* by Doherty; indeed, the latter (1889: 437) had specifically excluded *malayica* from his new genus, stressing that it was a true *Logania*. *Malais* remains, therefore, a valid and available genus-group name, which can be used as a subgenus, largely in the sense in which it was employed by Fruhstorfer, by those authors who consider that the differences between *Logania* and *Malais* are greater than those between species-groups. *Malais* is, however, still without a properly established type-species, and any author intending to use it will have to refer the matter to the International Commission on Zoological Nomenclature, as required under Article 70 of the *Code*, with a recommendation that *Logania marmorata* Moore, 1884, be designated as type-species.

The genus ranges from Peninsular India through the Archipelago to New Guinea and the Bismarcks, and comprises 10 species.

### Key to the species of *Logania*

1. **♂** underside of forewing with vein $M_3$ unswollen and clothed with normal cover scales. **♂** fore-tarsus, so far as known, ending in a tapered, down-curved point
2. **♂** underside of forewing with basal part of vein $M_3$ swollen and clothed with specialised scales. **♂** fore-tarsus ending abruptly, but with a small point directed downwards from its lower edge
3. Forewing apex not produced

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<td>1</td>
<td><strong>♂</strong> underside of forewing with vein $M_3$ unswollen and clothed with normal cover scales. <strong>♂</strong> fore-tarsus, so far as known, ending in a tapered, down-curved point</td>
<td>2</td>
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<td>2</td>
<td><strong>♂</strong> underside of forewing with basal part of vein $M_3$ swollen and clothed with specialised scales. <strong>♂</strong> fore-tarsus ending abruptly, but with a small point directed downwards from its lower edge</td>
<td>4</td>
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<tr>
<td>3</td>
<td>Forewing apex not produced</td>
<td>3</td>
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Logania malayica Distant
(Figs 38, 39, ♂ genitalia)

Logania malayica Distant, 1884: 208.

The species is instantly recognisable by the pointed and produced forewing apex. The sexes are alike, above white with a blackish forewing border expanding from less than 1-0 mm at the tornus to nearly mid-costa. Underside white densely mottled with reddish brown striae. The legs are buff-brown freckled with whitish scales, and the male fore-tarsus ends in a comparatively long, tapered, down-curved point.

The species occurs from Peninsular Thailand to Malaya, Sumatra, Borneo and the Philippines. There are two subspecies with somewhat different male genitalia.

Key to the subspecies of L. malayica
1 Underside irregularly mottled and blotchy, with some of the usual lycaenid markings apparent
- Underside regularly and densely mott. with none of the lycaenid markings apparent

Logania malayica malayica (p. 60)
- malayica malayica (p. 60)
- malayica subura (p. 60)
Logania malayica malayica Distant
(Fig. 38, ♂ genitalia)

Logania malayica Distant, 1884: 208, pl. 22, fig. 21 ♀, text-fig. 61 hind-leg. Holotype ♀, WEST MALAYSIA: Sungei Ujong (not located).

Logania malayica malayica Distant; Fruhstorfer, 1914: 23; 1916: 805. pl. 141f ♂; Corbet, 1940a: 111, fig. 1 ♂ valva; Fleming, 1975: 22, pl. 58, fig. L51 ♀; Eliot, 1978: 241, pl. 20, fig. 8 ♂.

On the underside the mottling is irregular and coalesced into blotches in places, and covers both wings except for a white area above the forewing dorsum in spaces 1a and 1b. The usual lycaenid markings can be partly made out with difficulty.

DISTRIBUTION. Peninsular Thailand; West Malaysia; Sumatra; Borneo, including Pulo Laut.

Logania malayica subura Fruhstorfer
(Fig. 39, ♂ genitalia)

Logania malayica Distant; Semper, 1889: 160, pl. 31, fig. 3 ♂.


On the underside the mottling of striae is regular and without blotches; none of the usual lycaenid markings can be made out. On the forewing the white area above the dorsum extends into space 2. The male genitalia differ more than usual in subspecies, and it may be that subura has achieved species status.

Fruhstorfer named subura from Semper's figure, so the male depicted therein is automatically the holotype.

DISTRIBUTION. Probably throughout the southern Philippines, but I have only seen examples from Mindanao and Samar.

Logania nehalemia Fruhstorfer stat. rev.
(Figs 40, ♂ genitalia; 78 ♂)

Logania nehalemia Fruhstorfer, 1914: 25; 1916: 808. Holotype ‘♀’ recte ♂, NEW GUINEA (BMNH) [examined].


Above, the forewing is white with a black border which curves in above the cell to the wing base; the hindwing has the basal half white and the outer half black. The underside is white, with dense, dark brown striae more or less corresponding with the areas which are black on the upperside.

In the unique male holotype, which has hitherto been regarded as a female, the legs are missing except
for the femur and tibia of one hindleg with the scales rubbed off; these hardly differ from the femur and tibia of *L. malayica*. The male genitalia are chiefly distinguished by the phallus, which is considerably stouter than that of its congeners except for *L. waltraudae*.

The holotype is labelled /Type [red]/New Guinea. Hewitson Coll. 79–69 Miletus 1/♀ holotype Logania nehalemia Fruhst. [in Corbet’s hand]/. Given its early date of capture, the type-locality is likely to lie in the north-western part of Irian Jaya.

**Logania waltraudae** sp. n.

(Figs 41, ♀ genitalia; 107 ♂)

♂ forewing 10.0 mm. Generally similar in appearance to the sympatric *L. malayica subura*, and like it with the basal portion of vein *M*₃ unswollen and clothed with normal cover scales; but differing in having the forewing apex rounded and veins *M*₁ and *R*₅ connate.

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**Fig. 40** *Logania nehalemia* Fruhstorfer; New Guinea. Male genitalia.

**Fig. 41** *Logania waltraudae* sp. n.; Samar. Male genitalia.
Upperside white; forewing with a blackish brown apical border running from just below vein $Cu_2$ on the termen to just above the cell apex on the costa; hindwing with a dark brown marginal hairline. Cilia dark brown. Underside pale brown very densely mottled with darker brown striae except on the forewing in most of spaces 1b and 2 and in the basal part of space 3, which are white. A dislocated series of postdiscal spots can just be made out on the forewing.

Antennae just under half the length of the forewing costa, thinner than in $L. \text{malayica}$, with probably 28–30 segments (both antennal clubs are broken off just before the tip after 26 segments). The middle shaft segments are just over twice as long as wide (in the remaining $Logania$ species these segments are nearly as wide as long). The nudum extends widely to the base of the shaft, which is brown on the upper surface with a central buff patch on each segment. The palpi are clothed with brown and a few buff adpressed scales and are exceptionally short, not protruding beyond the head, with the third segment comparatively stout and only a quarter the length of the second segment. The legs are about as long as those of $L. \text{malayica}$, which they resemble in having the fore-tarsus ending in a tapered, down-curved point; but they differ in several respects. The femora, tibiae and tarsi are subequal; the femora are broader and somewhat flattened; the foretibiae are narrow and cylindrical, and the middle tibiae are slightly swollen, the swelling being greatest in the upper half. The hind legs are missing. Body dark brown, slightly paler beneath; the abdominal hair tufts on the eighth sternum are smaller than in the other species of $Logania$. The male genitalia are broadly of $Logania$ type, but the phallus is distinctive, while the triangular vinculum flap and strut running parallel to the lower edge of the uncus plate recall those structures in $Allotinus$.

♀ unknown.

**Material examined**

Holotype ♀, **Philippines**: Samar, 18.viii.1980 (C. G. Treadaway) (coll. Treadaway, but will be deposited in due course in SM).

The species, which is named after Mrs Treadaway, occupies an isolated position in the genus, differing from the remainder in palpi, antennae, legs and male genitalia, and possibly deserves to be placed in a separate subgenus.

**Logania regina** (H. Druce)

(Fig. 42, ♀ genitalia)

*Miletus regina* H. Druce, 1873: 348.

This and subsequent species differ from the foregoing species in the male fore-tarsus, which is not tapered but ends abruptly in a rounded pad from the lower side of which a small, short point is directed downwards, as in *Allotinus*. The legs, in this and the next three species, are banded, most prominently on the tibiae, with whitish and brown, while in the remaining species they are freckled and sometimes have obscure longitudinal streaks.

A distinguishing character of $L. \text{regina}$ is the white ground colour of the underside of the hindwing, which is almost devoid of striae in a streak-like area running from the wing base to the termen through the upper part of the cell and space 6.

On the upperside the male has a fuscous border on the forewing tending to run narrowly along the costa to the wing base, and a fuscous costal area above vein 6 on the hindwing. The rest of the wings are whitish to bluish grey. The female has a narrower forewing border and the pale areas on both wings are whiter than in the male.

In the female of this species and of $L. \text{paluan}$ (infra) the abdomen is longer than in the other $Logania$ species, and extends just beyond the hindwing tornus.

The species has a restricted distribution in Sundaland, excluding Java, Palawan and the islands off the west coast of Sumatra, but has reached the Sulu Is. where it must be a recent immigrant. There are two subspecies.

**Key to the subspecies of *L. regina***

1. ♀ upperside of forewing with black border comparatively wide, filling whole of space 5. ♀ forewing border reaching dorsum; underside of forewing with a white area above dorsum usually reaching vein $M_2$ ..............................................................  
   regina regina  (p. 63)
   - ♀ upperside of forewing with black border narrower, not reaching base of space 5. ♀ forewing border fades out at, or just before, tornus; underside of forewing without a white area  
   regina sriwa  (p. 63)
Logania regina regina (H. Druce)

(Fig. 42, ♀ genitalia)

Miletus regina H. Druce, 1873: 348, pl. 32, fig. 4 ♂. Holotype ♂, BORNEO (BMNH) [examined].

Logania regina regina (H. Druce); Fruhstorfer, 1914: 23; 1916: 806.


Syn. n.

In the male most, if not all, the pale areas on the upperside are clothed with bluish grey scales. The female is much whiter, with a narrower forewing border which is usually about 1-5 mm wide at the tornus. On the underside of the forewing there is sometimes a narrow whitish area along the dorsum, the corresponding area in the female being much wider and usually extending into the basal half of space 4.

Distribution. Borneo; Sulu Is (only known from unique holotype). In BMNH there is a single male from Pulo Laut, in which the fore wing border is even narrower than in subsp. sriwa, while the pale areas are white, so that the general appearance is of a female; it probably represents a further subspecies.

Logania regina sriwa Distant

Logania sriwa Distant, 1886a: 531; 1886b: 452, pl. 44, fig. 16 ♀; Evans, 1932: 212. Holotype ♀, WEST MALAYSIA (not located).

Logania regina sriwa Distant; Fruhstorfer, 1914: 23; 1916: 805, pl. 141f ♀; Corbet, 1940a: 112, fig. 2 ♂ valva; Cantlie, 1967: 28; Fleming, 1975: 22, pl. 58, fig. L52 ♀; Eliot, 1978: 241, pl. 20, fig. 9 ♂

The male is usually whiter, with a narrower border, than nominate regina. In the female the forewing border usually fades out at or before the tornus. On the underside both sexes lack a white area above the forewing dorsum, and on the hindwing the white streak is narrower.

Distribution. West Malaysia; Sumatra; peninsular Thailand (Pinratana, 1981).

Logania paluana sp. n.

(Fig. 79 ♀)

This taxon, at present only known from two females, appears to replace L. regina, of which it may be a subspecies, in Sulawesi. It is larger, with forewing length 17-0 mm, compared with an average of 14-0 mm in regina, and differs additionally as follows. On the upperside the forewing border is narrower, ending beyond the middle of the costa. On the hindwing there is a black border measuring nearly 4-0 mm at the dorsum, expanding to 4-5 mm at vein Cu2 and thence decreasing to 1-0 mm at the apex whence it is continued as a blackish line along the costa to the wing base. The underside is generally marked as in
regina, but on the hindwing the comparatively well-defined white streak of regina is replaced by a wider and more obscure, because more heavily striated, white discal patch extending to vein Cu1 and the lower edge of the cell. The postdiscal markings are olive-brown and there is a well-defined marginal olive-brown line 0.5 mm wide on the forewing and between veins Cu2 and M2 on the hindwing.

**Material examined**

Paratype. 1 ♀, data as holotype (BMNH).

*Logania marmorata* Moore

(Fig. 43, ♂ genitalia)

*Logania marmorata* Moore, 1884: 22.

The species can be recognised by its crenulate forewing termen and banded legs, which are shorter and stouter than in any other *Logania* species. Except in the subspecies from Simeulue, both sexes always have a pale area on the forewing, which is more extensive in the female, but in the male of some subspecies it is reduced to a small discal patch. The hindwing of the male is normally brown, at least in the wet season, while that of the female bears some grey scales; but in Nias and south Sumatra the hindwing is partly grey in the male and nearly all white in the female.

The species ranges from central Burma to Vietnam and throughout Sundaland, the Lesser Sunda Is. and the Philippines into north Sulawesi. The dividing line between subspecies is difficult to draw because of the high degree of individual variation; 10 are provisionally recognised.

**Key to the subspecies of L. marmorata**

1 ♀ upper side of forewing with basal half whitish ........................................ 2
2 ♂ upper side of forewing unmarked brown ................................................ marmorata diehli (p. 66)
3 ♂ upper side of hindwing plain brown ......................................................... 3
4 ♀ upper side of hindwing partly white or grey ......................................... 11
5 ♀ upper side of forewing with some bluish grey scaling reaching wing base ............ 4
6 ♀ upper side of forewing with brown wing base .......................................... 6
7 ♀ upper side of forewing with pale area outwardly white becoming light bluish grey at wing base and in space 1a. ♀ upper side of hindwing with at least some grey scaling below vein 6 marmorata damis (p. 65)
8 ♀ upper side of forewing with white extending fully across space 1b. ♀ upper side of forewing without a whitish area beyond cell ................................................ marmorata hilaeira (p. 65)
9 ♀ upper side of forewing with white area not below mid-space 1b. ♀ upper side of forewing with a whitish area beyond cell extending from vein A1 to veins M2 or M1 dry season form of marmorata javanica (p. 67)
10 ♀ upper side of forewing without a prominent whitish area beyond the cell .......... 7
11 ♀ upper side of forewing with a broad whitish area beyond the cell stretching from vein A1 to vein M2. ♂ upper side of forewing with an ovate discal white patch about 2.5 mm wide at base of spaces 4, 3, 2 and sometimes just entering space 1b ................................ marmorata munichya (p. 66)
12 ♀ upper side of forewing with discal white patch at least 2.0 mm wide, reaching and often crossing vein Cu2. ♀ upper side of forewing with base more or less grey-scaled ................................ 8
13 ♀ upper side of forewing with discal patch about 1.25 mm wide and not below mid-space 2. ♀ upper side of forewing with base brown, bearing only a trace of grey scaling wet season form of marmorata javanica (p. 67)
14 ♀ upper side of forewing with white patch usually not below vein Cu2. Underside comparatively dark. Continental ........................................ wet season form of marmorata marmorata (p. 65)
15 ♀ upper side of forewing with white patch usually crossing vein Cu2. Underside comparatively light. Palawan ........................................ marmorata palawana (p. 67)
Logania marmorata marmorata Moore

Logania marmorata Moore, 1884: 22; 1886: 39, pl. 3, fig. 7; de Nicéville, 1890: 33, frontispiece, fig. 128 ♄ holotype; Bingham, 1907: 303; Swinhoe, 1910: 200, pl. 618, figs 1, 1a ‘♀ recte ♀; Evans, 1932: 213. Holotype ♄, BURMA: Mergui (ZSI).

[Malais sriwa (Distant) sensu Doherty, 1889: 436. Misidentification.]

Logania marmorata marmorata Moore; Fruhstorfer, 1914: 23; 1916: 806, pl. 141f ♄ ♀; Corbet, 1940a: 112; Cantlie, 1963: 29.

The subspecies occurs in two seasonal forms, at least in the northern part of its range. In the wet season both wings are brown, with a small white patch on the forewing above vein Cu1 in the male and a much larger white area which is greyish basally in the female. In the dry season the white areas of the forewing are much enlarged in both sexes, the hindwing is more or less overlaid below vein M1 with grey or whitish scales, especially in the male, and on the underside of the forewing there is no whitish area beyond the cell. Intermediate season examples may be indistinguishable from subsp. damis.

DISTRIBUTION. Burma, from Karen Hills to Mergui; Thailand; Vietnam.

Logania marmorata damis Fruhstorfer

Logania massalia damis Fruhstorfer, 1914: 24; 1916: 807. LECTOTYPE ♄, SINGAPORE (BMNH), here designated [examined].

Logania marmorata damis Fruhstorfer; Corbet, 1940a: 111; Fleming, 1975: 22, pl. 58, fig. L53 ♀; Eliot, 1978: 241, pl. 20, fig. 10 ♄.

In the wet and only seasonal form the pale areas on the forewing are whiter and more extensive than in any other subspecies except lahomius. In the male the pale area is outwardly white, inwardly rather pale bluish grey, reaches the dorsum and fills the cell; the hindwing is brown. In the female the pale area is whiter and broader, and the hindwing always bears at least some grey scales below vein M1.

I designate as lectotype of damis a male in BMNH labelled /Type [red]/Singapora II. 95/almost certainly type of Logania massalia damis Fruhst. [in Corbet's hand].

DISTRIBUTION. Peninsular Thailand; West Malaysia; Singapore; east coastal region of Sumatra.

Logania marmorata hilaeira Fruhstorfer

Logania obscura Distant & Pryer, 1887: 266. Syntypes, BORNEO: Sandakan (not located). [Secondary homonym of Logania obscura (Röber, 1886).]

Logania marmorata hilaeira Fruhstorfer, 1914: 23; 1916: 806; Corbet, 1940a: 112. LECTOTYPE ♄, SUMATRA (BMNH), here designated [examined].

Logania marmorata stenosia Fruhstorfer, 1914: 23 (nomen nudum); 1916: 806; Corbet, 1940a: 112. LECTOTYPE ♄, BORNEO (BMNH), here designated [examined]. Syn. n.

Logania marmorata obscura Distant & Pryer; Fruhstorfer, 1914: 23.

Logania massalia nada Fruhstorfer, 1914: 24; 1916: 807. LECTOTYPE ♄, SUMATRA (BMNH), here designated [examined]. [Synonymised by Corbet, 1940a: 112.]

Logania marmorata cineraria Fruhstorfer, 1916: 806; Corbet, 1940a: 112. [Replacement name for Logania obscura Distant & Pryer, 1887.] Syn. n.

Logania massalia sora Fruhstorfer, 1916: 807. LECTOTYPE ♄, BORNEO (BMNH), here designated [examined]. Syn. n.

Logania marmorata sora Fruhstorfer; Corbet, 1940a: 112.

Above, the male has a slightly wider forewing border than subsp. damis, and the base of the wing is darker with brown scales intermixed with the grey. The female generally has a darker hindwing which is often without any grey scales.

I designate as lectotype of hilaeira a male in BMNH labelled /Type [red]/CMB IV.94/Fruhstorfer Coll.

In his earlier work (1914) Fruhstorfer did not list or describe Logania marmorata stenosa, either through an oversight or lapsus calami, but he mentioned stenosa twice by comparison with his sub-spp. javanica and samosata. In 1916 he gave a brief description and type-locality, so that the name dates from 1916. I designate as lectotype of stenosa a female in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Sintang Dr. Martin H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/Marmorata stenosa Fr. [in Fruhstorfer’s hand].

I designate as lectotype of nada a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/CMB X.94/Fruhstorfer Coll. B.M. 1933-131/massalia nada Frhst. [in Fruhstorfer’s hand].

I designate as lectotype of sora a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Nord-Borneo ex coll. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/massalia sora Fr. [in Fruhstorfer’s hand].

**DISTRIBUTION.** Northern and western Sumatra at least as far south as Padang; Borneo, including Pulo Laut; Cagayan Sulu.

**Logania marmorata lahomius** (Kheil)

*Miletus lahomius* Kheil, 1884: 27, pl. 5, figs 28, 29 ♂. Syntypes, NIAS (not located).

*Logania regina lahomius* (Kheil) Fruhstorfer, 1914: 23.

*Logania lahomius* (Kheil); Fruhstorfer, 1916: 806.

*Logania marmorata lahomius* (Kheil); Corbet, 1940a: 113.

Above, both sexes are greyish white with the forewing border narrower than in the preceding subspecies. The hindwing of the male has a diffuse fuscous margin about 1.5 mm wide and the costal area is fuscous above vein M₁, but in the female the margin is vestigial or absent and there is only a little fuscous dusting below the costa.

**DISTRIBUTION.** Nias I. There is a pair in BMNH taken by Doherty at Liwa, in the extreme south-west of Sumatra, which differ only that in the female the fuscous scaling below the hindwing costa is solid as far as vein M₁; they are provisionally placed under *lahomius*.

**Logania marmorata diehli** subsp. n.

♂ upperside brown; forewing with a small, sullied, circular whitish patch 2-0 mm wide surrounding swollen portion of vein M₃ in spaces 2, 3 and 4. Underside generally pale, with postdiscal markings ill-defined; forewing without a trace of a white or paler discal area, as in the otherwise rather similar subspecies from Java.

♀ upperside entirely brown. Underside like male.

**Material examined**


Paratype. 1 ♂ (allotype), data as holotype (BMNH).

The subspecies is named in honour of the captor, Dr Edvard Diehl.

It is instructive that the two extremes of geographical variation in this species are found in the neighbouring islands of Nias and Simeulue, the former having the most extensive white markings, the latter the least; a good example of the haphazard course of evolution in small, isolated populations.

**Logania marmorata munichya** Fruhstorfer

*Logania massalia munichya* Fruhstorfer, 1914: 24; 1916: 807. LECTOTYPE ♂, JAVA (BMNH), here designated [examined].

*Logania marmorata javanica* Fruhstorfer; Corbet, 1940a: 112, partim.

In this and the remaining subspecies the males, at least in the dry season, have a brown forewing bearing a white discal patch and without grey scales at the wing base. In *munichya* the white patch is 2-5 mm wide and lies at the bases of spaces 4, 3 and 2 and just enters space 1b. The female resembles subs. *hilaeira* on the upperside but is distinctive in possessing, on the underside of the forewing, a white area 3-0–4-0 mm wide beyond the cell stretching from vein A₁ to vein M₂.
It seems likely that this subspecies and the east Javanese subsp. javanica may represent the ends of a cline, in which case Corbet's action in synonymising munichya with javanica would be justified.

I designate as lectotype of munichya a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/ Java occident. Sukabumi 2000' ex coll. Fruhstorfer/massalia munichya Frhst. [in Fruhstorfer's hand].

**Logania marmorata javanica** Fruhstorfer

*Logania marmorata javanica* Fruhstorfer, 1914: 23; 1916: 806; Corbet, 1940a: 112. LECTOTYPE ♂, JAVA (BMNH), here designated [examined].


*Logania marmorata* Moore; Piepers & Snellen, 1918: 18, pl. 20, fig. 21 ♀.

[Logania massalia] Doherty; Piepers & Snellen, 1918: 18, pl. 20, figs 22a ♂, 22b ♀. Misidentification.

The male differs from subsp. munichya in the smaller white patch on the forewing, which is 1-25 mm wide and does not descend below mid-space 2. The female differs in having the base of the forewing darker and, on the underside, in lacking the prominent white patch beyond the cell, this area being only slightly paler than the rest of the wing.

I designate as lectotype of javanica a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/ Ostjava Lawang 1897 ex coll. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/Logania javanica Frhst. [in Fruhstorfer's hand]/. Its left forewing is much discoloured, the basal two-thirds of the wing having an oily bluish sheen; the right forewing is undamaged. The figure in Piepers & Snellen (1918), showing only the left half of a male with a basally bluish forewing, was obviously made from the lectotype; Piepers said that he had himself seen no Javanese examples of *L. marmorata*. There are also in BMNH two females of the original type-series labelled /Logania javanica Frhst. [in Fruhstorfer's hand]/ which are paralectotypes.

I designate as lectotype of glypha a male in BMNH labelled /Type [red]/Ostjava Lawang 1897 ex coll. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/massalia glypha Frhst. [in Fruhstorfer's hand]/.

All the above lectotypes and paralectotypes appear to be wet season forms. There is in BMNH a series of 4 ♂, 7 ♀ from Sumbawa labelled /Sumbawa Doherty Sept '91/ which must represent the dry season form and which I provisionally place under subsp. javanica. The males have a white patch on the forewing similar to that of subsp. munichya, but the base of the wing is covered with rather dark bluish grey scales. The females also are rather similar on the upperside to that sex of subsp. munichya, but the hindwing is paler brown and may bear some grey scales, while on the underside of the forewing the whitish area beyond the cell is narrower and more sullied. There is also in BMNH a single female labelled /S. Flores xi.96. Dry s. Everett/ which, despite the label appears to be a wet season form as might be anticipated from the date of capture at the change of seasons. Above, it differs only slightly from females of subsp. javanica in having the base of the forewing browner, with only a very few overlying grey scales, while on the underside of the forewing the whitish patch beyond the cell is vestigial. Provisionally I attach it also to subsp. javanica.

**Logania marmorata palawana** Fruhstorfer

*Alloinus (Logania) distant* Staudinger, 1889: 93, pl. 1, fig. 3 ♀. Synotypes, PALAWAN (? MNHU). [Secondary homonym of Logania distant Semper, 1889.]

*Logania marmorata palawana* Fruhstorfer, 1914: 23; 1916: 806. [Replacement name for Logania distant (Staudinger, 1889).]

The male resembles subsp. munichya, but the forewing patch is a little larger and faintly bluish grey. The female is most like subsp. marmorata and hilaeira, especially on the underside, but on the upperside of the forewing the border is a little wider at the tornus.

Single females from Luzon in BMNH and Marinduque (coll. Treadaway) appear to belong to this subspecies.

**Logania marmorata samosata** Fruhstorfer


I have seen only two females and no males from Cebu. The former, which have the lower part of the hindwing lightly grey-scaled, differ additionally from subsp. palawana by a much darker underside with the forewing mostly blackish. A female from Mindoro is similar.

Fruhstorfer named the subspecies from Semper’s fig. 4, so the specimen depicted therein is automatically the holotype.

**Distribution.** Cebu; probably Mindoro.

*Logania marmorata faustina* Fruhstorfer

(Fig. 43, ♂ genitalia)

*Logania obscura* Distant & Pryer sensu Semper, 1889: 160 partim, pl. 31, fig. 5 ♀. Misidentification.]


All the females I have seen from Mindanao, Samar and Leyte have the underside of the hindwing plain blackish brown; otherwise they do not differ from subsp. *samosata*. The males resemble subsp. *palawana* on the upperside, but are readily separable by their much darker blackish undersides.

Fruhstorfer described the subspecies from Semper’s fig. 5, so the female from Mindanao depicted therein is automatically the holotype.

**Distribution.** Mindanao; Leyte; Samar (coll. Treadaway); Sulu Is.: Tawi Tawi (Tite, 1969).

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**Fig. 43** *Logania marmorata faustina* Fruhstorfer; Mindanao. Male genitalia.

*Logania obscura* (Röber)

(Fig. 44, ♂ genitalia; 80 ♂)

*Allotinus obscurus* Röber, 1886: 52, pl. 4, fig. 8 ♂. Syntypes, SUWASWEI (? SMT).

*Allotinus martinus* Fruhstorfer, 1913: 371; 1916: 814, pl. 141h ♀. Holotype ♂, SUWASWEI: BUTON I. (BMNH) [examined]. **Syn. n.**

*Logania donussa* Fruhstorfer, 1914: 24. LECTOTYPE ♀, SUWASWEI (BMNH), here designated [examined]. **Syn. n.**

*Logania distanti donussa* Fruhstorfer; Fruhstorfer, 1916: 807.


*Logania marmorata obscurus* (Röber); Corbet, 1940a: 112.

In the past *L. obscura* has been thought to replace *L. marmorata* in Sulawesi and its satellite islands, and it was treated as a subspecies thereof by Corbet. However, the very recent discovery of *L. marmorata* in north Sulawesi in a still undescribed subspecies indicates that *L. obscura* is a distinct species. Its status as such is further confirmed by the following characters. The female is all brown, whereas the male has a white forewing patch – a reversal of the usual sexual differences in *Logania marmorata* wherein the female has
more extensive white areas than the male (except in Simeuluē). The forewing termen and apex are more rounded and the crenulations are weaker. The legs are longer and thinner. The wing span is considerably larger. Finally, there is a small difference in the male valva.

The holotype of *martinus* has no head, legs nor right forewing. It bears a label /damaged in shelter by burst pipe, G.E.T./. The remaining wings show no significant difference to normal *L. obscura*.

I designate as lectotype of *donussa* a female in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/S. Celebes Bua-Kraeng 5000' Febr. 1896 H. Fruhstorfer/Fruhstorfer Coll. B.M. 1933-131/Logania donussa Fr. [in Fruhstorfer's hand]/.

A single male from Banggai I. in coll. Bedford Russell (Fig. 80) has the forewing patch suffused all over with fuscos scales, so that it hardly shows up, and the underside is darker and more densely striated than in typical examples. A male from the Toekan Besi 1s. in BMNH resembles the Banggai male on the upperside, but on the underside is paler than typical examples. These two males probably represent further minor subspecies.

**DISTRIBUTION.** Sulawesi.

*Logania distanti* Semper

(Figs 45, 46, ♂ genitalia; 81 ♂)

*Logania distanti* Semper, 1889: 161.

In this species I combine the subspecies which have hitherto been treated as pertaining to two distinct species, *L. distanti* and *L. massalia*. Fruhstorfer, and also Corbet in part, confused the *massalia* subspecies-group with *L. marmorata*, but the two species are easily distinguished by several characters. Firstly, in *L. distanti* the legs are longer, thinner and not banded, but speckled and streaked with brown on a whitish ground. Secondly, the forewing termen is barely crenulate. Thirdly, the underside is more ochreous and the striations are usually denser. In the male genitalia the phallus is much less strongly bent.

The male is brown above, normally with a whitish or bluish grey discal patch on the forewing, but in the Philippines and Malay Peninsula (and probably elsewhere) the upperside is sometimes unmarked. On the forewing vein *M₂* is briefly swollen and clothed with specialised scales. Females show very great individual variation, the forewing white or very pale greyish blue with a broad blackish border, while the hindwing, except in subsp. *staudingeri*, varies from brown to mainly whitish in any one area.

The species flies from India to the Malay Peninsula, Sumatra, Borneo and the Philippines. It is apparently absent from the islands off the west coast of Sumatra and from Java, records of *L. massalia* from the latter island applying to misidentified *L. marmorata*.

**Key to the subspecies of *L. distanti***

1 ♂ with upperside of forewing brown to brownish at base. ♀ with upperside of hindwing variable, but in the most lightly marked examples always with a fuscous border 1-0-2-0 mm wide ...
- **♂** upperside of forewing with pale bluish grey area reaching wing base. ♀ upperside of hindwing all white except for sparse fuscous dusting above vein M, .............. **distanti staudingeri** (p. 72)

2. **♂** upperside of forewing with discal patch, if present, pale bluish grey ......................... 3

- **♂** upperside of forewing with discal patch, if present, white .............. **distanti massalia** (p. 70)
- Philippine ................................................................. **distanti distanti** (p. 70)
- Bornean ................................................................. **distanti drucei** (p. 71)

**Logania distanti distanti** Semper

(Fig. 81 ♂)

*Logania distanti* Semper, 1889: 161, pl. 31, figs 6, 7 ♂, 21 ♀. Holotype ♀, PHILIPPINES: Cebu (SM) [examined].

*Logania distanti distanti* Semper; Fruhstorfer, 1914: 24; 1916: 807.

*Logania distanti apsines* Fruhstorfer, 1914: 24; 1916: 807. LECTOTYPE ♂, PHILIPPINES: Mindanao (SM), here designated [examined].

*Logania turdeta* Fruhstorfer, 1916: 807. Holotype '♂' recte ♀, PHILIPPINES: Cebu (SM) [examined].

**Syn.**

Semper originally described *L. distanti* from three examples: a male and female of large size from Mindanao, which he figured at figs 21 and 7 respectively, and a small female from Cebu figured at fig. 6. Although he labelled the male as type he unfortunately did not specify it as such, and this left the way open for Fruhstorfer later to restrict nominate *distanti* to Cebu and to name the Mindanao pair as subsp. *apsines*. Semper’s female from Cebu is, therefore, automatically the holotype of *distanti*.

Fruhstorfer’s action, taken at a time when it is evident that he had not even seen Semper’s specimens, is doubly regrettable, since a year later, after examining Semper’s collection, he named the Cebu female, which he then inexplicably mistook for a male, as a new species, *L. turdeta*, and remarked that Semper had confused it with *L. distanti*. At the same time he still recorded nominate *distanti* from Cebu and maintained *apsines* for Mindanao examples. Semper’s original female from Cebu, which is the holotype of both *distanti* and *turdeta*, is labelled /CEBU/Coll. C. Semper/206/1004/No 6/Typus [and on reverse] Logania turdeta (Fruh.). The small ticket reading ‘No 6’ obviously refers to Semper’s fig. 6. The specimen has extensive whitish dusting on the upperside of the hindwing and agrees fairly well with the butterfly figured by de Nicéville (1894: pl. 2, fig. 13) as *Logania luca*.

Semper’s pair from Mindanao may or may not be a valid subspecies; but as size, by which alone Fruhstorfer separated them as subsp. *apsines*, is an unreliable character. I treat *apsines* provisionally as a synonym of *distanti*. Fruhstorfer did not designate a type, so I now designate the male as lectotype; it is labelled /Log. Distanti typ. Semper/206/1004/16/Typus [red]/. The small ticket reading ‘16’ should refer to the figure in Semper’s pl. 31; but in fact the specimen is shown at fig. 21, while fig. 16 represents *Paragerythus punctatus*. Possibly the labels got transferred by mistake, as in other cases already mentioned (p. 37) during Fruhstorfer’s examination of the collection. Above, the specimen is unmarked brown, but as it is the only Mindanao male I have seen it would be premature to assume that an all-brown forewing is an unvarying character of the male in that island.

I have seen no males from Cebu, but have examined single males from Luzon and Negros kindly sent me by Dr Alistair Ballantine and Mr Yusuke Takanami respectively, both of which have been deposited in BMNH. The former is as large as the lectotype of *apsines*, but has a small diffuse bluish grey discal patch on the forewing. The latter is smaller, and has a more extensive bluish grey area which nearly reaches the base of the forewing. Judging by the three males I have seen I expect that it will be found that throughout the Philippines males most often have a pale discal patch on the forewing, but that unmarked males may occur anywhere from time to time, just as they do in the Malay Peninsula.

Apart from the two females in Semper’s type-series the only females I have seen are two from Samar in coll. Treadaway. Both have some grey dusting on the upperside of the hindwing, but in neither example is it as extensive as in the holotype of *distanti/turdeta*.

**DISTRIBUTION.** Probably throughout the Philippines, where it appears to be everywhere rare. Examples seen from Luzon, Negros, Cebu, Samar and Mindanao.

**Logania distanti massalia** Doherty stat. n.

(Fig. 45, ♂ genitalia)

*Logania massalia* Doherty, 1891b: 37 ‘♂’ recte ♂; Bingham, 1907: 304; Swinhoe, 1910: 202, pl. 618. figs 3, 3b ♂, 3a, 3c ‘♀’ recte ♂; Evans, 1932: 213. Holotype ♂, INDIA: Assam (BMNH) [examined].
Logania luca de Nicéville, 1894: 28, pl. 2, fig. 13 ♀; Evans, 1932: 213. 4 ♀ syntypes, Sumatra and West Malaysia (probably ZSI). Syn. n.

Logania luca luca de Nicéville; Fruhstorfer, 1914: 24; 1916: 806.

Logania massalia massalia Doherty; Fruhstorfer, 1914: 24; 1916: 807, pl. 141f ♀; Corbet, 1940a: 112.

Logania massalia luca de Nicéville; Corbet, 1940a: 112; Fleming, 1975: 22, pl. 58, fig. L54 ♀ ♂; Eliot, 1978: 241, pl. 20, fig. 10 ♂.

Usually the male has a circular white discal patch more or less dusted with grey scales on the forewing, but very occasionally the patch extends to the wing base where it is heavily dusted with bluish grey and fuscous scales, as in single males in BMNH from south India and Burma and in a male from the Malay Peninsula in coll. Fleming. Sometimes the white patch is wanting or vestigial, most often in examples from the Malay Peninsula. The hindwing is blackish brown.

Females show much individual variation, and cannot be reliably separated from that sex of the nominate subspecies. The hindwing may be unmarked blackish brown, but nearly always there is at least some grey scaling. De Nicéville described and figured as *L. luca* females from Perak and Sumatra in which the hindwing was more than half whitish, and even more extreme examples with paler undersides occur in Sumatra and in Assam and Burma during the dry season.

In BMNH there is a female labelled /Type [red]/Perak Jan.-Feb. '90 W. Doherty/Elwes Coll. 1915-207/ L. malais Doh. so named in Elwes Coll./Perak 2c Malais sp. undescribed ♀/Probably not a type but agrees exactly with fig. of luca Nic. in orig. desc. [in Corbet's hand]/. In fact this female, which may conceivably be one of de Nicéville's four female syntypes, does not agree closely with de Nicéville's figure, since the hindwing has hardly any whitish scaling.

**DISTRIBUTION.** South India (♂, Thantipandal, 60 m. NNW. of Madras); Nepal; north-east India (Sikkim to Manipur); Burma; peninsular Thailand; West Malaysia; Sumatra.

Logania distanti drucei Moulton

*Logania drucei* Moulton, 1911: 85, fig. 9 ♂; Fruhstorfer, 1914: 24; 1916: 807. Holotype ♂, BORNEO: Sarawak (BMNH) [examined].

*Logania massalia drucei* Moulton; Corbet, 1940a: 112.

Probably inseparable from subsp. *distanti*, but as I have seen few specimens of either subspecies I maintain it provisionally as distinct.

The only males I have seen have a circular bluish grey discal patch on the forewing and the females have a brown or very nearly plain brown hindwing. I have seen no females similar to the figure of *luca*.

**DISTRIBUTION.** Borneo, excluding Mt Kina Balu where it is replaced by subsp. *staudingeri*.
Logania distanti staudingeri H. H. Druce

(Fig. 46, ♂ genitalia)


Logania luca staudingeri Druce; Fruhstorfer, 1914: 24; 1916: 806.

Logania marmorata staudingeri H. H. Druce; Corbet, 1940a: 112.

The male differs from subsp. drucei in that the bluish grey patch extends to the base and dorsum of the forewing. The female is very pale bluish grey, with the usual blackish apical and marginal border, while the hindwing may be unmarked except for some fuscous scaling above vein $M_1$ and a marginal blackish hairline, or there may be a diffuse border up to 1-0 mm wide.

Distribution. Only known from Mt Kina Balu.

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Logania hampsoni Fruhstorfer

(Fig. 47 ♂ genitalia)

Logania hampsoni Fruhstorfer, 1914: 25 ‘♂’ recte ♀; 1916: 807. LECTOTYPE ♀, NEW GUINEA (BMNH), here designated [examined].


Logania hampsoni masana Fruhstorfer; D’Abrera, 1971: 384, figs ♂ ♀.


The species replaces L. distanti to the east of Weber’s Line and is rather doubtfully distinct. It differs chiefly in the browner underside markings and striae, which lack the characteristic ochreous tone of distanti. Individual variation, so conspicuous a feature of L. distanti, is virtually non-existent. The male is plain brown above, and the female has a white forewing with a broad brown marginal and apical border and a brown hindwing.

Fruhstorfer described L. hampsoni from the female, which he mistook for the male, and gave as type-locality Kumusi River in Papua New Guinea. As there were no specimens in his collection he must have described the species from memory of a series of females from that locality which he had seen in coll. Rothschild. I therefore designate as lectotype a female in BMNH labelled /Lectotype [purple]/Kumusi R. N. E. Brit. N. Guin. low elev. VIII-IX.07 (A. S. Meek)/Rothschild Bequest B.M. 1939-1/Lectotype L. hampsoni Fruhstorfer ‘♂’ recte ♀, designated by J. N. Eliot Nov. 1983/.

Fruhstorfer’s error over the sex of L. hampsoni was, no doubt, responsible for the mis-statement by
D'Abrera (1971) that the male of *L. hampsoni hampsoni* has a white basal area on the forewing, but can hardly explain his further mis-statement that the type-locality was north-western West Irian.

I designate as lectotype of *M. meeki* a male in BMNH labelled /Type [red]/Dampier Isl. Feb. & March 1914 (Meek’s Expedition)/Malais meeki Type Rothsch./.

**Distribution.** New Guinea, including Dampier I.; New Britain; North Moluccas: Obi I.

*Logania watsoniana* de Nicéville sp. rev.

(Fig. 48 ♂ genitalia)

*Logania watsoniana* de Nicéville, 1898: 143, pl. Z, figs 17 ♂, 18 ♀; Bingham, 1907: 303; Swinhoe, 1910: 201, pl. 618, figs 2, 2b ♂, 2a, 2c ♀ [intermediate form]; Fruhstorfer, 1914: 23. Syntypes, Burma: North Shan States (probably ZSI). [Dry season form.]


*Logania marmorata watsoniana* de Nicéville; Fruhstorfer, 1916: 806; Corbet, 1940a: 112; Cantlie, 1963: 29.

*Logania watsoniana watsoniana* de Nicéville; Evans, 1932: 213.

*Logania watsoniana subfasciata* Tytler; Evans, 1932: 213.

Structurally *L. watsoniana* is closer to *L. distantii* than to *L. marmorata*, with which, probably because of its crenulate forewing, it has sometimes been confused. It can easily be separated from the latter by its legs, which are even longer than those of *L. distantii* and are buff-brown streaked and speckled with whitish.
In the wet season form, *subfasciata*, the male is blackish with a small bluish grey discal patch in spaces 3 and 4 of the forewing, just extending into the upper part of space 2 and the base of space 5. The hindwing may have a few grey scales. The female has a more extensive pale patch, outwardly white and inwardly dark bluish grey, which may extend to the wing base and has its outer edge right-angled at vein $M_3$. The underside is much like that of *L. marmorata*.

In the dry season form, *watsoniana*, the pale patch on the forewing of the male extends to the wing base and is outwardly white and angled on its outer edge, and the hindwing is dusted with grey below vein $M_1$. In the female the pale areas are more extensive and mostly white, and on the underside of the forewing there is a large white area beyond and below the cell.

**Distribution.** Manipur; Burma as far south as Tavoy; Thailand.

**Genus LONTALIUS gen. n.**

Type-species: *Lontalius eltus* sp. n. Gender masculine. The generic name is an anagram of *Allotinus*.

The genus is described from single females from Pulo Laut and Samar.

Eyes glabrous. Antennae similar to those of *Paragerydus*, with slender shaft and gradually incrassate club; segments number about 55; nudum tapering almost to base of shaft. Labial palpi comparatively short, resembling those of *Logania* rather than *Allotinus*, with third segment barely longer than one-quarter of second segment. Legs (Fig. 49) unlike those of other miletine genera, about as long as those of *Allotinus*, generally thin, but with tibiae slightly swollen; long first segment of fore-tarsus arched, clothed with long hairs in place of normal scales, while the scales on remaining tarsal segments much longer than those on femur and tibia but in other respects of normal type. Wings crenulate, with a particularly long tooth on forewing at end of vein $M_3$. Venation (Fig. 49) especially distinguished by a strong humeral vein on hindwing which reaches a little over half-way across base of space 8. The single species is moderately large, brown on the upperside and marked on the underside much as in *Allotinus* (*Fabitarus*) *fabius*.

This monotypic genus appears to fall between *Allotinus* and *Logania*, having the antennae, pattern and size of the former, while the crenulate wings and short labial palpi are characteristic of the latter, but it differs from both in the peculiar fore-tarsi and strong humeral vein.

**Fig. 49** *Lontalius eltus treadawayi* subsp. n., ♀; Samar. Left, venation, indicating system of veins and spaces used in the text; centre, mid-leg; right, fore-leg.
Lontalius eltus sp. n.
(Figs 49, venation and legs; 82 ♀; 108 ♂)

The characters are those of the genus. The female sex only is known.

**Key to the subspecies of L. eltus**

1 Upperside reddish brown. Underside with normal lycaenid markings present and partly catenulate on hindwing ........................................... **eltus eltus** (p. 75)

- Upperside dull brown without reddish tinge. Underside with lycaenid markings barely developed ........................................... **eltus treadawayi** (p. 75)

**Lontalius eltus eltus** subsp. n.
(Fig. 82 ♀)

♀ forewing length 20·0 mm. Upperside reddish brown; cilia pale buff but dark brown at vein endings, broadly so on forewing and narrowly so on hindwing. Underside greyish white, freckled with chocolate-brown specks and striae which are more or less coalesced to give lycaenid-type markings. On forewing these comprise a series of broad postdiscal spots in spaces 4, 5 and 6, a broad cell-end bar and two spots in cell; on hindwing a complete postdiscal series of which the spots in spaces 2, 3 and 4 are inwardly darker-edged and catenulate, as well as a large spot mid-space 7 and a smaller spot in inner half of space 1b. Cilia as on upperside.

Venation differs from that shown in Fig. 49 – on the forewing veins $Cu_1$ and $M_3$ are connate, on the hindwing the humeral vein is straight, while the forewing termen is more strongly dentate at vein $Cu_2$.

Antennae with 55 segments; ringed on dorsal side of shaft with dark brown and whitish; club whitish in basal third, remainder dark brown except for unscaled tip; nudum reddish brown tapering gradually to within four segments of base of shaft. Labial palpi freckled with adpressed dark brown and whitish scales. Legs uniformly pale buff. Body brown above and buff below.

**Material examined**

Holotype ♀, **Borneo**: Pulo Laut, vi.1891 (W. Doherty) (BMNH).

Unique. The specimen is labelled /Type [red]/Pulo Laut Borneo June 1891 Doherty/Borneo Allotinus n. sp. ♀/Elwes coll. 1915-207/Sp. inc. so named in Elwes coll./Body loose and fixed 7.v.1948. A.S.C./Allotinus eltus Cbt. ♀ H.T./. Shortly after affixing the last two labels Corbet died, and the name eltus was not published.

**Lontalius eltus treadawayi** subsp. n.
(Figs 49, venation and legs; 108 ♂)

♀ forewing length 19·5 mm. Upperside dark brown without a reddish tinge. Cilia mainly worn away, but appear to be similar to those of subsp. eltus. Underside greyish white freckled with brown as in subsp. eltus, but lycaenid markings not apparent, the specks being only slightly denser to give an indication of postdiscal spots in spaces 4, 5 and 6 on forewing and on hindwing in spaces 6 and 7 as well as a suggestion of a spot in basal half of space 7.

**Material examined**

Holotype ♀, **Philippines**: central Samar, Bagacay, 900 ft, 11.viii.1979 (G. C. Treadaway) (coll. Treadaway). Regrettably the specimen is worn and in tattered condition, with the antennae broken after 38 segments and one middle leg and both hind legs missing.

**Genus MILETUS** Hübner


*Gerydus* Boisduval, 1836: pl. 23, fig. 2. Type-species: *Papilio symethus* Cramer, 1779, by original designation.

The genus is instantly recognisable by three external characters. The first segment of the tarsi is long, flattened and blade-like. There is no humeral vein on the hindwing. The pattern on the underside comprises normal catenulate lycaenid markings on a ground which is not striated or freckled. The male genitalia are typical of the tribe, with the arms of the juxta particularly strongly conjoined above the phallus. The twin abdominal hair tufts on the sternum of the eighth abdominal segment are usually permanently extruded.

The genus is distributed from India to south China and through the Malay Archipelago and Philippines to New Guinea. It was revised by Eliot (1961), and I have no reason to alter the arrangement proposed therein with the exception of a few amendments detailed below. However, as there are now a few additional species, I have thought it best to include herein a fresh key to the species. Opportunity has been taken to figure the new species as well as a few previously unfigured taxa, viz. M. nymphis eneus (Fig. 85, ♂), M. cellarius (Figs 86, ♂, 87, ♀), M. heracleion (Figs 94, 96, ♂, 95 ♀), M. mallus mallus (Fig. 83, ♂) and M. celinus (Fig. 104, ♂).

Key to the species of Miletus

1. ♂ valva with distal half not tapering distad, dorsal edge not narrowly folded inwards. ♂ forewing vein M₃ unwollen or basally swollen and clothed with specialised scales ........................................... 2
   - ♂ valva more or less tapering distad, dorsal edge narrowly folded inwards (Fig. 50D). ♂ forewing with vein M₃ always swollen and clothed with specialised scales (symethus-group) ........................................................................ 14
2. ♂ distal third of valva not trough-shaped. ♂ forewing vein M₃ swollen or unwollen .................................. 3
   - ♂ distal third of valva more or less rectangular, with edges curved inwards to form a U-shaped trough (Fig. 50C). ♂ forewing vein M₃ swollen (boisduvali-group) ................................................................. 11
3. ♂ distal third of valva subspatulate, with dorsal margin less convex than ventral margin, and with a terminal hook at apex (Fig. 50A) (chinensis-group) ................................................................. 4
   - ♂ distal third of valva spatulate, with terminal hook very small and in centre line (Fig. 50B) (zinckenii-group) ........................................................................... 8
4. ♂ forewing vein M₃ not or only weakly swollen, partly covered with normal scales .................................. 5
   - ♂ forewing vein M₃ strongly swollen and clothed with specialised scales ..................................... M. chinensis
5. ♂ ♀ upperside of forewing with white to whitish markings, which may be heavily sullied in wet season forms, comprising a patch beyond end-cell and smaller and usually separate spots in spaces 2 and 1b. ♂ forewing vein M₃ not swollen .................................................. 6
   - ♂ ♀ upperside of forewing not so marked. ♂ forewing vein M₃ weakly swollen or unwollen .... 7
6. Larger, forewing 20–24 mm. Underside of hindwing rather dark, variegated brown, usually becoming more or less blackish on disc, with reddish brown markings. Underside of forewing without a whitish streak above dorsum ................................................. M. croton
   - Smaller, forewing 14–22 mm. Underside of hindwing greyish to buff-brown, with markings only slightly more reddish than ground colour. Underside of forewing with a more or less developed whitish streak above dorsum ........................................... M. mallus
7. ♂ ♀ upperside of forewing with a continuous and more or less even white band M. nymphis
   - ♂ ♀ upperside of forewing usually unmarked brown, but markings similar to those of M. croton and M. mallus are occasionally faintly discernible (Fig. 84), most often in ♀ M. gaesa

Fig. 50  Valvae of species-groups of Miletus. A, M. chinensis C. Felder; B, M. zinckenii C. & R. Felder; C, M. boisduvali Moore; D, M. symethus (Cramer).
8  ♂ vein M₃ strongly swollen and clothed with specialised scales ........................................... 9
   ♂ vein M₃ unswollen and clothed with normal scales .............................................................. 10
9  ♂ ♀ upperside of forewing with white band outwardly more or less straight and oblique from
   vein A₁ to vein M₃, thence curved basad. ♀ hindwing strongly produced at vein M₃
   \hspace{1cm} M. gopara
   - ♂ ♀ upperside of forewing with white band outwardly angled at vein Cu₁, below which it is at
     right angles to dorsum. ♀ hindwing normal, barely toothed at vein M₃ .................. M. zinckenii
10  ♂ ♀ upperside of hindwing unicolorous brown .......................................................... M. valeus
   - ♂ ♀ upperside of hindwing mostly white .......................................................... M. boisduvali
11  ♂ upperside of forewing with white or whitish markings, except in smoky brown M. gaetulus
    sometimes .......................................................... M. drucei
   - ♂ ♀ upperside of forewing brown with a sephia tinge and unmarked .................. M. biggsii
   - ♂ ♀ upperside of forewing with white band not extending basad of outer quarter of cell .... 13
   - ♂ ♀ upperside of forewing with broad white band filling outer half of cell.
   \hspace{1cm} Underside markings very clearly defined (Figs 86, 87) .................. M. cellarius
12  ♂ ♀ variable; on upperside of forewing white markings may be absent, or form a diffuse
    whitish spot beyond end-cell in spaces 3–5, or may be clear white and extend into spaces 2
    and 1b commencing at base of space 2.
   - ♀ usually with a more or less circular white patch beyond end-cell, but a white band similar
     to that of well-marked males may be present. Philippines and North Borneo
     \hspace{1cm} M. drucei
   - ♂ ♀ less variable; white markings, at their most extensive, do not reach base of space 2
     \hspace{1cm} M. biggsii
13  ♂ ♀ outer half of valva tapering more or less evenly and ending in a blunt point or narrowly
    truncate (Figs 50D, 51) .......................................................... 15
   - ♂ ♀ outer half of valva tapering unevenly, apex broadly truncate or broadly rounded (Figs 52,
     53) .................................................................. 16
14  Underside of hindwing with postdiscal markings in spaces 4 and 5 equidistant from end-cell
    and termen, or very nearly so .......................................................... 18
   - Underside of hindwing with postdiscal markings in spaces 4 and 5 much closer to termen
     than end-cell .......................................................... 19
15  Forewing apex without a protruding point .................................................................. 20
   - Forewing apex produced to a short point, termen concave in space 6 (Figs 102, 103)
     \hspace{1cm} M. takanami
16  Upperside of hindwing with discocellular veins not darkened, without bluish grey scaling ...... 21
   - Upperside of hindwing with discocellular veins more or less darkened, with bluish grey scaling
     (except in some Philippine subspecies) (Figs 88–91) .................................. M. symethus
17  Upperside forewing base and all hindwing brown (but hindwing may be sullied with white
    scales in dry season M. ancon) .................................................................. 22
   - Upperside forewing base white and hindwing almost all pure white .......................... 23
18  Upperside of forewing with white band (if present) constricted and may be completely divided
    below basal half of vein Cu₁ .......................................................... 24
   - Upperside of forewing with white band not constricted below vein Cu₁ ............ 25
   - Upperside more reddish brown. Forewing with white markings much reduced (absent in ♂
     of nominate subspecies), with lower part of band widely separated from upper part, in space 2
     at most a round white spot .................................................................... M. archilochus
19  Underside of hindwing with markings in cell and spaces 3 and 4 darker than other markings.
    Smaller, forewing 17–18 mm .................................................................. M. gallus
   - Underside of hindwing with all markings of more or less same intensity. Larger, forewing 19–23
     mm .................................................................. M. heracleion
20  Underside of forewing with a black discal area which more or less completely blacks out cell
    markings .................................................................. M. gigantes
   - Underside of forewing with cell markings not blacked out ....................................... M. atimonicus
21  Forewing termen and apex normal .................................................................. M. leos
   - Forewing apex produced to a short point, termen strongly convex (Fig. 104) ........ M. celinus
22  ♂ valva with apex broadly truncate, slightly concave (Fig. 52) .................................... M. melanion
   - ♂ valva with apex broadly rounded (Fig. 53) .......................................................... M. bazilanus
Miletus mallus (Fruhstorfer)
(Fig. 83 ♂)

Gerydus croton mallus Fruhstorfer, 1913: 310.

In my original analysis of Miletus (Eliot, 1961) I treated M. mallus as a good species, but later (1967: 72) I suggested that it was conspecific with, and a subspecies of, M. gaesa. At the same time I erroneously recorded a montane form or microsubspecies of M. gaesa (Fig. 84) from the mountains of the Malay Peninsula as M. gaesa mallus. I now consider that M. mallus and M. gaesa should be treated as distinct allopatric species.

Until recently I was only able to examine four specimens of M. mallus from Vietnam, namely the male holotype of mallus from south Annam, which was taken in the dry season, and the male holotype and two females of gethusus, which were taken in Tonkin in the wet season. I presumed, mistakenly, that these represented seasonal forms of a single taxon. I have now been able to examine a series of mallus taken by Bedford Russell at Dalat in south Vietnam during the wet season. The males differ hardly at all from the holotype of mallus, but differ from gethusus in several particulars, notably in having quite well-developed whitish postdiscal markings on the upperside of the forewing and a blackish area in and beneath the cell on the underside. In consequence I consider that gethusus should be reinstated as a valid subspecies of M. mallus flying in north Vietnam.

Miletus symethus (Cramer)
(Figs 88 ♂; 89, 90 ♂; 91 ♀)

Papilio symethus Cramer, 1779: 84.

In my analysis (1961) I suggested that the dark subspecies philopator from Mindoro probably occurred in Luzon and other Philippine islands. I have now seen females from Luzon and both sexes from Marinduque, which bear little resemblance to philopator and constitute a new subspecies.

Miletus symethus phantus subsp. n.
(Fig. 88 ♂)

♂ broadly similar to subsp. edonus from Palawan, from which it differs by the reduction of the greyish blue scaling on the hindwing, so that the lower half of the wing looks greyish brown.

♀ differs from subsp. edonus in the same way as the male, namely in the considerably browner hindwing, which usually has a white streak in the basal three-quarters of spaces 4 and 5 and in the extreme end of the cell.

The subspecies approaches subsp. hierophantes (Fig. 89) from the Sulu Is and, in a form with a much darker underside (Figs 90, 91), from Mindanao, in which the usual bluish grey scaling on the hindwing is entirely absent, so that the non-white area of the wing is dark brown.

Material examined

Paratypes. Philippines: 1 ♀ (allotype), Marinduque, vii.1979 (ex coll. Takanami) (BMNH); 1 ♀, data as holotype (coll. Treadaway).
Excluded from type-series. Philippines: 2 ♀, Luzon, Bicol National Park, 28–29.viii.1980 (Y. Takanami) (BMNH). These differ from Marinduque females by a larger white area on the underside of the forewing; in addition, in one example (Fig. 88) the white streak on the hindwing is obsolescent.

Miletus ? symethus solitarius Okubo


I have not seen the unique holotype from Tioman, an island some 30 miles off the east coast of the Malay Peninsula. Okubo’s figures show a butterfly in which the white markings on the forewing comprise a triangular patch beyond the end of the cell which is separated by a broad dark bar from a smaller, elongated
spot in space 2, a larger more or less contiguous spot in space 1b and a narrow white streak in space 1a above the centre of the dorsum. I do not think it can be a subspecies of *M. ancon* since it possesses several discordant characters. It is smaller than any *ancon* I have seen, the forewing length being only 18.0 mm; the base of the forewing and all the hindwing below vein *M*₁ are paler; the discocellular veins of the hindwing are darkened; and on the underside of the forewing the markings in the cell are not blacked out. In fact, the butterfly accords much better with *M. symethus* than with any other species, and broadly resembles a frequent male variety of the nominate subspecies in Java, in which the white markings are similarly reduced.

The only two males of *M. symethus* from Tioman which I have examined differ from subsp. *petronius* from the nearby mainland in having the basal area of the forewing darker and more extensive, so that the white markings are reduced though not divided. On these grounds the local Tioman race appears to be a good subspecies. I suspect that the holotype of *solitarius* is just a variety of this race, in which the tendency for a darker and enlarged basal area is much increased. I therefore treat the name *solitarius* conditionally as that of the *symethus* subspecies flying in Tioman 1.

**Miletus archilochus siamensis** (Godfrey)

*Gerydus ancon siamensis* Godfrey, 1916: 134. Holotype ♀, THAILAND: east (BMNH) [examined].

*Miletus archilochus* (Fruhstorfer); Lewis, 1974: pl. 178, fig. 29 ♂.

In my analysis of 1961 I retained *siamensis* as a subspecies of *M. ancon*, as I thought that the two taxa were allopatric. Since then I have seen examples of nominate *ancon* from throughout Thailand apparently flying sympatrically with *siamensis*. So wide an overlap argues against conspecificity, and I now think that *siamensis* must be a subspecies of the sibling species *M. archilochus*. In *siamensis* the rather sullied white markings on the forewing decrease in extent from west to east. These markings are absent in the male of nominate *archilochus* and present, but obscure, in the female. I have seen no examples from the territory between Thailand and Tonkin (type-locality of *archilochus*), and I anticipate that these will prove to be intermediate and show that variation is clinal.

**Miletus gigantes** (de Nicéville)

*Gerydus gigantes* de Nicéville, 1894: 23.

In my analysis (1961) I considered this species to be a subspecies of *M. ancon* because of the absence of any known overlap in their distribution. Later (1978: 237) I restored *gigantes* to specific status. The phenotype, with the upperside mainly white, differs greatly from that of *M. ancon* and, in addition, there is an apparently constant difference in the male genitalia. In continental and Bornean *ancon* there is only a single spine-like cornutus in the phallos, whereas in *gigantes* there are two spines as in most other species of the genus.

**Miletus atimonicus** Murayama & Okamura stat. n.

(Figs 51, ♂ genitalia; 92 ♂; 93 ♀)


Hitherto only known from the female holotype, which the authors mistook for a male of a *M. symethus* subspecies. Recently I have been sent a male from Negros and a female from Luzon by Mr Yusuke Takesami. Both sexes bear a superficial resemblance on both surfaces to *M. gaetulius* (de Nicéville, 1894), and on the upperside to *M. gigantes*. In the male the basal third of vein *M*₂ of the forewing is swollen and clothed with specialised scales; this character immediately separates it from *M. gaetulius* wherein it is absent. It also differs from the latter on the underside by a browner ground colour and more reduced markings in the forewing cell. The underside is not at all like that of *M. gigantes*, lacking the prominent blackish discal areas found on the forewing of that species.

The male genitalia indicate that *M. atimonicus* belongs to the *symethus*-group. However, the valva is truncate just before the apex and shows a slight approach to the valva of *M. melanion*. The phallus, with a single spine-like cornutus, recalls that organ in *M. ancon*.
**Fig. 51** Miletus atimonicus Murayama & Okamura; Negros. Male genitalia.

**Miletus heracleion** (Doherty)

(Figs 94, 96 ♂; 95 ♀)

*Gerydus heracleion* Doherty, 1891b: 36.

This species has not been recorded from Sumatra, but there is in BMNH a male (West Sumatra, Lebong Tandai, March 1923, C. J. Brooks) which is somewhat larger but otherwise hardly differs from the nominate subspecies. There is also a male from Sarawak (Bidi, February 1909, C. J. Brooks) (Fig. 94) which is similar to the Sumatran male except that on the underside of the forewing the white band crossed by dark-dusted veins is little more than half as wide. It, and a female from Pulo Laut (Fig. 95) previously recorded as subsp. *arion* (Fig. 96) (Eliot, 1961: 171), but which has the white band on the forewing considerably narrower on the upperside but wider on the underside than in that subspecies, possibly represent a further minor subspecies, but they are provisionally placed under subsp. *heracleion*.

**Miletus melanion** C. & R. Felder

(Figs 52, ♂ genitalia; 97, 98 ♀)


It has been found that *melanion*, as treated by all authors up to and including Eliot (1961), comprises two superficially similar species with different male genitalia, namely *M. melanion* and *M. bazilanus* (Fruhstorfer, 1913). The former occurs throughout the Philippines (excluding Palawan) at least as far south as Mindanao, whilst the latter is at present known only from Mindanao and Bazilan. This distribution suggests that the two species evolved in the northern and southern island groups respectively, and that *melanion* was later able to spread south into Mindanao, where to-day it is a common species, without interbreeding with the endemic *bazilanus*.

*M. melanion* exhibits a good deal of individual variation, but broadly the males can be broken down into two dimorphs, which at first sight look as though they should represent distinct species. The male genitalia, however, reveal no significant differences, and the females cannot be separated into two groups. In the typical male (Fig. 97), figured by the Felders (1865: pl. 35, figs 32, 33), the brown forewing has a short, more or less sullied white subtornal streak in space 1b and the swollen portion of vein *M₃* is not surrounded by a white area, although a thin band of whitish scales below and a sullied white spot above the swelling may be present. On the underside of the forewing there are sullied white subtornal spots in spaces 1b and 2 and a sullied whitish streak beyond the cell. The dimorph, ♂-*albiguttatus* f. n. (fig. 98) (holotype ♂, Luzon, Lorquin, ex Felder coll. (BMNH)) is generally smaller and more blackish brown above; there is an additional whitish subtornal spot in space 2 and a prominent, usually clear white, more or less triangular spot surrounding the swollen portion of vein *M₃*, with its base extending from mid-space 3 to the cell apex.
On the underside of the forewing there is a broad white area crossed by dark-dusted veins, extending from the dorsum to vein $M_1$.

The female generally resembles $\sigma^\prime$-f. *albiguttatus*, but the white spots are usually larger. I do not think they are ever conjoined into a continuous white band, such as occurs frequently in *M. bazilanus*.

In the male genitalia the valva is slightly upturned and truncate before the apex and its outer edge is slightly concave.

**Key to the subspecies of *M. melanion***

1. $\sigma$ dimorphic. $\varphi$ upperside of forewing with white markings comprising a sullied streak in space 1a, a double subtornal spot in space 1b, an overlapping spot in space 2 separated by a dark bar from a much larger spot beyond the cell which extends above vein $R_5$, often as far as vein $Sc$.

   - $\sigma$ monomorphic, apparently only f. *melanion* being present. $\varphi$ upperside of forewing with subtornal white markings normally reduced to an often sullied white streak in upper part of space 1b, with the white spot beyond the cell smaller, not extending above vein $R_5$.

**Miletus melanion melanion** C. & R. Felder

(Figs 52 $\sigma^\prime$ genitalia; 97, 98 $\sigma^\prime$)

*Miletus melanion* C. & R. Felder, [1865]: 284, pl. 35, figs 32, 33 $\sigma^\prime$. LECTOTYPE $\sigma^\prime$, PHILIPPINES: Luzon (BMNH), here designated [examined].

*Gerydus melanion* (C. & R. Felder); Semper, 1889: 161, pl. 31, figs 13, 14 $\varphi$.

*Gerydus melanion melanion* (Felder); Fruhstorfer, 1913: 246; 1916: 822, pl. 14d $\sigma^\prime$.


The characters of the subspecies are given in the key.

Judging by material in BMNH, in Luzon f. *melanion* nearly always has a small, often sullied, white spot above the swollen portion of vein $M_3$. In the southern group of islands this white spot is seldom present, nearly all males resembling Fig. 97. It seems that fully marked f. *albiguttatus* is rare in Luzon, and many examples are intermediate to f. *melanion*; elsewhere the two forms remain more sharply distinct.

In BMNH there are three males from the Felders’ type-series, one of which is f. *albiguttatus* already designated as holotype. The other two are f. *melanion* with a sullied white spot above vein $M_3$. I designate as lectotype the one which most nearly resembles the example figured by the Felders and has the white spot very small and sullied; it is labelled /80/Luzon Lorquin [round blue]/Melanion n./Felder Colln. [round white]/Rothschild Bequest B.M. 1939/1.

**DISTRIBUTION.** Throughout the Philippines, excluding Mindoro, Palawan and the Sulu Is.

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Fig. 52 *Miletus melanion melanion* $\sigma^\prime$-f. *albiguttatus* f. n.; Negros. Male genitalia. Left, above, latero-dorsal view of interior of left valva and, below, ventral view of both valvae.
**Miletus melanion euphranor** (Fruhstorfer)

*Gerydus melanion euphranor* Fruhstorfer, 1914: 60; 1916: 822. LECTOTYPE ♂, PHILIPPINES: Mindoro (BMNH), here designated [examined].


The characters of this dark subspecies are given in the key.

In BMNH there are two male and one female syntypes. I designate as lectotype one of the males, labelled: /Syntype [blue]/Baco Dist. Mindoro 6.5.09/Adams Bequest B.M. 1912-399/; its genitalia were figured by Eliot (1961: fig. 24). The other male and female are paralectotypes.

**Distribution.** Mindoro. Also Leyte, whence some examples in BMNH tend to be even darker than those from Mindoro whilst others (Fig. 97) are inseparable from Luzon examples; it might have been expected that subsp. *melanion* alone would have occurred there.

**Miletus bazilanus** (Fruhstorfer) stat. n.

(Figs 53 ♂, genitalia; 99 ♂; 100, 101 ♀)

*Gerydus melanion bazilanus* Fruhstorfer, 1913: 246; 1916: 822. LECTOTYPE ♂, PHILIPPINES: Bazilan (BMNH), here designated [examined].

*Gerydus melanion vitelianus* Fruhstorfer, 1913: 246; 1916: 822. LECTOTYPE ♀, PHILIPPINES: Mindanao (BMNH), here designated [examined]. **Syn. n.**


The male is very similar to sympatric *M. melanion* f. *melanion*, but on the upperside of the forewing the white streak in space 1b is usually more prominent and about 3.5 mm long; the underside is slightly darker and the postdiscal markings are wider. However, to be absolutely certain of identification some males may need dissection.

The females generally have the white markings more extensive than *M. melanion*, and in typical examples (Fig. 100) there is a continuous white band on the forewing extending from the dorsum to vein *Sc*. However, some examples (Fig. 101) resemble normal *melanion* females, except by a slightly darker underside with wider postdiscal markings, and these are connected by intermediates to the typical form.

The male genitalia differ from those of *M. melanion* in three respects. The valva is distally broader, with the tip rounded; the paired, spine-like cornuti in the phallus are more than twice as large; the unci have a more elongated tip.

I designate as lectotype of *bazilanus* a male in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/

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**Fig. 53** *Miletus bazilanus* (Fruhstorfer); Mindanao. Male genitalia. Left, above, latero-dorsal view of interior of left valva and, below, ventral view of both valvae.
Philippines: Underside of forewing, Mindanao. 

I designate as lectotype of *vitelianus* a female in BMNH labelled /Type [red]/Type [Fruhstorfer orange]/Fruhstorfer Coll. B.M. 1933-131/melanion vitelianus Frhst. [in Fruhstorfer's hand]; it has vein Cu$_1$ dark-dusted across the forewing white band. There are no males from Mindanao ex Fruhstorfer coll. in BMNH, but his description of the male agrees reasonably well with *bazilanus*.

**Distribution.** Mindanao; Bazilan.

*Miletus takanamii* sp. n.  
(Figs 54, ♂ genitalia; 102 ♂; 103 ♀)

♂ forewing length 19.0 mm. Body and labial palpi dark brown. Legs buff-brown. Wing shape similar to that of the Celebesian *M. celinus* (Fig. 104), with the forewing concave in space 6 below a pointed apex, and with the basal quarter of vein $M_3$ swollen and clothed with the usual minute wedge-shaped specialised scales. Upperside blackish brown; forewing with a white patch 3.0 mm wide surrounding swollen portion of vein $M_3$, extending from mid-space 2 across spaces 3 and 4 and into space 5 as a narrow projection, and a white streak 5.5 mm long and 1.0 mm wide just below centre of vein $Cu_2$. Underside paler brown becoming reddish near middle of forewing termen; usual markings reddish brown, outlined by black lines except on outer side of postdiscal series of hindwing. Forewing with an irregular white area extending from just above dorsum to vein $R_5$, 5.0 mm wide in space 1b, increasing to 6.5 mm in space 2, then decreasing to 3.5 mm in space 6. Genitalia with valva tapering to a rounded point, as in most species of the *symethus*-group, phallus short, much as in *M. melanion* and *M. bazilanus*, but lacking cornuti.

♀ forewing 18.0 mm. Forewing termen more convex than in male, hindwing slightly dentate at vein $M_3$, as usual in the genus. Upperside blackish brown; forewing with an irregular, oblique white band running from vein $A_1$, where it is 5.0 mm wide, to vein $R_1$, where it is 2.0 mm wide, and entering outer part of cell; veins $Cu_1$ and $Cu_2$ are dark-dusted where they cross this band. Underside generally similar to male, but on hindwing lower half of area between discal and postdiscal spots dusted with black scales.

**Material examined**

Paratype. 1 ♀ (allotype), ii.1982, data otherwise as holotype (BMNH).

Apart from its distinctive wing shape the male most nearly resembles *M. melanion* f. *albiguttatus*, from which it differs in having a larger white patch astride the swollen portion of vein $M_3$ and in lacking a small white subtornal spot in space 2 and, on the underside, in a darker and more irregular ground colour and

Fig. 54 *Miletus takanamii* sp. n.; Mindanao. Male genitalia. Lower left, latero-dorsal view of interior of left valva.
wider white area on the forewing. The female is much like that sex of *M. basilanus*, but on the underside the ground colour is much darker and the white central area of the forewing is wider.

The species is named after Mr Yusuke Takanami, who generously presented the types to the BMNH.

**Genus MEGALOPALPUS Röber**

*Megalopalpus* Röber, 1886: 51. Type-species: *Megalopalpus simplex* Röber, 1886: 51, pl. 4, fig. 4, by original designation. Gender masculine. [See also Opinion 566, 1959.]

This genus appears to be closely allied to *Miletus*, of which it should perhaps be treated as a subgenus, having similar long legs with the foretarsi flattened and blade-like, and the undersurface of the wings similarly patterned with ctenulate markings, although these are sometimes obsolete. The only significant difference lies in the presence of a strongly developed humeral vein in *Megalopalpus*. Males also lack secondary sexual characters, but this condition is matched in some species belonging to the Oriental genera. The male genitalia are of the normal pattern for the tribe, but with some distinctive characters: the uncus/tegumen plates are triangular and bear a broad, lobe-like process directed ventrad, and the brachia are curved (see illustrations in Bethune-Baker, 1914; Stempffer, 1967; Eliot, 1973).

The genus is restricted to the forested regions of West Africa, from Liberia south to Angola and east to Uganda. The larvae are predators of Jassidae and Membracidae (Cottrell, 1984). Gilbert (1976) records and illustrates an adult feeding from the 'nectary' of a lycænid larva.

Species limits within *Megalopalpus* are very imperfectly understood. Aurivillius (1922), followed by Stempffer (1967) and Cottrell (1984), accepted four species: *metaleucus*, *simplex*, *zymna* and *angulosus*. Of these, Stempffer (1967) dissected specimens of the first three, and stated that 'The male genitalia of *M. zymna* and *M. metaleucus* are very similar to those of *simplex*. D'Abrera (1980) and Carcasson (1981), however, following Peters (1952), recognised only three species, *zymna* (to include *simplex*), *metaleucus* and *angulosus* - the last, representing the species not dissected by Stempffer, they regarded as doubtful, and possibly only a synonym of *zymna*. Berger (1981) also recognised only three species but, in contrast, these were *zymna*, *simplex* and *metaleucus* - no mention was made of *angulosus* (confounded by Berger with *metaleucus* - see below).

In the BMNH as apparently curated by Ms S. J. May, all four species listed by Aurivillius and Stempffer are purportedly represented. However, it is very difficult to see how *simplex* differs consistently from *zymna*, and under the former the following note appears: 'Probably some *simplex* in *zymna* series, as these were hitherto considered to be synonymous. SJM.' This note is doubly puzzling because not only have the two often been considered to be separate, there is no evidence of comprehensive dissection of the specimens segregated as *simplex* (and therefore, presumably, their distinguishing features must have been open to inspection). The basis of this separation, if indeed it is valid, is thus unclear or unknown. Carcasson (1981) implies, effectively, that there are just two species: large (*metaleucus*) and small (*zymna*). Unfortunately, the type of *zymna* is of intermediate size! However, there seems little doubt that there are at least three species, corresponding to the arrangement in Peters (1952) and illustrated by D'Abrera (1980). All four nominal species are grossly sympatric in some areas (e.g. Cameroun, Zaire), although Clench (1965) noted a 'strong correlation with geography' for the four forms (including *simplex*) that he described under *zymna*. Detailed field observations and reared material are probably essential for the solution of this problem.

In the following key, *simplex* and *zymna* are separated following Aurivillius (1922) and Berger (1981), but this is not very reliable if the identifications in the BMNH are correct; see also Clench (1965).

**Key to the species of the genus Megalopalpus**

1 Larger species, forewing length 17-23 mm; black border of forewing upperside does not extend broadly quite as far posterior as vein *A1*; ctenulate markings of hindwing underside darker than general ground colour, not solely forming a series of concentric bands.................. 2
   - Smaller species, forewing length 11-18.5 mm; black border of forewing upperside extends broadly and fully to vein *A1*; ctenulate markings of hindwing underside not appreciably darker than ground colour, outlined by pale scales, forming a series of roughly concentric bands................................................................. 3

2 Hindwing upperside very narrowly bordered (up to 1 mm) with dark scales along posterior margin; postdiscal ctenulate band of hindwing underside disrupted medially; hindwing underside pattern with overall appearance of veined marble.................. *metaleucus* (p. 85)
   - Hindwing upperside usually more broadly bordered (2-3 mm) with dark scales, affecting entire
outer margin; postdiscal catenulate band of hindwing underside reticulate medially; hindwing underside pattern with a more complex marbling effect ................................................................. \textit{angulosus} (p. 85)

3. Hindwing upperside with dark marginal band 3–5 mm in width, not interrupted in middle \textit{zymna} (p. 85)

- Hindwing upperside with dark marginal band no more than 3 mm in width (often much less), medially very narrow or completely interrupted ......................................................... \textit{simplex} (p. 85)

\textbf{Megalopalpus angulosus} Grünberg


This butterfly, judging by the underside and if correctly identified in the BMNH, is a good species and not merely a maculated or seasonal form of \textit{metaleucus}. \textit{M. angulosus} is known from Cameroun, Equatorial Guinea and Zaire. Specimens in the BMNH have a forewing length of 20–23 mm.

\textbf{Megalopalpus metaleucus} Karsch

[\textit{Allotinus zymna} (Westwood); Grose-Smith & Kirby, 1891: figs 1, 2. Misidentification.]

\textit{Megalopalpus metaleucus} Karsch, 1893: 217; Clench, 1965: 326, figs 198–201; D’Abrera, 1980: 470 (illusr.); Berger, 1981: pl. 197, figs 3, 4. 2 ♂ syntypes, Togo: Bismarckburg (?MNHU) [not examined].

\textit{M. metaleucus} is considered to occur from Liberia and Ivory Coast south to Cameroun and Zaire, and east to Uganda. Specimens in the BMNH have a forewing length range of 17–22 mm. Clench (1965) discusses a variation of the species.

\textbf{Megalopalpus simplex} Röber

\textit{Megalopalpus simplex} Röber, 1886: 51, pl. 4, fig. 4. ♀ syntype(s), \textit{Equatorial Africa}: ‘Borneo’ (patria falsa) (?SMT) [not examined].


\textit{Allotinus similis} Kirby, 1890: 262. Syntype(s), (sex?), \textit{Cameroun}: Barombi (Preuss.) (MNHU) [not examined]. [Synonymy from Aurivillius, 1922; Stempffer, 1967.]

\textit{Megalopalpus gigas} Bethune-Baker, 1914: 335, pl. 58, figs 9, 9a. ♂ syntypes, \textit{Cameroun}/\textit{Gabon} (BMNH) [examined]. [Synonymy from Stempffer, 1967.]

Material in BMNH identified as \textit{simplex} is very variable with respect to the hindwing dark border (see also \textit{zymna} below). As already discussed, the basis of the separation of \textit{simplex} from \textit{zymna} is elusive, and may not be real. The identification of specimens illustrated by Berger (1981) to represent both species should be regarded with caution. The forewing length of the BMNH material varies from 14.0–18.5 mm. The distributional range is thought to include Ghana, Liberia, Nigeria, Cameroun, Gabon, Zaire and Uganda.

\textbf{Megalopalpus zymna} (Westwood)

\textit{Pentila zymna} Westwood, 1851: pl. 76, fig. 7; 1852: 503. 1 ♂ syntype, \textit{Nigeria}: Ashanti (ex \textit{Wesleyan Missionary Society}) (BMNH) [examined].


As already noted, it is doubtful if \textit{simplex} can be reliably separated from \textit{zymna}. However, Clench (1965) recognised four more or less distinct forms under \textit{zymna}, including one apparently corresponding to \textit{simplex}, and the possibility that \textit{zymna} s.l. represents a species complex must be considered. Specimens identified in the BMNH as \textit{zymna} have a forewing length of 11–18 mm, with the lone syntype at 18.5 mm (despite this, the syntype is definitely of the correct general facies — it is not \textit{angulosus} or \textit{metaleucus} as currently understood). The distribution of \textit{zymna} encompasses that given for \textit{simplex}, and is considered to extend also to Macias Nguema (Fernando Poo), Equatorial Guinea, Angola, southern Sudan and Zimbabwe.
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Australian ichneumonids of the tribes Labenini and Poecilocryptini

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Synopsis

The Australian species of the labenine tribes Labenini and Poecilocryptini are revised and keys provided to the five genera and 36 species occurring on the continent. Twenty new species are described, but one is not formally named as its status requires further investigation. The remaining 16 species are redescribed and their diagnostic features emphasized. Asperellus Townes is newly placed as a junior synonym of Certonotus Kriechbaumer, Certonotus tasmaniensis Turner is treated as a junior synonym of C. nitidulus Morley and Poecilocryptus straminea Morley placed as a junior synonym of P. nigromaculatus Cameron. Lectotypes are designated for five species. Details of known hosts are given together with notes about the geographical distribution of each species. A brief introductory section discusses the systematic position of the subfamily and outlines possible relationships between species. A checklist of Australian species, and indexes to hosts and parasitoids complete the work.

Introduction

Amongst the most important of the natural enemies of insect pests are the parasitic Hymenoptera, a very large group of animals whose larvae develop at the expense of other insects (Askew, 1971). Under normal circumstances, the populations of many injurious insects are severely
limited by the attacks of Parasitica, and in several countries, including Australia, the ravages of accidentally imported pests have been curtailed by the introduction of one or more hymenopterans (Muldrew, 1967; Taylor, 1978). Other introduced pests have been severely attacked by native Australian parasitoids (Ttryon, 1900). During the past 30 years there has been an upsurge in interest in using Hymenoptera and other organisms for purposes of pest control (Wilson, 1960; Huffaker & Messenger, 1976) as an alternative to costly, ineffective and environmentally destructive chemical methods (Bosch, 1978). However, for biological control programmes to be successful an intimate knowledge is necessary of the life history and interactions of the pest and its parasites. A sound taxonomic basis is vital for the development of such knowledge (Hardy, 1982), for such work permits the accurate identification of an organism and hence provides constancy and universality in the usage of names, a prerequisite for the national and international communication of information.

The present work is a taxonomic study of two very distinct tribes of one of the apparently most primitive extant ichneumonid subfamilies, the Labeninae. These two tribes, the Labenini and Poecilocryptini, are virtually confined to the southern hemisphere with most species occurring in Australia and South America. The generic phylogeny of the Labeninae and their geographical distribution has recently been studied (Gauld, 1983) but no keys are currently available to facilitate identification of the species. This paper is an attempt to provide a means of determining the Australian species of this interesting group.

The terminology in this work follows that of Gauld (1984).

Material examined

The study is based on examination of almost all specimens available in collections of Australian ichneumonids. Special attention was paid to collections in agricultural institutions that contain a large number of reared specimens. Examination of these collections has been supplemented by extensive collecting, particularly in Tasmania and the south-east. Although the resulting sample is thought to be fairly representative of the fauna of the more humid eastern part of the continent, relatively little material has been examined from the west.

The following abbreviations have been used for museums containing Australian material.

AM Australian Museum, Sydney, New South Wales, Australia
ANIC Australian National Insect Collection, Canberra, Australian Capital Territory, Australia
BMNH British Museum (Natural History), London, U.K.
BPBM Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
MNHN Muséum National d'Histoire Naturelle, Paris, France
MNHU Museum für Naturkunde der Humboldt-Universität, Berlin, D.D.R.
NMV National Museum of Victoria, Melbourne, Victoria, Australia
NSWDA New South Wales Department of Agriculture, Rydalmere, New South Wales, Australia
QM Queensland Museum, Brisbane, Queensland, Australia
TC Townes Collection, Ann Arbor, Michigan, U.S.A.
WADA Western Australian Department of Agriculture, Perth, Western Australia, Australia

Checklist of Australian Labenini and Poecilocryptini

LABENINI

CERTONOTUS Kriechbaumer
Asperellus Townes syn. n.
anrewi sp. n.
annulatus Morley
apicalis Morley
avitus sp. n.
celes sp. n.
cestus sp. n.
farrugiai sp. n.
genpiculatus Morley
hinnuleus Krieger comb. rev.

humeralifer Krieger
leeuwinensis Turner comb. rev.
mogimbensis Cheesman comb. rev.
monticola Morley
nitidulus Morley
tasmaniensis Turner syn. n.
apaluma sp. n.
pineus sp. n.
rufescens Morley
sisyphus sp. n.
talus sp. n.
toolangi sp. n.  
zebus sp. n.  
species A  
LABENA Cresson  
anulata (Brullé)  
chadwickii (Parrott)  
grandis sp. n.  
jacunda sp. n.  
keira sp. n.  
malecasta sp. n.  
pudenda sp. n.  
POECILOCRYPTINI  
ALAOYTHRIS Gauld  
clongissimus Gauld  
POECILOCRYPTUS Cameron  
coloratus sp. n.  
galliphagus sp. n.  
nigriceps Turner & Waterston  
nigromaculatus Cameron  
straminea Morley syn. n.  
URANCYLA Gauld  
fulva Gauld  

Nomen dubium  
Certonotus varius Kriechbaumer  
From Kriechbaumer’s original description (1889: 308) it is apparent that this species is one of the larger Australian Certonotus. As we have seen no species that agrees with the description, nor can the type be located, we have no option but to treat this as an unrecognized taxon.

Subfamily LABENINAE  
The Labeninae is a moderately large subfamily. Amongst the ichneumonid subfamilies it is unique in being a Gondwanic group. Most genera and species are confined to Australasia and/or South America; only a dozen or so taxa occur outside this area (Table 1). All other ichneumonid subfamilies are well represented, if not actually most diverse, in the Holarctic region. Phylogenetic analysis suggests that the Labeninae radiated in West Gondwanaland, prior to the separation of Australia, Antarctica and South America, some 55 mya (Gauld, 1983). The group is only represented by some highly derived species in India and South Africa, suggesting that the Gondwanic radiation occurred after the separation of these continents (c. 100 mya). Many labenines are associated with the southern temperate rain forests, the areas floristically dominated by Nothofagus, Araucaria and Podocarpus. One labenine genus is known to oviposit into the seeds of an Araucaria in Australia.

Structurally labenines exhibit many of the plesiomorphic features of ichneumonids, and the larvae are particularly primitive (Short, 1978). Biologically they also show many of the so-called primitive features of ichneumonids – they are ectoparasitoids and many are known to parasitize wood-boring insects.  
It is not clear what the sister-group to the labenines is. The more primitive taxa (Labenini) closely resemble some Pimplinae, but all the similarities can, we believe, be interpreted as either symplesiomorphies, or parallel adaptations to the wood-boring habit. We suggest that the shared specializations shown by labenines and rhyssines are parallelisms rather than synapomorphies because of the striking differences in oviposition behaviour between the groups. Labenines manipulate the ovipositor with a specialized guide on the antero-medial surface of the hind coxa; rhyssines achieve similar control with specialized claspers on the ventral surface of the gaster. It is not impossible that these taxa share a close common ancestor (a wood-borer with no specialization to control the ovipositor), but there is no conclusive phylogenetic evidence to support such speculation. We suggest that the labenines are a primitive offshoot of the earliest ichneumonid radiation, and that at an early stage in their evolutionary history they became isolated on a southern continent prior to undergoing a modest radiation, that has in some respects paralleled that of other ectoparasitic ichneumonids (see Gauld, 1983; 1984).

The Labeninae comprises four morphologically distinctive tribes, Labenini, Groteini, Poeci-locryptini and Brachycyrtini, all of which are well represented in Australia (Table 1). Both the Groteini and Brachycyrtini include some genera for which relatively insufficient material is at hand to justify undertaking a taxonomic revision at present. Quite good series of some species of Labenini and Poecilocryptini are available for systematic study, and as there are far more species than the few described the opportunity has been taken to monograph these taxa.
Table 1  The distribution of the Labeninae.

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<th>New Zealand</th>
<th>Malaccas</th>
<th>New Guinea</th>
<th>Australia</th>
<th>South America</th>
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Key to tribes of Labeninae

1  Mandible long and slender, labrum very large, almost as long as clypeus (Fig. 1); female with ovipositor barely projecting beyond apex of gaster, dorsoventrally depressed....................... GROTEINII
   - Mandible rather short and not particularly slender, labrum from moderately small to virtually concealed (Fig. 2); female with ovipositor projecting beyond apex of gaster by at least 0-5 times length of hind tibia............................................ 2
2  Fore wing with abscissa of Cu_{1}, between 1m-cu and Cu_{1a} at least 1-4 times as long as Cu_{1b} (Fig. 3); hind coxa of female with a furrow on anterior surface internally; base of valvula 3 bearing distinct sclerotized lobe (Fig. 4).......................................................... LABENINI(p. 110)
   - Fore wing with abscissa of Cu_{1}, between 1m-cu and Cu_{1a} from subequal to, to conspicuously shorter than Cu_{1b} (Figs 5, 6); hind coxa of female without a furrow on anterior surface internally; base of valvula 3 without a distinct sclerotized lobe.......................................................... 3
3  Fore wing with 2m-cu with one long bulla, sometimes with an indistinct trace of a vein centrally (Fig. 5); occipital carina dorsally absent...................................................... POECILOCRYPTINI(p. 137)
   - Fore wing with 2m-cu with two short bullae widely separated from each other (Fig. 6); occipital carina dorsally complete................................................................. BRACHYCYRTINI

The Groteini and Brachycyriniti are not discussed further in this paper.

Tribe LABENINI

Labenines are characterized by having a distinct sclerotized lobe at the base of the third valvula. Most species also have fine file-like teeth at the distal apex of the ovipositor. The tribe contains four genera: Labena, Certonotus, Apechoneura and Xenothyris. The last two are exclusively Neotropical, and Apechoneura may well be a specialized species-group of Certonotus. Labena and Certonotus are most commonly found in Australia and South America, and there is evidence to suggest that the group is an ancient southern one that originated in the cool temperate forests of Gondwanaland (Gauld, 1983). As far as is known, the native hosts of the group are
coleopterous larvae boring in wood (Townes, 1969; Gauld, 1984), though one species has adapted to parasitizing introduced siricids (Hocking, 1967).

Structurally, labenines are amongst the most primitive ichneumonids. Virtually all species have clearly developed parapsidal furrows, a primitive hymenopterous feature found widely amongst Symphyta and some lower Aculeates. An apparently unique feature of the group is the presence of a distinct sclerotized lobe at the base of the third valvula (Fig. 4). In other ichneumonids a slightly broadened, rounded area is present in a homologous position and this may well represent a precursor of the valvular lobe. Quite what this structure is, at present is unclear, as recent morphological treatises make no mention of such a structure (e.g. Smith, 1970; Matsuda, 1976). Short (1978) comments on the primitive structure of labenine larvae.

Key to genera of Labenini occurring in Australia

1 Mesoscutum punctate or puncto-striate; occipital carina mediodorsally complete or only narrowly interrupted; apex of fore tibia with a conspicuous long curved spine on outer distal margin; female with third fore tarsal segment produced apically into a lobe that reaches beyond apex of fourth segment (Fig. 7) .......................................................... LABENA Cresson (p. 111)
   - Mesoscutum with transverse rugae; occipital carina dorsally entirely absent; apex of fore tibia with a short tooth on outer distal margin; female with fore tarsus simple

CERTOÑOTUS Kriechbaumer (p. 117)

LABENA Cresson


Caryoeus Walsh, 1866: 30. Type-species: Mesochorus fusciennis Brullé (= Cryptus grallator Say), by monotypy.


Dyseidopus Kriechbaumer, 1890: 489. Type-species: Dyseidopus sericeus Kriechbaumer, by monotypy.

Dysidopus Schulz, 1906: 103. [Unjustified emendation.]


Moderately large to large insects, fore wing length 6–20 mm; clypeus small, flat or concave, very thin with margin arculate; labrum barely projecting; mandible tapered, twisted 30° with upper tooth slightly the longer; outer mandibular surface with a median longitudinal groove bearing hairs; malar space shorter than basal mandibular width. Occipital carina complete or narrowly interrupted centrally; eye margin slightly indented opposite antennal socket. Antenna almost cylindrical, that of female with a small flat sensillum on extreme distal apex. Mesoscutum punctate or striate transversely, with notauli vestigial; notaular crests well developed. Propodeum rather short, convexly rounded with spiracle elliptical; propodeal areae usually defined, area superomedial usually larger than area petiolaris; gaster inserted high on propodeum, above level of hind coxae. Fore tibia of female inflated (so it often collapses in dried specimens) with a large curved spine on outer distal margin; fore tarsus with segment 3 lobed, the lobe reaching nearly to centre of segment 5, segment 4 reduced; hind coxa of female flattened internally with a short basal groove; tarsal claws large, simple. Fore wing with cu-a more or less opposite base of Rs&M; 3r-m present, areollet large, rhombic or with very short anterior side; 2m-cu sinuous with two bullae. Hind wing with distal abscissa of Cu4 present, sometimes not joining to first abscissa of Cu1, if joined, then first abscissa of Cu1 is shorter than cu-a; basal cell slender; Sc with one or two hamuli. Gaster quite long, cylindrical; tergite 1 with spiracles a little before centre; sternite 1 usually reaching to or slightly beyond level of spiracles; laterotergites 2–4 membranous; last visible tergite with a small, weakly defined dorsal plate differentiated. Ovipositor projecting beyond apex of gaster by 1.8–4.4 times length of hind tibia; upper valve with apex bearing blunt serrations, lower valve apically almost enclosing the upper, usually with series of close file-like teeth and a fine coriaceous patch just proximal to these teeth, rarely with teeth quite strongly developed.

REMARKS. Labena is a large genus with most species occurring in the Neotropics. Two species occur in North America, and in this work seven are recognized from Australia.

Labena species are easily separated from other Labenini by the specialized fore tarsus and the possession of a sensillum on the extreme apex of the antenna. It resembles the Neotropical genus Xenothyris Townes in having a relatively smooth mesoscutum, though in the latter taxon rugae are present on the anterior part of the median lobe. Unlike Xenothyris, Labena species have simple claws.
The relationships of the Australian species. As the vast majority of the Neotropical species are undescribed and virtually unstudied it is impossible as yet to state whether the Australian Labena constitute a holophyletic group, so no formal cladistic analysis is presented here. However, the seven Australian species are clearly divisible into two monophyletic species-groups, each of which is characterized by several apomorphic features. The annulata-group contains four taxa (L. annulata, grandis, chadwickii and malecasta). All these species have Cu1 in the hind wing incomplete and have the white flagellar band at the distal apex of the antenna. The keira-group contains three taxa (L. keira, jacunda and pudenda). These species have virtually a smooth mesopleuron, and the male genitalia are specialized in that the apex of the gonosquama is flattened or impressed and surrounded by a fringe of very long hairs (Figs 9, 10).

The interrelationship of the taxa within these species-groups is less clear. Within the keira-group, keira and pudenda share two apparently apomorphic features, a specialized mid tibia and a medially interrupted yellow band on the central female gastral segments. The unspecialized mid tibia found in L. jacunda may represent a reversal to the plesiomorphic condition unless the apomorphic state has been derived independently in both the keira and annulata lineages (and probably also in various Neotropical groups). It is therefore arguable that the possible sister-relationship between keira and pudenda is only supported by the colour character. Contradicting this relationship are two features shared by pudenda and jacunda – the coarse ovipositor teeth (Fig. 21) and the large imposed area on the apex of the male gonosquama. The latter is quite clearly an apomorphic condition but the polarity of the former is controversial as the possession of coarse teeth is probably plesiomorphic for ichneumonids. Other Labenini all have fine, file-like ovipositor teeth and it is considered that this condition is an apomorphy of the tribe (Gauld, 1983) and consequently plesiomorphic for Labena species. Thus the possession of coarse teeth can be regarded as a further apomorphic development, albeit a reversal, supporting the group pudenda and jacunda.

Within the annulata-group the three species grandis, chadwickii and malecasta seem to form a subgroup characterized by possession of transverse striations on the mesoscutum. This subgroup apparently has a sister-relationship to L. annulata (Fig. 65).

Key to species of Labena occurring in Australia

1 Hind wing with distal abscissa of Cu1 present in membrane, not confluent with Cu1 and cu-a (Fig. 11); mesopleuron quite closely punctate or punctocoriaceous, often submatt; male gonosquama not distally strongly flattened, with a fringe of fine hairs (Fig. 8) or a single tuft of long hairs (annulata-group) ................................................. 2

- Hind wing with distal abscissa of Cu1 complete (Fig. 12); mesopleuron smooth and polished, at most with sparse punctures; male gonosquama distally flattened or impressed, with this area fringed with long hairs (Figs 9, 10) (keira-group) ......................................................... 5

2 Tergites 2-4 of gaster coarsely and very closely punctate, matt (Fig. 13); ovipositor 2-0 or less times as long as hind tibia ................................................................. annulata (Brullé) (p. 113)

- Tergites 2-4 of gaster smooth and polished, at most with very fine punctures (Fig. 14); ovipositor at least 2-5 times as long as hind tibia ................................................................. grandis sp. n. (p. 114)

3 Posterior end of gaster with mediodorsal margin thickened and produced into a rounded prominence (Fig. 15); pronotum with a median lateral conical tubercle; metapleuron strongly verrucose ......................................................... 4

- Posterior end of gaster with mediodorsal margin thin, slightly concave, not produced (Fig. 16); pronotum, at most, with a median lateral convex swelling, usually virtually flat; metapleuron punctate or puncto-striate ................................................................. chadwickii (Parrott) (p. 113)

4 Female with ovipositor at least 3-5 times as long as hind tibia; occipital carina mediodorsally complete; male with a tuft of long hairs on distal apex of gonosquama .... malecasta sp. n. (p. 116)

- Female with ovipositor at most 3-0 times as long as hind tibia; occipital carina (of female at least) mediodorsally, narrowly interrupted; male with gonosquama distally evenly rounded and uniformly hirsute .................................................................................... chadwickii (Parrott) (p. 113)

5 Mid tibia slender, subcylindrical (Fig. 17); tergites 4-5 of gaster with broad posterior yellow marginal band; hind coxa of female with ovipositor guide barely differentiated ................................................................. jacunda sp. n. (p. 115)

- Mid tibia distally swollen, proximally narrowed and at least slightly flattened (Fig. 18); tergites 4-5 of gaster with posterior marginal yellow band centrally interrupted or yellow band indistinct; hind coxa of female with ovipositor guide well developed ................................................................. keira sp. n. (p. 115)

6 Apex of fore wing infumate; mid tibia with a longitudinal row of 3-6 spine-like bristles on outer surface (Fig. 18); submetapleural carina evenly and weakly broadened anteriorly (Fig. 19); ovipositor about 3-0 times as long as hind tibia .................................................................
Apex of fore wing very uniformly hyaline; mid tibia without obvious spine-like bristles on outer surface; submetapleural carina anteriorly abruptly expanded into a rounded lobe (Fig. 20); ovipositor about 4-0 times as long as hind tibia. 

**Labena annulata** (Brullé)

(Figs 8, 11, 13)

*Ephialtes annulatus* Brullé, 1846: 86. Holotype ♀, TASMANIA (MNHN) [examined].

*Labena annulata* (Brullé) Townes et al., 1961: 112.

**Female.** Moderately large species, fore wing length 7-13 mm. Malar space 0-4 times as long as basal mandibular width. Occipital carina mediodorsally narrowly interrupted, ventrally joining hypostomal carina and continuing to mandibular base as a distinct carina, not developed into a flange. Pronotum laterally almost flat; mesothorax laterally and ventrally bearing dense, short, white pubescence; mesoscutum closely and coarsely punctate; horizontal mesopleural furrow indistinct; metapleuron closely and coarsely punctate; submetapleural carina anteriorly expanded into a rounded lobe. Propodeum with anterior transverse carina present centrally separating area superomedia from area basalis. Fore wing with 3r-m and 2r-m converging, widely separated at junction with Rs. Hind wing with distal abscissa of Cu₄ present in membrane, not confluent with Cu₃ and cu-a. Mid tibia with a longitudinal row of spine-like bristles on outer surface, proximally slender, distally swollen with a trace of groove in inner surface. Gaster with sternite 1 0-7 times as long as the hind coxa, reaching to level of spiracle; tergites 2-4 coarsely and very closely punctate, matt; apex of terminal plate of tergite 8 simple. Ovipositor projecting beyond apex of gaster by 1-8-2-0 times length of hind tibia, the apex bearing very fine teeth.

Coloration. As for *L. pudenda* although some specimens with fore and mid legs entirely yellow.

**Male.** Similar to female but with fore wing length 7-8 mm; malar space 0-4 times basal mandibular width; gaster with sternite 1 0-7-0-8 times as long as hind coxa. Gonosquama with an apical tuft of fine, long hairs.

**Remarks.** *L. annulata* is one of the most distinctive species of Australian *Labena* and can easily be recognized by its very close, coarse punctured microsculpture, particularly on the tergites of the gaster. The ovipositor is shorter than that of any other species. This species is widespread in Australia though it seems to be most common in the south and west.

**Host records.** Cerambycidae: *Uracanthus strigos Pascoe* (NMV).

**Material examined.**

Holotype ♀, *Tasmania*: no further data (MNHN).

Queensland: 1 ♀, 14 km W. by N. Hope Vale Mission (15-16S 144-59E), x.1980 (Cardale) (ANIC). New South Wales: 2 ♀, 1♀, Kinchega NP, i.x.1980 (Rodd) (AM). Victoria: 1 ♀, Baxter, parasite on *Uracanthus strigosus* (Dixon) (NMV); 1 ♀, Healesville, xi.1983 (NMV). Northern Territory: 2 ♀, Arengya, 600 m, viii (TC). Tasmania: 2 ♀, Hobart, i.x.1921 (Cole) (NMV); 1 ♂, Ridgeway i.x.1943 (Cole) (NMV); 1 ♀, 1867 (Sichel) (TC) (compared with type). Western Australia: 1 ♀, 13 km WNW. Northampton (28°18'S 114°31'E), x.1981 (Naumann & Cardale) (ANIC); 1 ♀, no further data (BMNH).

**Labena chadwickii** (Parrott)

(Fig. 14)

*Neonotus chadwickii* Parrott, 1955: 230. Holotype ♀, NEW SOUTH WALES (NSWDA) [examined].


**Female.** Moderate to large species, fore wing length 6-17 mm. Malar space 0-5 times as long as basal mandibular width. Occipital carina mediodorsally narrowly interrupted at least in female, ventrally joining hypostomal carina and continuing to base of mandibular base as distinct carina, not developed into a flange. Pronotum laterally with a median swelling; mesothorax laterally and ventrally bearing sparse, short, white pubescence; mesoscutum punctate, at least transversely striate in centre, in larger specimens uniformly striate; horizontal mesopleural furrow distinct; metapleuron punctate; metapleural carina expanded anteriorly into a small rounded lobe. Propodeum with anterior transverse carina present centrally, separating area superomedia from area basalis. Fore wing with 3r-m and 2r-m converging, almost joining at junction with Rs. Hind wing with distal abscissa of Cu₄ present in membrane, not confluent with Cu₃ and cu-a. Mid tibia with a longitudinal row of spine-like bristles on outer surface, proximally slender, distally swollen and with indication of groove on inner surface. Gaster with sternite 1 0-8 times as long as hind coxa, reaching from opposite to well behind level of spiracle; tergites 2-4 smooth.
and polished, at most with very fine punctures; apex of terminal plate of tergite 8 simple. Ovipositor projecting beyond apex of gaster by 2-2.5-3.0 times length of hind tibia, the apex bearing very fine teeth.

Coloration. Black. Palps, labrum, clypeus, face (except median longitudinal area), genae, orbits, anterolateral margin of mesonotum, tegula, posterior 0.5 of subalar process, posterior 0.5 of scutellum, postscutellum, posterior 0.5 of propodeum, posterior margins of tergites 1-7, distal end of each coxa, fore and mid legs with trochanters, distal 0.5 of femur, tibia and tarsus, hind legs with distal 0.1 of femur and tibial spurs yellow. Median area of frons, mesonotum, mesopleuron, metapleuron, upper surface of hind coxa partly deep red. Antenna with disruptive mark subapical, last 2-3 flagellar segments black.

Male. Similar to female but with fore wing length 6-9 mm; malar space 0.5 times basal mandibular width; gaster with sternite 1 0.5 times as long as hind coxa. Gonosquama distally evenly rounded and uniformly hirsute. Coloration as for female with less deep red areas.

Remarks. *L. chadwickii* is the commonest and most widespread eastern species in Australia. Of the species with an apical white flagellar band, complete yellow posterior margined gastral tergites and incomplete Cu1 in the hind wing only *chadwickii* has a simple terminal plate, smooth gastral tergites and incomplete occipital carina. The females are rather similar to *L. malecasta* but differ in having a shorter ovipositor and the genal orbits more broadly yellow and confluent with the yellow on the face. *L. malecasta* has only narrow yellow marks on the genae and these are not confluent with the facial yellow.

Host records. Buprestidae: *Ethon affine* Laporte & Gory (Parrott, 1955). Several individuals have been reared in Tasmania from logs of *Pinus radiata* infested by *Sirex.*

Material examined

Holotype ♀, **New South Wales**: Middlecove Point, Willoughby, Sydney (Chadwick) (NSWDA). 

**Queensland**: 1 ♀, Eungella, xi (TC); 1 ♀, 6 km N. of Kuranda, 11.i.1967 (McAlpine & Holloway) (AM); 1 ♀, Mt Cootha, iv (TC); 1 ♀, Mt Glorious, vi.1977 (Hiller) (BMNH); 1 ♀, Mt Glorious, xii.1976 (Boucek) (BMNH); 2 ♀, Mt Glorious, i (TC); 2 ♀, Mt Nebo, ii (TC); 1 ♀, Mt Tambourine, iii.1950 (Burns) (NMV); 4 ♀, Mt Tambourine, xii (TC); 1 ♀, O'Reilly's Guest House, iii.1980 (BMNH); 1 ♀, Palm Is., near Townsville, x (TC); 1 ♀, Stanthorpe, 1982 (Sedlacek) (TC). **New South Wales**: 1 ♀, Eucambene Dam, i.1961 (Leipa) (ANIC); 3 ♀ (paratypes), same data as holotype (AM, ANIC, NSWDA); 1 ♀, Monga, ix.1957 (ANIC); 6 ♀, Tomah, ix.1982 (Rodd) (AM); 1 ♀, Mt Tomah, xi.1978 (Rodd) (AM); 1 ♀, Wentworth Falls, Blue Mtns, xi.1982 (McAlpine) (AM). **Australian Capital Territory**: 1 ♀, Lees Ck, xi.1977 (Daniels) (AM). **Victoria**: 1 ♀, 6 km S. Aberfeldy, xi.1976 (Calder) (NMV); 1 ♀, Blackwood Ra., x.1953 (Neboiss) (NMV); 2 ♀, Ferntree Gully, x.1951 (Oke) (NMV); 1 ♀, Gippsland (AM); 1 ♀, Kinglake W., x.1954 (Neboiss) (NMV); 1 ♀, Lal Lal, i.1954 (Neboiss) (NMV); 1 ♀, 12 km SE. Merrijig, Howqua R., xi.1971 (Neboiss) (NMV); 1 ♀, Mitta Mitta R., x.1973 (NMV); 1 ♀, 1 ♀, Mt Dandenong, 200 m, ii (TC); 1 ♀, Mt Drummier, xi.1956 (Riek) (ANIC); 1 ♀, Warburton, xii.1972 (Sedlacek) (TC); 1 ♀, Woori Yallock, x.1932 (Burns) (NMV). **Tasmania**: 1 ♀, Bronte Park, i (TC); 1 ♀, Cambridge, i.1965, ex *Pinus radiata* log (Taylor) (ANIC); 1 ♀, Cambridge, xii.1964, ex *Pinus radiata* logs (Taylor) (BMNH); 1 ♀, 2 ♀, Hobart, xi.1922 (Cole) (NMV); 1 ♀, Hobart, xii.1915 (Cole) (NMV); 2 ♀, Launceston, x.1927 (Cole) (NMV); 1 ♀, Leven R., xi.1975 (Neboiss); 1 ♀, Ridgway, ix.1942 (Cole) (NMV); 2 ♀, Roseberry, i (TC); 1 ♀, Strahan, iii (TC).

*Labena grandis* sp. n.

(Fig. 15)

**Female.** Large species, fore wing length 17 mm. Malar space 0.5 times as long as basal mandibular width. Occipital carina mediodorsally complete, ventrally joining hypostomal carina and continuing to mandibular base as distinct carina, not forming a flange. Pronotum laterally with a median conical tubercle; mesothorax laterally and ventrally bearing sparse, short, white pubescence; mesoscutum strongly, transversely striate; horizontal mesopleural furrow distinct, at least posteriorly; metapleuron vermiculate; submetapleural carina strongly broadened into a triangular striate lobe. Propodeum with anterior transverse carina present centrally, separating area superomedial and area basalis. Fore wing with 2r-m converging towards 3r-m, almost joining it at junction with Rs. Hind wing with distal abscessa of Cu1 present on membrane, not confluent with Cu1 and cu-a. Mid tibia with longitudinal row of spine-like bristles on outer surface, the distal end swollen somewhat, proximally slender and with a diagonal internal furrow present. Gaster with sternite 1 0.5 times as long as hind coxa, reaching to level of spiracle; tergites 2-4 smooth and polished; apex of terminal plate of tergite 8 specialized. Ovipositor projecting beyond apex of gaster by 2-5 times length of hind tibia, the apex bearing very fine teeth.

Coloration. Black. Palps, labrum, clypeus, inner orbits, outer orbits, anterolateral margin of mesoscut-
tum, tegula, posterior 0.5 of subalar process, posterior 0.4 of propodeum, posterior margin of tergites 1-7, fore and mid legs (except inner surface of femur and tibia), hind leg with distal tip of coxa, trochanter, femur, proximal end of tibia and tarsus yellow.

**Male.** Unknown.

**Remarks.** Only a single specimen of this species is known. It is immediately distinguished by possession of a uniquely specialized tergite 8, having the metapleuron strongly vermiculate and having a swollen pronotum. The hind coxae are shorter and stouter than those of other species and the petiole is considerably more robust.

**Material Examined**

Holotype ♀, **Western Australia:** Yallingup, Cape Naturaliste, ix–x.1913 (*Turner*) (BMNH).

**Labena jacunda** sp. n.

(Fig. 17)

**Female.** Large species, fore wing length 13–14 mm. Malar space 0.6 times as long as basal mandibular width. Occipital carina mediodorsally complete, ventrally joining hypostomal carina far from base of mandible. Pronotum laterally weakly convex; mesothorax laterally and ventrally bearing sparse pubescence; mesoscutum with superficial punctures; horizontal mesopleural furrow indistinct; metapleuron finely sparsely punctate; submetapleural carina broadened anteriorly into ribbed lobe. Propodeum with anterior transverse carina complete so area superomedia is distinctly delineated. Fore wing with 3r-m slightly inclined, 2r-m strongly convergent anteriorly. Hind wing with distal abscissa of Cu1 complete. Mid tibia slender, cylindrical, with scattered spines on outer surface. Gaster with sternite 1 0.6-0.7 times as long as hind coxa, reaching to level of spiracle, the membranous portion unusual in being a pair of well-developed crests; tergites 2-4 smooth and polished; apex of terminal plate of tergite 8 simple. Ovipositor projecting beyond apex of gaster by about 3-5 times length of hind tibia, apex bearing 8 distinct strong teeth.

Coloration. Black. Face, frontal and genal orbits narrowly, tegula, small mark on subalar prominence, scutellum, posterior part of propodeum and posterior margins of all tergites yellow; mesopleuron and base of petiole reddish; anterior two pairs of legs predominantly yellow; hind legs black, distal apex of coxa and femur and proximal end of tibia and basitarsus yellow.

**Male.** Similar to female but with fore wing length 13–14 mm; malar space 0.3 times basal mandibular width; gaster with sternite 1 1.0 times as long as hind coxa. Gonosquama distally flattened, impressed, the impressed area surrounded by a fringe of long hairs. Black with face, frontal and genal orbit, tegula, subalar prominence, scutellum, postscutellum, hind margin of propodeum, broad posterior bands on g внут 4 tergites, anterior 2 pairs of legs, hind trochanter and trochantellus, proximal 0.5 of tibia, entire basitarsus and extreme proximal apex of second tarsal segment yellow. Flagellum black, with a subapical whitish mark that is not a complete band.

**Remarks.** The female of this species is immediately recognizable by the slender mid tibia and ventral petiolar prominences which are unique features of this species amongst Australian Labena. The broad yellow bands on the gaster distinguish the male of *jacunda* from *pudenda* and *keira*, the only other species with ornamented male gonosquamae.

**Material Examined**

Holotype ♀, **Victoria:** Chiltern (NMV).
Paratypes. **Victoria:** 2 O’, Mt Buffalo, 4,500’, 13.i.1955 (*Neboiss*) (NMV).

**Labena keira** sp. n.

(Figs 9, 12, 18, 19)

**Female.** Large species, fore wing length 11–16 mm. Malar space 0.5 times as long as basal mandibular width. Occipital carina mediodorsally complete, ventrally joining hypostomal carina and forming a flange. Pronotum laterally with a slight median swelling; mesothorax laterally and ventrally bearing no white pubescence; mesoscutum smooth, with sparse fine punctures; horizontal mesopleural furrow distinct and widening posteriorly; metapleuron smooth and polished; submetapleural carina slightly broadened anteriorly, not produced into a lobe. Propodeum with anterior transverse carina present centrally, separating area superomedia from area basalis. Fore wing with 3r-m and 2r-m convergent, sometimes almost joining at junction with Rs. Hind wing with distal abscissa of Cu1 complete. Mid tibia with a longitudinal row of spine-like bristles on outer surface, proximally slender and slightly flattened, distally
swollen. Gaster with sternite 1 0·7 times as long as hind coxa, just reaching to slightly behind level of spiracle; tergites 2–4 smooth and polished; apex of terminal plate of tergite 8 simple. Ovipositor projecting beyond apex of gaster by 3 times length of hind tibia, the apex bearing very fine teeth.

Coloration. Black to deep red. Palps, labrum, clypeus, face, outer orbits, frons (except ocellar triangle and vertex), scutellum, scutellar ridges, postscutellum, postscutellar ridges, tegulae, subalar process, small mesopleural macula, posterior 0·5 of propodeum, posterior margin of tergites 1–8 (often divided medially), fore and mid legs except sometimes distal 0·5 of mid femur, hind trochanters, basal 0·5 of tibia and basal tarsal segment yellow. Disruptive mark of antenna medially placed, apex of fore wing infumate.

**Male.** Similar to female but with fore wing length 8–13 mm; malar space 0·4 times basal mandibular width; gaster with sternite 1 0·9 times as long as hind coxa. Gonosquama distally flattened and fringed partially by very fine hairs. Coloration. As for female, sometimes with less yellow on gaster and no white disruptive marks on antenna.

**Remarks.** *L. keira* is immediately recognizable by the infumate mark on the distal apex of the fore wing. Structurally it is rather similar to *L. pudenda* from which it may be separated by the submetapleural carina being barely expanded, spinose mid tibia and centrally complete anterior transverse carina of the propodeum. This is one of the most widely distributed species of *Labena* and is recorded from Victoria north to central Queensland. It is also known to occur on Lord Howe Island.

**Material examined**

Holotype ♀, New South Wales: Mt Tomah, 28.iii.1980 (Rodd) (AM).

Paratypes. **Queensland:** 1 ♀, Bunya Mtns, i.1938 (Geary) (AM); 3 ♂, Eugenella, ix.1923 (NMV); 2 ♀, Eugenella, xi (TC); 1 ♀, 9 ♀, Montville, ix.1955 (Burns) (NMV); 1 ♂, 9 ♂, Mt Glorious, xi & i (TC); 4 ♀, 1 ♂, Mt Tambourine, x.1977 (Galloway) (BMNH); 7 ♀, 8 ♂, Mt Tambourine, xi–xii (TC); 1 ♀, Mt Tip Tree (17-02S 145-37E), x.1980 (Cardale) (ANIC); 1 ♂, Westwood, xi.1924 (Burns) (NMV); 1 ♂, Wilson’s Peak, Killarney, 9.i.1977 (Boucek) (BMNH). **New South Wales:** 1 ♂, Lord Howe Is., (AM); 1 ♂, Lord Howe Is., 30.xi.1955 (Paramonov & Leipa) (ANIC); 1 ♂, Lord Howe Is. xii.1977 (Liepa) (ANIC); 1 ♂, Mooney Mooney Creek, near Gosford, xi.1975 (McAlpine & Schneider) (AM). **Australian Capital Territory:** 1 ♀, Mt Gingera, i.1957 (Riek) (ANIC).

**Labena malecasta** sp. n.

(Fig. 16)

**Female.** Large species, fore wing length 13–15 mm. Malar space 0·8 times as long as basal mandibular width. Occipital carina mediodorsally complete, ventrally joining hypostomal carina and continuing to mandibular base as a distinct carina, not developed into a flange. Pronotum laterally with a median swelling; mesothorax laterally and ventrally bearing sparse, long, white pubescence; mesoscutum finely punctate with indications of weak transverse striae; horizontal mesopleural furrow indistinct; metapleuron indistinctly puncto-striate; submetapleural carina anteriorly abruptly expanded into an almost quadrate lobe. Propodeum with anterior transverse carina present centrally, separating area superomedia from area basalis, latter with transverse striae. Fore wing with 3r-m converging towards 2r-m, almost joining at junction with Rs. Hind wing with distal abscessa of Cu1 present in membrane, not confluent with Cu1 and cu-a. Mid tibia with a longitudinal row of spine-like bristles on outer surface, proximally slender, distally swollen, with an oblique furrow on inner surface. Gaster with sternite 1 0·7 times as long as hind coxa, reaching to well behind level of spiracle; tergites 2–4 smooth and polished with sparse, fine punctures; apex of terminal plate of tergite 8 simple. Ovipositor projecting beyond apex of gaster by at least 3·5 times length of hind tibia, the apex bearing distinct teeth.

Coloration. Black to red. Palps, clypeus, inner orbit of face, emargination of orbit opposite antennal socket, thin line on outer orbit, antero-lateral corner of mesocutum, tegula, subalar process, posterior 0·3 of scutellum, postscutellum, posterior 0·3 of propodeum, posterior margin of tergites 1–7, fore leg (except coxa and distal part of femur), mid leg with distal end of femur, tibia and tarsal segments 1–4, hind leg with distal end of tibia and basal tarsal segment yellow. Antennal disruptive mark at distal end except for last 1–2 segments which are blackish.

**Male.** Similar to female but with fore wing length 12 mm; malar space 0·5 times basal mandibular width; gaster with sternite 1 0·9 times as long as hind coxa. Gonosquama with an apical tuft of long hairs. Coloration similar to female.

**Remarks.** This large species is structurally rather similar to *L. chadwickii*. The female has a subtly different colour pattern and a longer ovipositor whilst the male is distinct in bearing a tuft of long hair on the gonosquama. *L. malecasta* is only known from Tasmania, Victoria and the southern alps of New South Wales.
Material examined

Holotype ♀, Tasmania (BMNH).


Labena pudenda sp. n.

(Figs 10, 20, 21)

Female. Large to very large species, fore wing length 13–20 mm. Malar space 0.7 times as long as basal mandibular width. Occipital carina mediodorsally complete, ventrally joining hypostomal carina and forming flange. Pronotum laterally with a median convex swelling; mesothorax laterally and ventrally bearing sparse, short white pubescence; mesoscutum smooth with sparse fine punctures; horizontal mesopleural furrow distinct; mesopleuron smooth and polished; metapleuron smooth and polished; submetapleural carina anteriorly expanded with a large rounded striate lobe. Propodeum with anterior transverse carina absent centrally so areae superomedia and basalis are confluent. Fore wing with 3r-m slightly inclined, 2r-m strongly converging towards 3r-m, both widely separated at junction with Rs. Hind wing with distal abscissa of Cu1 complete. Mid tibia without obvious spine-like bristles on outer surface, proximally slender and slightly flattened, distally swollen. Gaster with sternite 1 0.7–1.0 times as long as hind coxa, reaching behind level of spiracle; tergites 2–4 smooth and polished; apex of terminal plate of tergite 8 simple. Ovipositor projecting beyond apex of gaster by 4.0–4.4 times length of hind tibia, the apex bearing strong teeth.

Coloration. Black to deep red. Palps, labrum, clypeus, inner and outer orbits, ventral corner of propodeum, tegula, subalar process, scutellum, postscutellum, posterolateral corner of propodeum, posterior margin of tergites 1–7 (may be divided medially), fore and mid leg with distal part of coxa, trochanter, femur, distal and proximal ends of tibia and tarsal segments 1–4, hind leg with distal end of each segment including tarsal segment 1 and entire tarsal segments 2–4 yellow.

Male. Similar to female but with fore wing length 10–11 mm; malar space 0.9 times basal mandibular width; gaster with sternite 1 0.9 times as long as hind coxa. Gonosquama distally flattened and fringed almost entirely by very fine hairs. Coloration similar to female.

Remarks. This large, rather slender species is easily recognized by the very long ovipositor of the female. The tip of this organ is distinctive in having much coarser teeth than are usually found in species of Labena. Males have the most specialized gonosquamae of any Australian Labena species. L. pudenda seems to be a southern temperate forest species and has been recorded from New South Wales, Victoria and the Australian Capital Territory.

Material examined

Holotype ♀, Victoria: Bogong High Plains, xii.1931 (Kubala) (NMV).

Paratypes. New South Wales: 1 ♂, Dainer’s Gap (36-12S 148-43E), xi.1973 (Morrow) (ANIC); 1 ♀, Kosciusko, xii.1922 (Goldfinch) (AM); 1 ♀, Mt York, x.1930 (NMV). Australian Capital Territory: 1 ♀, Lees Springs, xi.1953 (Riek) (ANIC). Victoria: 1 ♀, 1 ♂, ‘Alps’, xii.1910 (NMV); 1 ♀, Mt Buffalo, 1600 m, ii (TC); 1 ♀, 2 ♂, ‘Victoria’, ii.1901 (French) (BMNH); 1 ♀, Yarra Falls, S. Warburton, i.1907 (Barnard) (NMV).

CERTONOTUS Kriechbaumer

Cernetotus Kriechbaumer, 1889: 308. Type-species: Cernetotus varius Kriechbaumer, by monotypy.


Small to very large insects, fore wing length 4–17 mm; clypeus flat, transverse, margin thin, evenly arcuate; labrum barely projecting; mandible short, stout but tapered, twisted 25–30°, with upper tooth the longer; outer mandibular surface with a groove bearing hairs; malar space trans-striate, usually a little longer than basal mandibular width. Occipital carina dorsally absent; eye not indented next to antennal socket. Antenna slightly clavate, apically pointed, without a flat sensillum. Mesoscutum with transverse rugae, notauli weak, notaular crests very weak. Propodeum usually quite short, convexly rounded with spiracle elliptical; anterior transverse carina usually complete except centrally, other carinae often reduced, area superomedia usually not delineated; gaster inserted high up on propodeum, above level of hind coxae. Fore tibia with a short tooth on outer distal margin; fore tarsus unspecialized; hind coxa of female with an anterior carina continued ventrally as a process, the area behind this carina concave and closely punctate;
tarsal claws simple. Fore wing with cu-a opposite or proximal to base of Rs\&M; 3r-m usually present, areolet almost triangular, often petiolate above; 2m-cu sinuous, with two close bullae. Hind wing with distal abscissa of Cu₁ present or incomplete or absent; first abscissa of Cu₁ shorter than cu-a; basal cell slender; Sc with one or two hamuli. Gaster quite long, tergite 1 from stout to quite slender, with spiracles before centre; sternite 1 usually reaching nearly to level of spiracles; laterotergites 2–4 membranous, folded under; tergite 8 highly modified, projecting laterally as a pair of prominences at either side of ovipositor base, dorsally with a detached plate projecting through concave orifice in hind margin, tergite 7 often mediadorsally incised. Ovipositor projecting beyond apex of gaster by 3.0–8.0 times length of hind tibia, its apex compressed, the upper valve with weak blunt serrations, the lower valve enclosing the upper and bearing fine file-like teeth.

REMARKS. Certonotus is a large genus centred in Australia with a few species present in New Guinea, New Zealand and South America. Previously, the species now included in this taxon were divided between Certonotus and Asperellus (Townes, 1969; Gauld, 1984) but more detailed study has revealed that the latter genus is almost certainly polyphyletic. In the present work 23 species are recognized as occurring in Australia.

Certonotus species are easily recognized by the possession of transverse rugae on the mesoscutum, a feature immediately distinguishing the genus from all other Australian labenines. Certonotus species may inadvertently be confused with Rhyssini, especially Epirhyssa species. Unlike rhyssines, which have an undeveloped submetapleural carina, Certonotus has a broad expanded lobe present anteriorly. Furthermore, Certonotus has fine file-like teeth on the ovipositor apex, not the coarse teeth found in Epirhyssa (Gauld, 1984).

The relationships of the Australian species. Gauld (1984) suggested that Asperellus, as defined by Townes (1969), was merely a specialized species-group of Certonotus. Further study suggests that Asperellus is not even a monophyletic group, but rather an assemblage of species of Certonotus that lack the distal abscissa of Cu₁. The majority of species (farrugiai, pineus, mogimbensis, zebrus, toolangi, hinnuleus and leeuwiniensis) do comprise a natural group, the leeuwiniensis-group. All have rather similar propodeal carination, in that the posterior transverse carina is absent but a large smooth area is enclosed by the anterior carina and the lateral carinae; they possess a very small areolet, have one or more spine-like bristles present on the hind tibia and have a slightly convex face. Most have a rather short first sternite, a quite deeply divided tergite 7 and a pronounced lobe on tergite 8. Only in farrugiai is tergite 7 barely indented posteriorly. The species ixion, paluma, celeus and Certonotus species A would all run to Asperellus in Townes’ (1969) key but these do not appear to be closely related to the others (i.e. the leeuwiniensis-group). The first three are closely related to Certonotus talus and belong to the humeralifer-group, which is defined by having a very deeply divided tergite 7 and possessing rather long narrow processes on tergite 8. The group includes seven Australian species – humeralifer, apicalis, talus, cestus, ixion, paluma and Certonotus species A. The New Zealand species C. fractinervis apparently also belongs to this group.

The majority of other Australian species (annulatus, nitidulus, geniculatus, rufescens, andrewi, avitus, sisyphus and celeus) constitute a third group, having a weakly to moderately deeply divided tergite 7, rounded lobes on tergite 8 and a relatively long first sternite. Within the nitidulus-group one rather distinctive lineage can be recognized comprising rufescens, geniculatus, sisyphus and celeus. These species all have flat lower faces, and most have the posterior end of the lateral propodeal carina broadened to form a raised keel.

The remaining Australian species, C. monticola, belongs to the flaviceps-group which is characterized by possession of elongate glossae and a very short occipital carinal stub. Males of species in this group are specialized in having a very elongate gaster (with tergite 7 about 1.5 times as long as broad or longer). Frequently the hind margins of the tergites are concave. This elongate form of the gaster is characteristic of wood-boring species in which the male copulates with the female prior to her emergence from the burrow (see Nuttall, 1973). The male of C. fractinervis resembles males of the flaviceps-group though the structure of the female suggests the species is best placed in the humeralifer-group.

The relationships of the species-groups are difficult to determine as there is considerable conflict in the characters. The leeuwiniensis-group, a holophyletic clade, may well be the sister-lineage of the humeralifer-group. Both have a similarly deeply divided tergite 7 and many often possess spine-like bristles on the hind tibia and show reduction in the distal abscissa of Cu₁. This arrangement leads to difficulty in placing C. farrugiai which has tergite 7 barely divided. The humeralifer-group could be paraphyletic with respect to the leeuwiniensis-group. The nitidulus-group could well be a paraphyletic assemblage, the stem group from which all others have arisen, although the rufescens-subgroup is clearly a holophyletic clade. The flaviceps-group is also undoubtedly a holophyletic clade.

The geographical distribution of the species-groups is as follows:
nitidulus-group: New Guinea, Australia;
rufescens-subgroup: Australia;
humeralifer-group: Australia, New Zealand;
flaviceps-group: Moluccas, New Guinea, tropical Australia;

Key to species of Cetonotus occurring in Australia

1  Hind wing with distal abscissa of Cu₁ complete ................................................. 2
   - Hind wing with distal abscissa of Cu₁ either incomplete, that is present in membrane but not
     joining Cu₁ & cu-a, or entirely absent ................................................................. 13

2  Gaster more or less entirely yellowish or orange-brown, the tergites in dorsal view, unicolorous
   or slightly infurcate along posterior margin ......................................................... 3
   - Gaster dark reddish brown or black, usually with conspicuous yellow spots or bands along
     margin of tergites, some marks with gaster unicolorous dark brown .......................... 7

3  Subalar prominence, in dorsal view, strongly raised, with a blunt, back-curved, thorn-like
   protuberance which is more sharply pointed in the male than the female (Fig. 22); malar
   space long (Fig. 25), in female 0-9–1-0 times as long as basal mandibular width, in male
   0-8–0-9 times as long; submetapleural carinal flange with a ridge delimiting an anterolateral
   triangular area ................................................. rufescens Morley (p. 133)
   - Subalar prominence in dorsal view at most convex, not produced into a spine-like protuberance
     (Figs 23, 24); malar space fairly short (Fig. 26), in female 0-7–0-8 or male 0-4–0-6 times as
     long as basal mandibular width; submetapleural carinal flange without a delimited triangular
     area anterolaterally ................................................................. 4

4  Pronotum in dorsal view with part before upper corner strongly convex or pyramidal (Figs 23,
   24); anterior transverse carina of propodeum present centrally (Fig. 27); 2r-m and 3r-m fused
   anteriorly so areolet is petiolate (Fig. 30) ......................................................... 5
   - Pronotum in dorsal view with part before upper corner flat to weakly convex; anterior
     transverse carina of propodeum absent centrally (Figs 28, 29); 2r-m and 3r-m joining Rs
     separately so areolet not petiolate (Fig. 31) ......................................................... 6

5  Upper part of pronotum pyramidal in dorsal view (Fig. 24); female with ovipositor about 5
   times as long as hind tibia; hind tibia with one spine-like bristle on posterior margin;
   flagellum entirely black .............................................................................. humeralifer Krieger (p. 127)
   - Upper part of pronotum simply strongly convex in dorsal view (Fig. 23); female with ovipositor
     7-5 or more times as long as hind tibia; hind tibia without a spine-like bristle or posterior
     margin; flagellum with distal end white ......................................................... apicalis Morley (p. 122)

6  Posterior transverse carina of propodeum centrally strongly raised (Fig. 28); antenna with
   apical 10 or so segments whitish; spiracular area bounded posteriorly by carina, thus being
   separated from lateral area ........................................................................... annulatus Morley (p. 121)
   - Posterior transverse carina of propodeum absent centrally (Fig. 29); antenna with apical
     segments black but with a subapical white band; spiracular area confluent with lateral area
     andrewi sp. n. (p. 121) ................................................................. 8

7  Males and females with tergites 2–5 with yellow band along hind margin .......................... 8
   - Females with tergites 2–5 with paired yellow spots or the males either with paired yellow spots
     or without yellow marks at all ................................................................. 9

8  Metapleuron centrally with conspicuous longitudinal wrinkles; propodeum with a tubercle
   below spiracle (Fig. 32); flagellum distally uniformly black; anterolateral part of mesoscutum
   without yellow marks ....................................................................................... geniculatus Morley (p. 124)
   - Metapleuron centrally smooth; propodeum without a tubercle below spiracle (Fig. 33);
     flagellum distally white-marked; anterolateral part of mesoscutum yellow-marked
     nitidulus Morley (p. 131) ................................................................. 9

9  Subalar prominence bearing a long slender back-curved spine (Fig. 34); female with tergite 8
   posteriorly extended into a narrow truncate projection (Fig. 35) ................ talus sp. n. (in part) (p. 135)
   - Subalar prominence without a spine; female with tergite 8 bluntly rounded apically (Figs 36,
     37) ................................................................. 10

10 Labium with glossae very long and slender, extending ventrally a distance of approximately the
    height of the eye; occipital carina represented by a short vestige at its junction with
    hypostomal carina (Fig. 38); propodeum (at least part behind anterior transverse carina)
    yellow ........................................................................ monticola Morley (p. 130)
- Labium with glossae short, barely projecting below head; occipital carina present ventrally, at least as long as abscissa of hypostomal carina between mandible and junction with occipital carina (Fig. 39); propodeum not or only partially yellow-marked behind anterior transverse carina ........................................ 11

- Propodeum with anterior and posterior transverse carinae strong, complete and almost parallel to each other (Fig. 40); lateromedian carinae not present between transverse carina; hind tibia uniformly reddish; females with malar space brown .......... sisyphus sp. n. (p. 134)

- Propodeum with anterior or posterior transverse carina weak or missing in part, the carinae not parallel and often with discernible traces of lateromedian longitudinal carinae between them (Fig. 41); hind tibia proximally pale-marked; females with malar space whitish ................. 12

- Sternite 1 long, extending behind spiracles and being about length of hind coxa; submetapleural carina anteriorly broadened to form a rectangular flange (Fig. 42); mesoscum with pair of pale stripes extending back from anterior margin .......... avitus sp. n. (p. 123)

- Sternite 1 short, reaching at most (in males) to level of spiracles, and being distinctly shorter than length of hind coxa; submetapleural carina anteriorly broadened to form a rounded lobe (Fig. 43); mesoscum with a median pale rectangular mark .............. cestus sp. n. (p. 123)

- Hind wing with distal abscissa of Cu1 absent; hind tibia with posterior margin bearing one or more spine-like bristles .......... 14

- Hind wing with distal abscissa of Cu1 present in membrane, not joining nervellus; hind tibia with posterior margin devoid of spine-like bristles ............... 22

- Tergite 2 of gaster entirely white; alitrunck anteriorly reddish brown, propodeum infuscate, gaster in greater part black (Fig. 58); wings uniformly infumate; antenna of female black; female with posterior margin of tergite 7 only slightly indented ........... farrugiai sp. n. (p. 126)

- Tergite 2 of gaster yellowish brown, or dark brown or pale spotted but never entirely white (Figs 59–62); alitrunck variously coloured, if brownish then concolorous with much of gaster; wings hyaline or apically infumate; antenna of female with white bands; female with posterior margin deeply indented medially .......... 15

- First segment of gaster exceptionally long and slender, the sternite far longer than length of hind coxa; propodeum with first and second lateral areae clearly defined and separated (Fig. 44); apex of fore wing of female narrowly infumate .......... celeus sp. n. (p. 125)

- First segment of gaster stouter, the sternite not longer than hind coxa; propodeum with first and second lateral areae confluent, often not defined laterally (Fig. 45); apex of fore wing not infumate ......... 16

- Gaster more or less uniformly yellowish or orange; female with at least distal two flagellar segments entirely black so white ruptive mark is a subapical band .......... 17

- Gaster predominantly black with white maculae; female with distal end of flagellum white except for tip of apical segment which is black ......... 18

- Pronotum convexly produced before upper hind corner, the convexity almost pyramidal in dorsal view (Fig. 46); female with tergite 9 in dorsal view transverse; female hind tarsus black; male with 3r-m present .......... pineus sp. n. (p. 132)

- Pronotum weakly convex before upper hind corner (Fig. 47); female with tergite 9 in dorsal view elongate; female hind tarsus yellow; male with 3r-m absent. mogimbensis Cheesman (p. 129)

- Tergite 2–5 with hind margin banded with yellow, occasionally with bands very faint so tergite is almost unicolorous .......... 19

- Tergite 2–5 with yellow spots on posterolateral corners, these marks not confluent centrally ....... 21

- Propodeum with area superomedialia distinct, hexagonal, with only posterolateral sides rather weak (Fig. 48); tergite 8 produced into long slender processes (Fig. 50); tergites 1–2 not clearly whitish or yellow-marked .......... species A (p. 137)

- Propodeum with area superomedialia undefined laterally and posteriorly (Fig. 49); tergite 8 produced into blunt or moderately long processes (Fig. 51); tergites 1–2 clearly whitish or yellow-banded posteriorly (Fig. 59) ......... 20

- Metapleuron closely punctate; lower face distinctly transverse (Fig. 52); hind coxa dorsally brown; propodeum in lateral aspect brownish .......... leeuwinensis Turner (p. 128)

- Metapleuron virtually smooth; lower face longer than broad (Fig. 53); hind coxa entirely black; propodeum in lateral aspect predominantly whish ......... zebrus sp. n. (p. 136)

- Pronotum convexly produced before upper hind corner; propodeum in lateral view extensively whitish; metapleuron virtually impunctate; hind tibia with an indistinct yellowish mark proximally .......... hinnuleus Krieger (p. 126)
- Pronotum very weakly convex before upper hind corner; propodeum in lateral view brown (Fig. 60); metapleuron closely punctate; hind tibia with proximal 0-5 whitis toolangi sp. n. (p. 136)

22 Subalar prominence bearing a long slender back-curved spine (Fig. 34); female flagellum with a subapical white band, the distal 5 or so segments black.......................... talus sp. n. (in part)(p. 135)
- Subalar prominence simple; flagellum with apical segments white, only extreme distal apex of last segment blackish or entirely black ........................................... 23

23 Tergites 4 and 5 of gaster with anterolateral corners broadly white (Fig. 62); hind coxa in profile rather short and stout, the ovipositor guide reaching to about the centre (Fig. 54); process on tergite 8 very slender; ovipositor about 4 times as long as hind tibia ............ paluma sp. n. (p. 132)
- Tergites 4 and 5 of gaster with only small white triangular marks in posterolateral corners (Fig. 61); hind coxa in profile slender, the ovipositor guide reaching about 0-3 of its length (Fig. 55); process on tergite 8 moderately slender; ovipositor about 5-5 times as long as hind tibia ixion sp. n. (p. 128)

Certonotus andrewi sp. n.

(Fig. 29)

*Female.* Medium to large-sized species, fore wing length 7–14 mm. Labium with glossae unspecialized. Lower face at narrowest point 1-0–1-1 times as broad as high; malar space 0-7–0-8 times as long as basal mandibular width. Occipital carina ventrally more than twice as long as absicissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, almost flat, in dorsal view barely projecting beyond scutal margin; subalar prominence moderately convex. Scutellum transversely striate, crest strong; metapleuron smooth and polished; submetapleural carina anteriorly expanded into a moderately broad, rather long lobe; metanotum with very strong tooth opposite anterior end of lateral carina. Propodeum moderately short with anterior transverse carina incomplete centrally; posterior transverse carina absent centrally; lateromedian longitudinal carina present only before anterior carina; pleural carina complete, but weak posteriorly; area superomedial undefined; area spiracularis confluent with first lateral area; first and second lateral area separated by a carina. Fore wing with 3r-m converging towards 2r-m, joining Rs separately; 2m-cu joining M 0-25 to 0-50 from 3r-m towards 2r-m. Hind wing with distal absicissa of Cu1 distinct to wing margin. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 short, the sternite 0-5–0-6 times as long as hind coxa, reaching to level of spiracle. Tergite 7 mediodorsally without any indentation; tergite 8 posteriorly with process short and rounded; tergite 9 in dorsal view transverse. Ovipositor projecting beyond apex of gaster by 3-5 to 4-0 times length of hind tibia.

*Coloration.* Orange-yellow species with frons centrally, vertex, mesoscutal stripes, most of gaster and hind legs more brownish or orange; flagellum black with subapical white band. Pterostigma brown, wings hyaline.

*Male.* Similar to female.

*Remarks.* Very like *C. annulatus* which it resembles in colour, venation, possession of short malar space and an almost flat pronotum. *C. andrewi* appears to be a more southern species than *annulatus* as it has been collected in southern Queensland, New South Wales and Victoria.

*Material Examined*

Paratypes. *Queensland*: 1 ♀, Brisbane, xii.1972 (*Sedlacek*) (TC); 4 ♀, Mt Glorious, near Brisbane, xii.1976 (*Bouček*) (BMNH); 1 ♀, 6 ♂, Mt Glorious, xi (TC). *New South Wales*: 1 ♀, Cabbage Tree Ck, Clyde Mtn, ix.1979 (*Naumann & Cardale*) (ANIC); 1 ♀, Iluka, Clarence R., rain forest, xi.1970 (*McAlpine*) (AM); 1 ♀, Warren, ix.1982 (*Holloway*) (AM). *Victoria*: 1 ♀, ‘Victoria’ (NMV).

Certonotus annulatus Morley

(Figs 28, 31)

*Certonotus annulatus* Morley, 1913: 31; Turner, 1919: 551. LECTOTYPE ♀, *Queensland* (BMNH), here designated [examined].

*Female.* Moderately large species, fore wing length 9–13 mm. Labium with glossae very slightly lengthened. Lower face at narrowest point 0-9 times as broad as high; malar space 0-7–0-8 times as long as basal mandibular width. Occipital carina ventrally about as long as absicissa of hypostomal carina between it and
mandibular base. Upper part of pronotum, slightly before posterior corner, very weakly convex, in dorsal view projecting only slightly beyond scutal margin; subalar prominence weakly convex. Scutellum punctate, transverse crest distinct; metapleuron virtually smooth except for a few striae ventrally and posteriorly; submetapleural carina anteriorly expanded into a broad rounded lobe that usually bears concentric striae; metanotum with a blunt tooth opposite anterior end of lateral carina. Propodeum moderately long with anterior transverse carina centrally absent; posterior transverse carina centrally present; lateromedian longitudinal carina complete only anteriorly and with stub behind anterior transverse carina; pleural carina complete; area superomedian indicated, but incomplete anteriorly and laterally; area spiracularis complete; first and second lateral areareae separated, distinctly delineated. Fore wing with 3r-m converging towards 2r-m, joining Rs separately; 2m-cu joining M 0-2-0.3 from 3r-m towards 2r-m. Hind wing with distal abscissa of Cu1 distinct to wing margin. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 short, the sternite 0.5-0.6 times as long as hind coxa, reaching behind level of spiracle. Tergite 7 mediadorsally with a short, narrow slit on posterior margin; tergite 8 posteriorly with process long and truncate; tergite 9 in dorsal view elongate and weakly rounded posteriorly. Ovipositor projecting beyond apex of gaster by 4.5 times length of hind tibia.

Coloration. Orange species with face and orbits, notauli, subalar prominences, scutellar margins and hind margins of gasteral tergites more yellowish; flagellum black with distal 10 or so segments white. Pterostigma blackish, wings very weakly infumate.

Male. Similar to female but with fore wing length 8 mm; malar space 0.4 times basal mandibular width; 3r-m present; gaster with segment 1 moderately slender, the sternite 0.5 times as long as hind coxa. Apex of gonosquama flattened, bearing a tuft of long hairs. Coloration as for female.

Remarks. *C. annulatus* is rather similar to and probably the sister species of *C. andrewi*. The two species are fairly easily separated by the characters given in the key.

*C. annulatus* seems to be a north Queensland species.

Material examined
Lectotype \(\varphi\), Queensland: Kuranda near Cairns, xii.1901 (BMNH).

Queensland: 2 \(\varphi\) (paralectotypes), Kuranda, xii.1901, iv.1902 (BMNH); 1 \(\varphi\), Kuranda, ii.1935 (Burns) (NMV); 1 \(\varphi\), Mission Beach, near Tully, iv.1971 (Moulds) (AM); 1 \(\varphi\), 2 \(\sigma\), Moses Ck, 4 km N. by E. Mt Finnigan (15-47S 145-17E), at light, x.1980 (Cardale) (ANIC); 2 \(\sigma\), Paluma (19-00S 146-12E), 900 m, Malaise trap, x.1980 (Frith) (ANIC); 1 \(\varphi\), Shipton's Flat (15-47S 145-14E), at light, x.1980 (Cardale) (ANIC).

*Certonotus apicalis* Morley

(Fig. 23)

*Certonotus apicalis* Morley, 1913: 31; Turner, 1919: 551. LECTOTYPE \(\varphi\), QUEENSLAND (BMNH), here designated [examined]

Female. Large species, fore wing length 12-15 mm. Labium with glossae slightly lengthened. Lower face at narrowest point 1-0-1-1 times as broad as high; malar space 0.7-0.8 times as long as basal mandibular width. Occipital carina ventrally sinuous, more than twice as long as abscissa of hypostomal carina between it and base of mandibles. Upper part of pronotum, slightly before posterior corner, convex, in dorsal view projecting as a rounded protuberance; subalar prominence quite strongly convex. Scutellum punctate, transverse crest weak; metapleuron with fine sparse punctures; submetapleural carina anteriorly expanded into a broad rounded lobe; metanotum with a weak swelling in front of lateral carina. Propodeum moderately short with anterior transverse carina complete; posterior transverse carina present centrally; lateromedian longitudinal carina present before anterior carina only; pleural carina strong anteriorly, weak posteriorly; area superomedian not defined laterally; area spiracularis complete; first and second lateral areareae more or less completely separated, the latter usually undefined externally. Fore wing with 3r-m fused anteriorly with 2r-m, so areolet is petiolate; 2m-cu joining M 0-20-0-25 basal of 3r-m. Hind wing with distal abscissa of Cu1 distinct to wing margin. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 short, the sternite 0.5 times as long as hind coxa, not reaching level of spiracle. Tergite 7 mediadorsally divided about 0.5 times its length; tergite 8 posteriorly with long narrow process; tergite 9 in dorsal view transverse, rounded apically. Ovipositor projecting beyond apex of gaster by 7-5 or more times length of hind tibia.

Coloration. Yellowish brown species, antenna black with distal segments white, the apical one or two segments slightly infuscate. Pterostigma black, wings weakly infumate.

Male. Similar to female but with fore wing length 9 mm; malar space 0.5 times basal mandibular width;
3r-m fused anteriorly with 2r-m; gaster with segment 1 short, the sternite 0-7 times as long as hind coxa, apex of gonosquama flattened, with a tuft of long close hairs. Colour similar to female but pterostigma dark brown.

REMARKS. The females of this species are easily distinguished by their very long ovipositors, the apices of which are fairly bluntly pointed. The fore femur is also rather distinctive, being slender proximally, then abruptly inflated proximocent rally. This is most similar to C. humeralifer and the two are probably sister-taxa. C. apicalis is a tropical species, only recorded from Queensland.

MATERIAL EXAMINED
Lectotype ♀, Queensway: Kuranda near Cairns, iv.1902 (BMNH).
Queensland: 3 ♀ (paralectotypes), same data as holotype (BMNH); 1 ♂, Kuranda, v–vi.1913 (Turner) (BMNH); 1 ♀, Paluma, mv lamp, i.1970 (Holloway) (AM).

Certonotus avitus sp. n.
(Figs 41, 42)

Female. Medium-sized species, fore wing length 8–10 mm. Labium with glossae unspecialized. Lower face at narrowest point 1·0 times as broad as high; malar space 0·4–0·6 times as long as basal mandibular width. Occipital carina ventrally sinuous, more than 3 times as long as abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, almost flat, in dorsal view barely projecting beyond scutal margin; subalar prominence weakly convex. Scutellum finely punctate, crest strong; metapleural finely punctate, obsolescent striae posteriorly; submetapleural carina anteriorly expanded into a rectangular elongate flange; metanotum laterally produced into a stout tooth in front of lateral carina. Propodeum moderately long with anterior transverse carina incomplete centrally; posterior transverse carina absent except laterally; lateromedian longitudinal carina present only before anterior carina; pleural carina incomplete posteriorly; area superomedia indistinct; area spiracularis complete; first and second lateral areae separated, the second not defined laterally. Fore wing with 3r-m converging towards 2r-m, widely separated on Rs; 2m-cu joining M 0·3 from 3r-m towards 2r-m. Hind wing with distal abscissa of Cu1 distinct to wing margin. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 long, the sternite 1·2 times as long as hind coxa, reaching well behind level of spiracle. Tergite 7 mediodorsally with indentation to 0·25 of tergite length; tergite 8 posteriorly with short, rounded process; tergite 9 in dorsal view transverse. Ovipositor projecting beyond apex of gaster by 5 times length of hind tibia.

Coloration. Flagellum black, distal apex white; head brown, orbits entirely and all of lower face whitish; alitrunk dark brown, notaular stripes, subalar prominence, tegula, scutellum, postscutellum, mesopleural stripe and posterior part of propodeum/metapleuron yellow. Gaster reddish brown, tergites laterally yellow and with posteralateral yellow spots. Tergite 1 anteriorly yellowish. Anterior two pairs of coxae whitish, hind ones brown with white apices; all tibiae and tarsi infuscate; femora brown, distally pale. Pterostigma dark brown; wings hyaline.

Male. Similar to female but with fore wing length 8 mm; malar space 0·3–0·4 basal mandibular width; 3r-m present; gaster with segment 1 slender, the sternite 1·0 times as long as hind coxa. Gonosquama with apex slightly flattened, with a tuft of close moderately long hairs. Similar in colour to female.

REMARKS. C. avitus is a distinctive species with a very characteristic submetapleural carina. For its size this species has a rather large areolet and a fairly long first sternite.

It is known from eastern Australia, from southern Queensland to Victoria.

MATERIAL EXAMINED
Holotype ♀, New South Wales: Mt Tomah, Blue Mtns, viii.1979 (Rodd) (AM).
Paratypes. Queensland: 1 ♀, Eungella, xi (TC); 1 ♀, Mt Glorious, i (TC); 1 ♂, Mt Nebo, viii (TC); 1 ♀, Mt Tamborine, ix–x.1978 (Galloway) (BMNH). Victoria: 1 ♂, Healesville, xi.1943 (NMV); 1 ♀, King Lake, x.1953 (Burns) (NMV); 1 ♂, King Lake, x.1954 (Burns) (NMV); 4 ♀, 1 ♂, Toolangi, xi.1982 (Farrugia) (BMNH).

Certonotus cestus sp. n.
(Figs 37, 43)

Female. Medium-sized species, fore wing length 9 mm. Labium with glossae unspecialized. Lower face at narrowest point 1·1 times as broad as high; malar space 1·0 times as long as basal mandibular width.
Occipital carina ventrally longer than abscissa of hypostomal carina between it and lobe of mandible. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view barely protruding beyond scutal margin; subalar prominence quite strongly convex. Scutellum coarsely punctate, crest strong; metapleurum small and polished; submetapleural carina anteriorly expanded into a rounded lobe, metanotum barely produced before lateral carina. Propodeum moderately long with anterior transverse carina obsolescent centrally; posterior transverse carina weak but more or less complete; lateromedian longitudinal carina present anteriorly and weakly between transverse carina; pleural carina anteriorly strong, posteriorly weaker or absent; area superomedia more or less distinct, not defined anteriorly; area spiracularis complete; first and second lateral areae separated, the first very short, the second ill-defined externally. Fore wing with 3r-m converging towards 2r-m, joining Rs separately; 2m-cu joining M opposite 3r-m. Hind wing with distal abscissa of CuI distinct to wing margin. Hind tibia with posterior margin with two spine-like bristles. Gaster with segment 1 short and broad posteriorly, the sternite 0-5 times as long as hind coxa, reaching almost to level of spiracle. Tergite 7 mediodorsally with broad indentation; tergite 8 posteriorly short and rounded; tergite 9 in dorsal view very broad. Ovipositor projecting beyond apex of gaster by 6 times length of hind tibia.

Coloration. Very dark brown species, flagellum with a white subapical band; facial, frontal and genal orbits, upper and lower margin of pronotum, mesoscutum in a central quadrate spot and indistinctly laterally, scutellum, postscutellum, subalar prominence, anterior and posterior mesopleural spots, most of hind part of propodeum and metapleuron whitish. Gaster dark brown with large anterolateral spots. Anterior coxa whitish, hind coxa brown with whitish mark. Pterostigma blackish, wings hyaline.

**Male.** Similar to female but with fore wing length 9 mm; malar space 0-7 times basal mandibular width; 3r-m present; gaster with segment 1 quite stout, the sternite 0-5 times as long as hind coxa. Apex of gonosquama with a small lobe that bears scattered long hairs. Colour similar to female but face entirely pale.

**Remarks.** This species is readily recognizable by its colour pattern. Structurally it seems to be related to the *C. humeralifer*-group as it has tergite 7 very deeply divided. Tergite 8 is less pronounced apically in this species than others in the *humeralifer*-group.

It is known from Queensland and New South Wales.

**Host record.** Buprestidae: *Diadoxus* sp. (ANIC).

**Material examined**

Holotype ♀, New South Wales: State Forest 854, viii.1952 (Martin) (ANIC), parasite of Diadoxus.

Paratype. Queensland: 1 ♂, viii.1926 (Jarvis) (BMNH).

*Certonotus geniculatus* Morley

(Fig. 32)

*Certonotus geniculatus* Morley, 1913: 28. LECTOTYPE ♀, VICTORIA (BMNH), here designated [examined].

**Female.** Large species, fore wing length 12–17 mm. Labium with glossae slightly lengthened. Lower face at narrowest point 1-1-1-2 times as broad as high; malar space 0-9–1-0 times as long as basal mandibular width. Occipital carina ventrally about as long as abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, very weakly convex, in dorsal view barely projecting beyond scutal margin; subalar prominence weakly convex. Scutellum punctate with strong transverse crest; metapleuron longitudinally striate; submetapleural carina anteriorly expanded into a moderately broad lobe; metanotum produced into a tooth opposite anterior end of lateral carina. Propodeum quite short with anterior transverse carina incomplete centrally; posterior transverse carina vestigial; lateromedian longitudinal carina present only as vestige anteriorly; pleural carina strongly raised into tubercle below spiracle, posteriorly obsolescent; area superomedia undefined; area spiracularis not completely delineated posteriorly; first and second lateral areae separated, but not clearly delineated internally or laterally. Fore wing with 3r-m and 2r-m converging but not joining anteriorly. Hind wing with distal abscissa of CuI distinct to hind margin. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 long and narrow, the sternite 1-0–1-3 times as long as hind coxa, reaching behind level of spiracle. Tergite 7 mediodorsally with very small indentation on posterior margin; tergite 8 posteriorly short and rounded. Tergite 9 in dorsal view broad. Ovipositor projecting beyond apex of gaster by 5-5 to 7-0 times length of hind tibia.

Coloration. Antenna black; head black, lower face, frontal and genal orbits yellow. Alitrunk red-brown with periphery of sclerites infuscate, only tegula, scutellum posteriorly, postscutellum and hind end of
propodeum yellow. Gaster reddish brown, tergite 1 anteriorly, laterally and posteriorly yellow, other tergites with lateral and posterior margins yellow. Fore leg yellow, proximal part of femur black; mid leg yellow, coxa basally, femur proximally and tarsus black. Hind leg black, coxa distally, trochanter segments, distal apex of femur, base and apex of tibia yellow. Pterostigma dark brown, wings virtually hyaline.

Male. Similar to female but with fore wing length 11 mm; malar space 0-7-0-9 times basal mandibular width; 3r-m present; gaster with segment 1 very slender, the sternite 1-3 times as long as hind coxa. Apex of gonosquama flattened with a dense tuft of long hairs. Colour similar to female.

Remarks. C. geniculatus belongs to the rufescens-subgroup of the tasmaniensis-group. It is probably the sister-species of C. rufescens. Both have the prementum and glossae somewhat lengthened, have a very flat face, the anterior portion of the lateral carina strongly raised and the pleural carina raised into a tubercle below the propodeal spiracle. C. geniculatus is most easily distinguished by the possession of a longitudinally striate metapleuron.

This is a southern species, only recorded from Victoria.

Material examined

Lectotype ♀, Victoria: Nulla Wurren, near Berwick (BMNH).

Victoria: 1 ♀, 2 ♂ (paralactotypes), same data as lectotype (BMNH); 1 ♀, Buckland River, xi.1964 (Neboiss) (NMV); 1 ♂, Fernshaw (NMV); 1 ♀, 1 ♂, Trafalgar (NMV).

Cerotonotus celeus sp. n.

(Fig. 44)

Female. Medium-sized species, fore wing length 8-9 mm. Labium with glossae slightly lengthened. Lower face at narrowest point 0-9 times as broad as high; malar space 1-3-1-4 times as long as basal mandibular width. Occipital carina ventrally slightly longer than abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, very weakly convex, in dorsal view projecting slightly beyond mesoscutal margin; subalar prominence moderately convex. Scutellum sparsely punctate with strong crest posteriorly; metapleuron smooth, very sparsely punctate; submetapleural carina anteriorly strongly expanded into a quadrate lobe that is abruptly narrowed posteriorly; metanotum with a weak lateral tooth. Propodeum quite long with anterior transverse carina complete; posterior transverse carina complete; lateromedian longitudinal carina present only anterior to anterior carina; pleural carina complete; area superomedia not defined; area spiracularis clearly delineated; first and second lateral areae distinct, separated. Fore wing with 3r-m converging towards 2r-m, joining Rs separately; 2m-cu joining M 0-3 from 3r-m towards 2r-m. Hind wing with distal abscissa of CuI absent. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 very long and narrow, the sternite 1-2-1-6 times as long as hind coxa, reaching well behind level of spiracle. Tergite 7 mediadorsally with shallow indentation; tergite 8 posteriorly short and rounded; tergite 9 in dorsal view short and pointed. Ovipositor projecting beyond apex of gaster by 4-5 times length of hind tibia.

Coloration. Red-brown species, flagellum black with subapical white band, lower face yellowish, anterior leg orange. Pterostigma dark brown; wings hyaline, apex of fore wing strongly infumate.

Putative male. Similar to female but with fore wing length 8 mm; malar space 0-6 times basal mandibular width; 3r-m present; propodeal carinae weaker; gaster with segment 1 slender, the sternite 0-9 times as long as hind coxa. Apex of gonosquama rounded, with scattered fine hairs. Pale orange, antenna black, head yellowish and wings uniformly hyaline.

Remarks. A distinctive species on account of the infumate tip to the fore wing of the female, the very long petiole, long hind coxa and rather flat face. It is probably related to C. rufescens though it is the only species in this subgroup without the distal abscissa of CuI. The male, here tentatively associated, has similarly long coxae and a rather flat face but has no clear posterior transverse propodeal carina nor has the wing apices infumate.

It is only known from Queensland.

Material examined

Holotype ♀, Queensland: Baldy Mtn Rd, via Atherton, Malaise trap, vi.1981 (Brown) (QM).

Paratypes. Queensland: 1 ♀, same data as holotype (BMNH); 1 ♂, Eungella Nat. Park, xi.1976 (Bouček) (BMNH); 1 ♀, Windsor Tableland, iii.1981 (Storey) (BMNH).
Certonotus farrugiai sp. n.

(Fig. 58)

**Female.** Medium-sized species, fore wing length 6-10 mm. Labium with glossae unspecialized. Lower face at narrowest point 1·1-1·2 times as broad as high; malar space 1·2-1·3 times as long as basal mandibular width. Occipital carina ventrally as long as abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, almost flat, in dorsal view barely projecting beyond mesoscutal margin; subalar prominence quite strongly convex and medially raised in dorsal aspect. Scutellum smooth, virtually impunctate with weak transverse carina apically; metapleuron anteriorly smooth, posteriorly with few coarse punctures; submetapleural carina anteriorly expanded into a broad rounded lobe; metanotum with a small lateral tooth before vestige of lateral carina. Propodeum moderately short with anterior transverse carina complete; posterior transverse carina absent; lateromedian longitudinal carina absent; pleural carina present, posteriorly obsolescent; area superomedial undefined; area spiracularis defined except medially; first and second lateral areae confluent. Fore wing with 3r-m converging towards 2r-m, joining latter at Rs or sometimes slightly separated; 2m-cu joining M slightly basad of 3r-m. Hind wing with distal abscissa of Cu1 absent. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 short and broad, the sternite 0·4-0·6 times as long as hind coxa, reaching to level of spiracle. Tergite 7 mediadorsally with wide indentation; tergite 8 posteriorly short and broadly rounded; tergite 9 in dorsal view short and broad. Ovipositor projecting beyond apex of gaster by 3·0-3·5 times length of hind tibia.

Coloration. Head and anterior part of alitrunk reddish brown; antenna, much of metapleuron and propodeum black; gaster black, tergite 2 entirely and posterior margins of tergites 3+ white; anteriorly red-brown, partially infuscate; hind leg mainly black. Pterostigma black, wings strongly infumate.

**Male.** Similar to female but with fore wing length 6 mm; malar space 0·8 times basal mandibular width; 3r-m present; gaster with segment 1 stout, the sternite 0·6 times as long as hind coxa. Apex of gaster rounded, bearing long scattered hairs. Similar in colour to female but with gaster entirely red; mid leg brownish.

**Remarks.** C. farrugiai is probably the most distinct species in the genus on account of its striking colour pattern which resembles that of a number of other unrelated species of Hymenoptera occurring in south-eastern Australia. Structurally it is also distinctive in having the posterior margin of tergite 7 only weakly indented.

This species occurs from south-eastern Queensland to Victoria.

**Material examined**

Holotype ♂, **Victoria**: Toolangi, xii.1982 (Farrugia) (AM).

Paratypes. **Queensland**: 4 ♂, Mt Glorious, xi–iii (TC); 1 ♂, Mt Nebo, 500 m, iii (TC); 1 ♂, Tambourine, x.1977 (Galloway) (BMNH); 1 ♂, Mt Tambourine, iv.1935 (Turner) (BMNH); 1 ♂, 2 ♀, Mt Tambourine, x–xii (TC). **Victoria**: 2 ♂, same data as holotype (BMNH).

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*Certonotus hinnuleus* Krieger comb. rev.

*Certonotus hinnuleus* Krieger, 1901: 123; Turner, 1919: 551. Holotype ♂, **New South Wales** (MNHU) [not examined].

*Certonotus* n. sp.; **Fullaway**, 1942: 244.

*Asperellus hinnuleus* (Krieger) **Townes et al.**, 1961: 114.

**Female.** Fairly small species, fore wing length 4–7 mm. Labium with glossae unspecialized. Lower face at narrowest point 1·2 times as broad as high; malar space 1·2–1·4 times as long as basal mandibular width. Occipital carina ventrally almost twice as long as abscissa of hypostomal carina between it and mandible base. Upper part of pronotum, slightly before posterior corner, very convex, in dorsal view appearing as a conical projection; subalar prominence moderately convex. Scutellum sparsely punctate with strong transverse keel; metapleuron smooth and polished; submetapleural carina anteriorly expanded into a broad triangular lobe; metanotum without a tooth. Propodeum short with anterior transverse carina complete, close to anterior margin; posterior transverse carina absent; lateromedian longitudinal carina present before anterior transverse carina; pleural carina present anteriorly, posteriorly absent; area superomedial not delineated; area spiracularis not delineated internally; first and second lateral areae indistinctly delineated, confluent. Fore wing with 3r-m converging towards 2r-m, sometimes forming a petiolate areolet or joining at one point on Rs; 2m-cu joining M at 3r-m or slightly basad. Hind wing with distal abscissa of Cu1 absent. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 short and broad, the sternite 0·6 times as long as hind coxa, reaching to level of spiracle. Tergite 7...
mediodorsally with large indentation; tergite 8 posteriorly short, broad, truncate; tergite 9 in dorsal view short, rounded posteriorly. Ovipositor projecting beyond apex of gaster by 5-0-5.5 times length of hind tibia.

Coloration. Antenna black, distal flagellar segments white; head white, vertex, interocellar area and frons centrally whitish; mesoscutum brownish or blackish with a yellow central quadrate mark; most of pronotum, tegula, subalar prominence, metapleuron and propodeum almost entirely yellowish; metapleuron brownish. Gaster dark brown with lateral margins and spots near posterolateral corners yellow; legs brownish; tibia proximally and femur distally somewhat paler; fore coxa whitish. Pterostigma blackish, wings very weakly infumate.

**Male.** Similar to female but with fore wing length 3-6 mm; malar space 0.9-1.0 times basal mandibular width; 3r-m present; gaster with segment 1 quite stout, the sternite 0.5 times as long as hind coxa; apex of gonosquama quite weakly sclerotized, slightly flattened, bearing long fine hairs. Colour similar to female but mid coxa yellow.

**Remarks.** *Certonotus hinnuleus* belongs to the leeuwinensis-group. It is the most distinctive taxon in the group on account of the swollen pronotal corner. Structurally it is most closely related to *C. zebrus* from which it differs in having a longer ovipositor and shorter stouter petiole. In Australia it has only been recorded from New South Wales and Victoria. The female from Western Australia referred to by Morley (1913) is a distinct species, *C. ixion*. Townes et al. (1961) note that this species occurs in New Caledonia.

**Material Examined**

**New Caledonia:** 2 ♀, 7 km SE. La Foa, i.1945 (Remington) (TC) (compared with type); 1 ♂, hills behind Noumea, x.1940 (Williams) (TC). **Queensland:** 1 ♀, N. slope, Bluff Range, Biggenden, viii.1976 (Frauca) (ANIC); 1 ♂, Broken R., near Eungella, xii.1961 (McAlpine & Lossin) (AM); 1 ♀, 1 ♂, Kuranda, v-vi.1913 (Turner) (BMNH); 1 ♂, Mackay, 1909 (Turner) (BMNH); 3 ♂, Mt Cootha, iv-v (TC); 1 ♂, Mt Glorious, i (TC); 2 ♂, Mt Tambourine, xi.1977 (Galloway) (BMNH).

**Certonotus humeralifer** Krieger

(Figs 24, 26, 27, 30)

*Certonotus humeralifer* Krieger, 1901: 121. Lectotype ♀, NEW SOUTH WALES (MNHU), designated by Townes et al., 1961: 113 [examined].

**Female.** Medium to large species, fore wing length 7-14 mm. Labium with glossae unspecialized. Lower face at narrowest point 1.2-1.3 times as broad as high; malar space 0.7-0.8 times as long as basal mandibular width. Occipital carina ventrally sinuous, at least twice as long as absissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, very strongly swollen, in dorsal view pyramidal, projecting; subalar prominence strongly convex. Scutellum punctate, crest distinct, metapleuron smooth and polished; submetapleural carina anteriorly expanded into a tooth before lateral carina. Propodeum moderately short with anterior transverse carina weak centrally but usually complete; posterior transverse carina absent; lateromedian longitudinal carina present anteriorly; pleural carina strong anteriorly, posteriorly vestigial; area superomedial not delineated; area spiracularis not clearly delineated posteriorly; first and second lateral area confluent, weakly defined laterally. Fore wing with 3r-m fused anteriorly with 2r-m, so areolet petiolate; 2m-cu joining *M.* basad by 0.2 from 3r-m. Hind wing with distal absissa of *Cu* distinguish to wing margin. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 short, the sternite 0.5 times as long as hind coxa, reaching to level of spiracle. Tergite 7 mediadorsally with wide indentation narrowing to silt to 0.5 of tergite length; tergite 9 in dorsal view short, rectangular. Ovipositor projecting beyond apex of gaster by 5 times length of hind tibia.

Coloration. Bright yellow species; flagellum, interocellar area, mesoscutum in central spot and scutoscutellar groove black; hind tarsus infuscate. Pterostigma black, wings hyaline.

**Male.** Similar to female but with fore wing length 7-8 mm; malar space 0.6 times basal mandibular width; 3r-m present; gaster with segment 1 quite stout, the sternite 0.5 times as long as hind coxa; apex of gonosquama strongly flattened, with periphery bearing only fine sparse hairs. Similar in colour to female.

**Remarks.** The bright yellow ground colour of this species and the conical pronotal process distinguish *C. humeralifer* from other Australian *Certonotus* species. *C. humeralifer* belongs to the humeralifer-group; it appears to be most closely related to *C. apicalis*. Both have a characteristically specialized fore femur.

*C. humeralifer* has been collected in Queensland and New South Wales.
Certonotus ixion sp. n.

(Figs 55, 61)

Female. Medium-sized species, fore wing length 8 mm. Labium with glossae unspecialized. Lower face at narrowest point 1-2 times as broad as high; malar space 0-9 times as long as basal mandibular width. Occipital carina ventrally slightly longer than abscessa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view parallel with mesoscutal margin; subalar prominence moderately convex. Scutellum closely, finely punctate with strong transverse crest; metapleuron with close shallow punctures; submetapleural carina anteriorly abruptly expanded into a broad lobe. Propodeum moderately short with anterior transverse carina complete; posterior transverse carina almost complete; lateromedian longitudinal carina absent except for vestiges before anterior carina; pleural carina obsolescent posteriorly; area superomedia not delimited laterally; area spiracularis almost complete; first and second lateral areae barely delineated laterally, confluent. Fore wing with 3r-m strongly converging towards 2r-m, joining Rs separately; 2m-cu joining M at 3r-m. Hind wing with distal abscessa of Cu1 present over distal 0-5 to wing margin, not joined to first abscessa of Cu1. Hind tibia with posterior margin with a small spine-like bristle. Gaster with segment 1 long and narrow, the sternite 0-8 times as long as hind coxa, reaching behind level of spiracle. Tergite 7 mediodorsally with narrow indentation to 0-5 of length; tergite 8 posteriorly short and truncate; tergite 9 in dorsal view broad. Ovipositor projecting beyond apex of gaster by 5-7 times length of hind tibia.

Coloration. Antenna blackish, apex (except extreme distal part of last segment) whitish; head reddish brown, lower face, frontal orbits and most of genae whitish; alitrunk reddish, peripherally darker; scutellum posteriorly, postscutellum, tegula, subalar prominence and upper margin of pronotum yellowish. Gaster dark red-brown; tergites 1-6 with posterolateral triangular yellow marks, tergites 2-3 with anterolateral pale spots. Legs predominantly reddish brown, anterior two pairs of coxae and distal apices of fore and mid femora whitish. Pterostigma red-brown, wings hyaline.

Male. Quite similar to female but with fore wing length 5-7 mm; malar space 0-6 times basal mandibular width; 3r-m present; gaster with segment 1 slender; sternite 1-0 times as long as hind coxa; apex of gaster with a small lobe bearing long scattered hairs. Colour similar to female but with mesopleuron white-marked and pale maculae on gaster smaller, rather inconspicuous, flagellum entirely black.

Remarks. The species is one of the three Certonotus that have incomplete distal abscessa of Cu1. It is most similar to C. paluma from which it differs strikingly in colour pattern, length of ovipositor and shape of tergite 8. The coxae are more elongate than in many other species and the sculpture of the alitrunk is coarser than that of C. paluma.

C. ixion has been collected in Queensland and Victoria.

Material examined

Lectotype ♀, New South Wales (MNHU).

Queensland: 1 ♂, Brisbane, 1956 (Ken) (NMV); 2 ♀, Fraser Island, ix.1930 (BMNH); 1 ♀, 1 ♂, Mt Glorious, 650 m, x-xiii (TC); 1 ♀, Mt Nebo, 500 m, iii (TC); 5 ♀, 1 ♂, Mt Tambourine, x-xi.1977 (Galloway) (BMNH); 1 ♀, Mt Tambourine, xii.1991 (Hacker) (BMNH); 2 ♀, Mt Tambourine, xi-xii (TC); 1 ♂, Toowoomba, iii (TC). New South Wales: 1 ♀, Terrigal, 1900 (Froggatt) (BMNH); 1 ♀, ‘New South Wales’ (NMV).

Certonotus leeuwinensis Turner comb. rev.

(Figs 49, 52)

Certonotus leeuwinensis Turner, 1919: 551. Holotype ♂, WESTERN AUSTRALIA (BMNH) [examined].

Asperellus leeuwinensis (Turner) Townes et al., 1961: 115.

Female. Medium-sized species, fore wing length 6-7 mm. Labium with glossae unspecialized. Lower face at narrowest point 1-2-1-3 times as broad as high; malar space 1-1-1.2 times as long as basal mandibular width. Occipital carina ventrally weak, only slightly longer than abscessa of hypostomal carina between it and mandibular base. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view slightly protruding from mesoscutal margin; subalar prominence weakly convex. Scutellum sparsely
punctate, with strong transverse keel; metapleuron closely, quite finely punctate; submetapleural carina anteriorly expanded into a moderately broad, triangular lobe; metanotum with weak lateral tooth. Propodeum quite short with anterior transverse carina complete; posterior transverse carina absent; lateromedian longitudinal carina present before anterior transverse carina; pleural carina more or less complete; area superomedia undefined; area spiracularis incomplete internally; first and second lateral areae confluent. Fore wing with 3r-m convergent towards 2r-m in some specimens; 2m-cu joining M just basad of 2r-m. Hind wing with distal abscissa of Cu₁ absent. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 short, the sternite 0-5 times as long as hind coxa, reaching nearly to level of spiracle. Tergite 7 mediodorsally with indentation to 0-5 its length; tergite 8 posteriorly long and rounded; tergite 9 in dorsal view short and broad. Ovipositor projecting beyond apex of gaster by 5-5 times length of hind tibia.

Coloration. Antenna black with apical segments white (except for distal apex of last segment which is black); head black, orbits entirely whitish, lower face centrally brownish; alitrunk reddish brown, the sclerites often margined with black irregularly; pronotum dorsally as a stripe, ventrally, tegula, subalar prominence, scutellum and postscutellum pale whitish yellow; gaster brownish or even blackish, tergites 1–7 laterally and posteriorly margined with yellow. Legs with fore and mid coxae yellow above, black below; hind coxa brown above, blackish below; anterior two pairs of legs otherwise brownish except for distal apices of femora which are yellow; hind femur brownish; hind tibia darker brown, proximally indistinctly paler, tarsus infuscate. Pterostigma dark brown, wings hyaline.

**Male.** Similar to female but with fore wing length 3–6 mm; malar space 0-9 times basal mandibular width; 3r-m present; gaster with segment 1 moderately stout, the sternite 0-6 times as long as hind coxa; apex of gonosquama flattened slightly and bearing long scattered hairs. Colour similar to female but lower face and anterior two pairs of coxae almost entirely yellow.

**Remarks.** _Certonotus leeuwinensis_ belongs to the _leeuwinensis_-group. It is structurally most similar to _C. toolangi_ in having a noticeably punctate metapleuron. The most obvious difference between the two species is in coloration. The gaster of _leeuwinensis_ has the hind margins of tergites 2–5 banded with yellow whereas those of _toolangi_ are spotted with yellow. The hind tibia of _toolangi_ is bicoloured, that of _leeuwinensis_ is almost unicolorous. _C. leeuwinensis_ has a slightly longer ovipositor and malar space than _toolangi_.

**Material examined**

Holotype ♂, Western Australia: Yallingup near Cape Naturaliste ix–x.1913 (Turner) (BMNH).

New South Wales: 1 ♀, Killara, xii.1935 (Day) (ANIC). Tasmania: 1 ♀, Coles Bay, ii–iii (TC); 1 ♂, Georgetown, xi.1917 (Cole) (NMV); 1 ♀, Mt Barrow, 1200 m, xiii–i (TC). Western Australia: 1 ♀ (paratype), same data as holotype (BMNH); 1 ♂, 21 km SW. by S. Donnybrook (23-44S 115-41E), x.1981 (Naumann & Cardale) (ANIC); 1 ♀, Mt Chudalup, S. of Northcliffe, x.1970 (Colless) (ANIC); 1 ♂, Yallingup, near Cape Naturaliste, ix–x.1913 (Turner) (BMNH).

*Certonotus mogimbensis* Cheesman comb. rev.

(Fig. 47)

*Certonotus mogimbensis* Cheesman, 1936: 180. Holotype ♀, NEW HEBRIDES (BMNH) [examined].

*Asperellus mogimbensis* (Cheesman) Townes et al., 1961: 115.

**Female.** Small species, fore wing length 5 mm. Labium with glossae slightly elongate. Lower face at narrowest point 1-0 times as broad as high; malar space 0-8–1-0 times as long as basal mandibular width. Occipital carina ventrally from slightly shorter to slightly longer than abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view parallel to mesoscutal margin; subalar prominence very weakly convex. Scutellum punctate with strong transverse keel; metapleuron smooth with some fine punctures posteriorly; submetapleural carina anteriorly expanded into a rounded lobe; metanotum without a lateral tooth. Propodeum short with anterior transverse carina complete; posterior transverse carina absent; lateromedian longitudinal carina vestigial; pleural carina complete; area superomedia undefined; area spiracularis not defined internally; first and second lateral areae confluent. Fore wing with 3r-m present for half the distance or less from Rs towards M; 2m-cu joining M well distad of 2r-m. Hind wing with distal abscissa of Cu₁ absent. Hind tibia with posterior margin with one or two spine-like bristles. Gaster with segment 1 short and broad, the sternite 0-5 times as long as hind coxa, reaching to level of spiracle. Tergite 7 mediodorsally with indentation to 0-5 of length; tergite 8 posteriorly long and rounded; tergite 9 in dorsal view elongate. Ovipositor projecting beyond apex of gaster by 4-0–4-5 times length of hind tibia.
Coloration. Antenna black with a subapical broad white band; head whitish; clypeus and mouth parts brownish, frons centrally and interocellar area dark brown. Alitrunk, legs and gaster uniformly orange. Pterostigma dark brown, wings hyaline.

**Male.** Similar to female but with fore wing length 3–4 mm; malar space 0-9-1-1 times basal mandibular width; 3r-m absent; gaster with segment 1 moderately slender; the sternite 0-6 times as long as hind coxa; apex of gonosquama with small lobe bearing fine scattered hairs. Similarly coloured to female but with head uniformly orange, flagellum entirely black, hind tibia and tarsus weakly to strongly infuscate, some tergites of gaster infuscate and wings slightly infumate.

**Remarks.** *C. mogimbensis* most closely resembles *C. pineus* in colour and structure and the two may be closely related. However, *mogimbensis* is distinctive, not only in having a flatter pronotum but in having 3r-m incomplete in the male and lacking dark maculae on the mesoscutum. This species is known to occur in tropical Queensland and on Vanuatu (New Hebrides).

**Material Examined**

Holotype ♂, **New Hebrides**: Malekula, Ounua, ii.1929 (*Cheesman*) (BMNH).

Queensland: 1 ♀, 1 ♂, Claudie R., near Mt Lamond, xii.1971 (*McAlpine & Holloway*) (AM); 1 ♂, Shipton’s Flat (15-47S 124-14E), x.1980 (*Cardale*) (ANIC).

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**Certenotus monticola** Morley, 1913: 29. Holotype ♂, **Queensland** (BMNH) [examined].

*Certenotus monticola* Morley, 1913: 29. Holotype ♂, **Queensland** (BMNH) [examined].

**Female.** Medium-sized species, fore wing length 9–12 mm. Labium with glossae elongate, projecting beyond clypeus by a distance equal to or greater than facial height. Lower face at narrowest point 0-9-1-0 times as broad as high; malar space 0-5-0-6 times as long as basal mandibular width. Occipital carina ventrally obsolescent, represented by a stub that is shorter than abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view barely projecting beyond scutal margin; subalar prominence very weakly convex. Scutellum closely and coarsely punctate, with transverse crest; metapleuron anteriorly punctate, posteriorly and dorsally; submetapleural carina anteriorly abruptly expanded into a broad rounded lobe; metanotum without a tooth before lateral carina. Propodeum quite short with anterior transverse carina centrally incomplete; posterior transverse carina absent; lateromedian longitudinal carina present only before anterior carina; pleural carina complete; area superomedial not delineated; area spiracularis complete, short; first and second lateral areae confluent. Fore wing with 3m-r converging on 2r-m but joining Rs separately; 2m-cu joining M midway between 3r-m and 2r-m. Hind wing with distal abscissa of Cu1 distinct to wing margin. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 short and broad, the sternite 0-7 times as long as hind coxa, reaching just beyond level of spiracle. Tergite 7 mediodorsally with small indentation; tergite 8 posteriorly elongate and narrow; tergite 9 in dorsal view long and truncate. Ovipositor projecting beyond apex of gaster by 4-5 times length of hind tibia.

Coloration. A reddish brown species with lower face, frontal and genal orbits, central mesoscutal spot, scutellum, most of pronotum, much of mesopleuron and virtually all of metapleuron/propodeum behind spiracle, yellow. Gaster dark brown, tergites 2+ with anterolateral triangular marks. Fore leg brownish yellow, coxa infuscate; mid leg blackish brown, femur distally yellow marked, coxa darker; hind leg with coxa black with dorsal yellow marks, femur and tarsus strongly infuscate, tibia less strongly infuscate. Pterostigma black, wings weakly infumate.

**Male.** Slender gaster, otherwise similar to female but with fore wing length 7–11 mm; malar space 0-5-0-6 times basal mandibular width; 3r-m present; gaster exceptionally elongate with segment 1 quite stout, the sternite 0-6 times as long as hind coxa; gonosquama long, apex a little flattened, with scattered hairs of various length. Male similar in general colour pattern to female, although with fewer yellow maculae.

**Remarks.** *C. monticola* belongs to the *flaviceps*-group. It is the only taxon in this complex to occur in Australia where it is easily recognizable by the elongate glossae and short occipital carina. *C. monticola* is known to occur in both north Queensland and Papua New Guinea.

**Material Examined**

Holotype ♂, **Queensland**: Tambourine Mt (BMNH).

Queensland: 1 ♀, Middle Claudie R., Iron Range, x.1974 (*Daniels*) (AM). Papua New Guinea: 1 ♀, Amuk, 165 m, i.1960 (*Maa*) (BPBM); 1 ♀, 2 ♂, Bulolo, ix.1981, ex *Myristica* sp. (*Roberts*) (BMNH); 7 ♀,
Certonotus nitidulus Morley

(Fig. 33)

Certonotus nitidulus Morley, 1913: 29. Holotype ♂, VICTORIA (BMNH) [examined].

Female. Medium to large species, fore wing length 7–14 mm. Labium with glossae unspecialized. Lower face at narrowest point 1.0–1.1 times as broad as high; malar space 0.6–0.7 times as long as basal mandibular width. Occipital carina ventrally strong, slightly longer than abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view barely projecting beyond scutal margin; subalar prominence weakly convex. Scutellum punctate, transverse keel strong; metapleuron smooth with isolated punctures; submetapleural carina anteriorly expanded into a broad rounded lobe; metanotum with a weak tooth opposite anterior end of lateral carina. Propodeum quite short with anterior transverse carina centrally incomplete; posterior transverse carina absent; lateromedian longitudinal carina present only before anterior carina; pleural carina present, complete but rather weak; area superomediala undefined; area spiracularis complete, defined posteriorly by an archcarina that is very close to spiracle; first and second lateral areae separated, distally delineated. Fore wing with 3r-m converging towards 2r-m, joining Rs separately; 2m-cu joining M to 0.3 basal of 3r-m. Hind wing with distal abscissa of Cu3; distinct to wing margin. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 short, the sternite 0–6 times as long as hind coxa, reaching behind level of spiracle. Tergite 7 mediodorsally with indentation almost to 0.5 length of tergite; tergite 8 posteriorly short and rounded; tergite 9 in dorsal view transverse. Ovipositor projecting beyond apex of gaster by 5–0 times length of hind tibia.

Coloration. Colour somewhat variable but generally with antenna black, distally, except for apex of last segment, white. Head red-brown, lower face laterally to entirely, genal and frontal orbits pale yellow. Alitrunk reddish brown, yellow marks on pronotum medially, anterior ‘corners’ and central spot on mesoscutum, scutellum laterally, tegula, subalar prominence, anterior and posterior mesopleural spots, postscutellum and hind part of propodeum. Gaster reddish with tergites posteriorly and laterally yellowish margined, and also with spots in anterolateral corners. Fore leg yellow, femur red centrally, peripherally black with distal apex yellow. Mid leg similar with coxa black-marked and tibia and tarsus infuscate. Hind leg as mid leg but with coxa reddish brown, ventrally black. Pterostigma black, wings hyaline.

Male. Similar to female but with fore wing length 7–10 mm; malar space 0.4–0.6 times basal mandibular width; 3r-m present; gaster with segment 1 moderately slender, 0–6 times as long as hind coxa; apex of gonosquama flattened, bearing two widely separated dense tufts of long hairs. Similarly coloured to female.

Remarks. C. nitidulus is apparently one of the commonest species in the genus as it has adapted to parasitizing an introduced siricid in Pinus radiata plantations in Victoria and Tasmania (Hocking, 1967). In coloration C. nitidulus most strongly resembles C. geniculatus (from which it can be separated by reference to couplet 8 in the key) but structurally it is most similar to C. annulatus and C. andrewi. C. nitidulus differs from both in colour pattern and in the form of the propodeal carinae. This is a quite widespread species in the south-east, extending from southern Queensland to Tasmania.


Material examined
Holotype ♂ (Certonotus nitidulus Morley), VICTORIA (BMNH). Holotype ♂ (Certonotus tasmaniensis Turner), TASMANIA: Mt Wellington, i–ii.1913 (Turner) (BMNH).

Queensland: 1 ♀, Mt Glorious, xi.1972 (Monteith) (ANIC).

New South Wales: 1 ♀, Barrington Nat. Park, i.1977 (Daniels) (AM); 1 ♂, Leather Barrel Ck, Kosciusko, xi.1961 (Colless) (ANIC); 1 ♀, Lord Howe Is., ii–iii.1957 (Leipa) (BPBM); 1 ♀, Monga, x.1957 (Riek) (ANIC); 1 ♀, Mooonee, xi.1947 (NMV); 1 ♂, Moss Vale, xi.1919 (Duquet) (AM); 1 ♀, 2 ♂, Mt Tomah, xi.1983 (Rodd) (AM); 1 ♂, Pebble Beach, xi.1960 (Common & Upton) (ANIC); 1 ♂, Tubrubucca, xi.1953 (Burns) (NMV). Victoria: 1 ♀, Dynamite Ck, Bonang Hwy, x.1961 (Colless) (ANIC); 1 ♀, Harrietville, i.1924 (Oke) (NMV); 3 ♂, Healesville,
Ceretonotus paluma sp. n.

(Figs 54, 62)

Female. Medium-sized species, fore wing length 8–10 mm. Labium with glossae unspecialized. Lower face at narrowest point 1:1–1:2 times as broad as high; malar space 0.8 times as long as basal mandibular width. Occipital carina ventrally as long as absissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, very weakly convex, in dorsal view almost parallel with mesoscutal margin; subalar prominence weakly convex. Scutellum sparsely punctate, with a posterior transverse crest; metapleuron polished, smooth, virtually impunctate; submetapleural carina anteriorly expanded into a broad rounded lobe; metanotum barely produced opposite anterior margin of lateral carina. Propodeum quite short with anterior transverse carina complete; posterior transverse carina present at least centrally; lateromedian longitudinal carina present only anterior to anterior transverse carina; pleural carina complete anteriorly, posteriorly obsolescent; area superomedial not bounded laterally; area spiracularis completely delineated; first and second lateral areae separated by carina. Fore wing with 3r-m converging towards 2r-m, joining the latter at Rs; 2m-cu joining M at 3r-m. Hind wing with distal absissa of Cu4 present over distal 0.5 to wing margin, not joined to first absissa of Cu1. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 long and narrow, the sternite 0–7 times as long as hind coxa, reaching to level of spiracle. Tergite 7 medidorsally with narrow indentation, over 0.5 of its length; tergite 8 posteriorly long and narrow; tergite 9 in dorsal view short and pointed. Ovipositor projecting beyond apex of gaster by 4 times length of hind tibia.

Coloration. Antenna black, distally white with extreme apex of last segment black; head black with face and orbits white; alitrunk black or reddish black, with central mesoscutal stripe, scutellum, pronotum, tegula, subalar prominence, mesopleuron centrally, metapleuron and propodeum laterally white; gaster black with very large lateral triangular areas white. Anterior two pairs of legs white with femora, tibiae and tarsi variously infuscate; hind leg black, coxa dorsally with white spot. Pterostigma blackish, wings hyaline.

Male. Unknown.

Remarks. C. paluma is one of the three quite closely related Ceretonotus species that have an incomplete distal absissa of Cu4 in the hind wing. It is distinguishable from Ceretonotus sp. A by its unspecialized subalar prominence. It is structurally similar to C. ixion, from which it may be separated by reference to the key.

Material examined


Ceretonotus pineus sp. n.

(Figs 45, 46)

Female. Medium-sized species, fore wing length 7–9 mm. Labium with glossae unspecialized. Lower face at narrowest point 1:0–1:1 times as broad as high; malar space 0.9–1.0 times as long as basal mandibular width. Occipital carina ventrally almost 3 times as long as absissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, very convex, in dorsal view subpyramidal; subalar prominence moderately convex. Scutellum moderately, closely punctate, trans-
verse keel weak; metapleuron anteriorly smooth, posteriorly punctate; submetapleural carina anteriorly expanded into a broad almost quadrate lobe; metanotum with a very weak tooth before vestige of lateral carina. Propodeum quite short with anterior transverse carina present, very close to anterior part of propodeum; posterior transverse carina absent; lateromedian longitudinal carina vestigial before anterior carina, otherwise absent; pleural carina more or less complete; area superomedial undefined; area spiracularis more or less complete except internally; first and second lateral areae not separated. Fore wing with 3r-m only slightly convergent towards 2r-m, joining Rs away from 2r-m, making areolet quadrature; 2m-cu joining M at 3r-m. Hind wing with distal abscissa of Cu$_2$ absent. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 short and broad, the sternite 0-3 times as long as hind coxa, just not reaching level of spiracle. Tergite 7 mediodorsally with indentation to 0-5 its length; tergite 8 posteriorly long and rounded; tergite 9 in dorsal view short and broad. Ovipositor projecting beyond apex of gaster by 4-5 times length of hind tibia.

Coloration. Antenna black, with subapical white band; head yellowish, only interocellar area and edges of mandibles blackish. Alitrunk and gaster yellowish; mesoscutum with lateral marks, anterocentrally infuscate; tip of tergite 8 blackish. Legs yellow, hind tarsus and sometimes distal apex of tibia blackish. Pterostigma black, wings hyaline.

**Male.** Similar to female but with fore wing length 4 mm; malar space 0-7 times basal mandibular width; 3r-m present; gaster with segment 1 quite stout, the sternite 0-3 times as long as hind coxa; apex of gonosquama rounded, bearing scattered hairs. Similar in colour to female but with yellowish areas a little paler, more strongly contrasted with infuscate areas; flagellar white mark very indistinct.

**Remarks.** A stocky species easily recognized by the almost pyramidal pronotal convexity. The virtually quadrate areolet and very short first sternite are also quite characteristic of this species. _C. pineus_ is only known to occur in Queensland.

**Material examined**

Holotype ♀, Queensland: Moses Ck, 45 km N. by E. Mt Finnigan (15-47S 145-17E), x.1980 (Cardale) (ANIC).

Paratypes. Queensland: 1 ♀, Lake Barrine, ii.1935 (Burns) (NMV); 1 ♀, Mt Webb Nat. Park (15-04S 145-07E), iv.1981 (Naumann) (ANIC); 1 ♀, Palm Is. near Townsville, x (TC).

**Certonotus rufescens** Morley

(Figs 22, 25)

*Certonotus rufescens* Morley, 1913: 30. LECTOTYPE ♀, QUEENSLAND (BMNH), here designated [examined].

**Female.** Moderately large to large species, fore wing length 8-16 mm. Labium with glossae slightly lengthened. Lower face at narrowest point 0-9-1-0 times as broad as high; malar space 0-9-1-0 times as long as basal mandibular width. Occipital carina ventrally rather straight, more than twice as long as abscissa of hypostomal carina between it and mandible base. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view rounded, just protruding beyond scutal margin; subalar prominence very strongly raised, in dorsal view with a blunt, back-curved, thorn-like protuberance. Scutellum punctuate, with a moderately strong transverse crest; metapleuron smooth, virtually impunctate; submeta- pleural carina anteriorly expanded into a broad almost quadrate lobe which usually has ridge near anterior corner delimiting a narrow triangular area; metanotum with small tooth opposite anterior end of lateral carina. Propodeum moderately long with anterior transverse carina complete; posterior transverse carina present as lateral vestige; lateromedian longitudinal carina present before anterior carina; pleural carina very strong anteriorly, absent behind anterior carina; area superomedial not delineated laterally; area spiracularis complete; first and second lateral areae confluent, not delineated laterally. Fore wing with 3r-m converging towards 2r-m and joining latter at Rs; 2m-cu joining M at 3r-m to 0-3 towards 2r-m. Hind wing with distal abscissa of Cu$_1$, distinct to wing margin. Hind tibia with posterior margin with one to three spine-like bristles. Gaster with segment 1 long and narrow, the sternite 0-9-1-0 times as long as hind coxa, reaching behind level of spiracle. Tergite 7 mediodorsally at most only slightly indented on posterior margin; tergite 8 posteriorly with process short and rounded; tergite 9 in dorsal view elongated and bluntly pointed posteriorly. Ovipositor projecting beyond apex of gaster by 4-5 times length of hind tibia.

Coloration. Brownish orange; flagellum black with a white subapical band which is usually well developed but is entirely absent in specimens from the northern part of the range. Pterostigma dark brown, wings hyaline.

**Male.** Similar to female but with fore wing length 5-7 mm; malar space 0-8-0-9 times basal mandibular...
width; 3r-m present; gaster with segment 1 long, slender, the sternite 0-8-1·0 times as long as hind coxa; apex of gonosquama simply truncate, not broadened, but with long sparse hairs. Similarly coloured to female, flagellum without a white band.

Remarks. C. rufescens is easily distinguished from other Australian species by the thorn-like subalar prominence. The face of this species is flatter than the other Certonotus and laterally it is abruptly, almost angularly rounded before the malar space. The characteristic submetapleural carina and possession of a strong, usually Y-shaped vestigial carina above the insertion of the hind coxa are useful confirmatory characters. A widespread species extending from northern Queensland south to near Melbourne, Victoria.

Material examined
Lectotype ♀, Queensland: Mackay, ix.1901 (BMNH).

Queensland: 2♀ (parallectotypes), same data as lectotype (BMNH); 2♂, Mackay, 1909 (BMNH); 1♀, Montville, ix.1935 (Burns) (NMV); 1♂, Moses Ck, 4 km N. by E. Mt Finnigan (15-47S 145-17E), x.1980, at light (Cardale) (ANIC); 1♀, Mt Glorious, xii.1979 (Galloway) (BMNH); 1♀, Mt Glorious near Brisbane, xii.1976 (Bouček) (BMNH); 3♂, Mt Glorious, i-iii (TC); 2♀, Mt Tambourine, x-xi.1978 (Galloway) (BMNH); 2♀, 4♂, Mt Tambourine, x-xi.1977 (Galloway) (BMNH). New South Wales: 1♀, 19 km S. Coff’s Harbour, i.1958 (Riek) (ANIC); 1♂, Otford, xii.1962 (Colless) (BMNH); 1♀, Sassafrass Gully, Springwood, ix.1972 (McAlpine) (AM). Victoria: 2♀, Toolangi, i-ii.1983 (Farrugia & Gauld) (BMNH); 1♂, Yellingbo, xi.1976 (Neboïss) (NMV).

Certonotus sisyphus sp. n.

(Figs 36, 39, 40)

[Certonotus hinnuleus Krieger; Morley 1913: 32. Misidentification.]

Female. Medium to large-sized species, fore wing length 8-18 mm. Labium with glossae slightly lengthened. Lower face at narrowest point 1·1-1·3 times as broad as high; malar space 0-9-1·0 times as long as basal mandibular width. Occipital carina ventrally sinuous, much longer than abscessa of hypostomal carina between it and mandibular base. Upper part of pronotum, slightly before posterior corner, weakly convex, in dorsal view projecting slightly beyond scutal margin, subalar prominence very strongly convex, in dorsal view slightly pyramidal. Scutellum sparsely punctate, transverse crest distinct; metapleuron smooth with scattered punctures, on larger specimens with punctures closer; submetapleural carina anteriorly expanded into a rectangular flange; metanotum with strong tooth opposite end of lateral carina. Propodeum moderately long with anterior transverse carina complete; posterior transverse carina strong, complete, almost parallel to anterior carina; lateromedian longitudinal carina present only as vestiges before anterior carina; pleural carina weak, posteriorly evanescent; area superomedia not defined; area spiracularis complete; first and second lateral areae clearly separated though latter weakly defined externally. Fore wing with 3r-m strongly converging towards an almost vertical 2r-m, joining Rs separately; 2m-cu joining M 0·2 from 3r-m towards 2r-m. Hind wing with distal abscessa of Cu; distinct to wing margin. Hind tibia with posterior margin with one to three spine-like bristles. Gaster with segment 1 long and narrow, the sternite 1·0-1·2 times as long as hind coxa, reaching behind level of spiracle. Tergite 7 mediodorsally with wide indentation to 0·5 length of tergite; tergite 8 posteriorly short and rounded; tergite 9 in dorsal view as long as wide with blunt point posteriorly. Ovipositor projecting beyond apex of gaster by 4-5 times length of hind tibia.

Coloration. Reddish brown, flagellum darker with subapical white band; clypeus, facial, frontal and genal orbits. Subalar prominence, pair of central stripes on mesoscutum, scutellum, mesopleural spot, spots in posterolateral corners of tergites 1+ and also on lateral margins of 3+ yellow. Legs yellowish brown, anterior two pairs of coxae and distal apex of mid femur yellow. Pterostigma dark brown, wings hyaline.

Male. Similar to female but with fore wing length 8 mm; malar space 0-7 times basal mandibular width; 3r-m present; gaster with segment 1 slender, the sternite 1·1 times as long as hind coxa; apex of gonosquama with a small angulate lobe that bears scattered long hairs. Similar in colour to female but with face entirely yellow, mid tibia yellow and yellow maculae on gaster virtually absent.

Remarks. The fairly elongate petiole, rather flat face and posteriorly flanged lateral propodeal carina suggest this species is related to C. rufescens though the pleural carina is not tuberculate as it is in rufescens and geniculatus. Superficially C. sisyphus is similar to C. avitus from which it can be distinguished, not only by the characters in the key, but also in having a distinctly longer prementum and having the hypostomal and occipital carinae meeting further from the base of the mandible than the basal mandibular width.
Widely distributed in the south-east of Australia; recorded from New South Wales, Victoria and Tasmania.

**Material examined**

Holotype ♀, **Victoria**: Toolangi, xi–xii.1982 (*Farrugia & Gould*) (AM).

Paratypes. **Victoria**: 8 ♀, 1 ♂, same data as holotype (BMNH). **New South Wales**: 2 ♀, Acacia Plateau, 3000 ft, x.1961 (*Common & Upton*) (ANIC). **Tasmania**: 1 ♀, Duck River, 6 km SE. Roger R., xii.1974 (*Neboiss*) (NMV); 1 ♀, Meridith R., 20 km from Corinna, i.1954 (*Campbell*) (ANIC); 1 ♀, Mt Field Nat. Park, 250 m, i–ii.1983 (*Gauld*) (BMNH); 1 ♀, Picton R. bridge, i.1983 (*Gauld*) (BMNH); 1 ♀, no data (ANIC).

*Certonotus talus* sp. n.

(Figs 34, 35)

**Female.** Medium-sized species, fore wing length 8–12 mm. Labium with glossae unspecialized. Lower face at narrowest point 1.1 times as broad as high; malar space 0.7–0.8 times as long as basal mandibular width. Occipital carina ventrally more than twice as long as abscessa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, very weakly convex, in dorsal view barely projecting beyond scutal margin; subalar prominence convex, with a long sharp back-curved spine. Scutellum punctate with strong transverse keel; metapleuron very sparsely punctate; submetapleural carina anteriorly expanded into a broad triangular lobe; metanotum with a large tooth before anterior end of lateral carina. Propodeum moderately long with anterior transverse carina complete; posterior transverse carina almost complete; lateromedian longitudinal carina vestigial, discernible only before anterior carina; pleural carina strong anteriorly, posteriorly poorly developed or obsolescent; area superomedia not delineated; area spiracularis complete, posteriorly very weakly delineated; and second lateral areae present, separated by strong carina. Fore wing with 3r-m converging towards 2r-m, joining latter at Rs; 2m-cu joining M at 3r-m. Hind wing with distal abscessa of Cu1 distinct to wing margin. Hind tibia with posterior margin with or without one spine-like bristle. Gaster with segment 1 short, the sternite 0.8–1.0 times as long as hind coxa, reaching behind level of spiracle. Tergite 7 mediadorsally with wide indentation almost to 0.7 length of tergite; tergite 8 posteriorly with long, narrow process; tergite 9 in dorsal view long and evenly rounded. Ovipositor projecting beyond apex of gaster by 5 times length of hind tibia.

Coloration. Antenna black with subapical white band; head reddish brown, orbits and Clypeus entirely pale; alitrunk reddish, mesoscutum with longitudinal stripes, tegula, subalar prominence, scutellum partly, postscutellum, anterior mesopleural spot and paired spots on hind edge of propodeum yellow; gaster reddish, lateral margins of all tergites yellow and tergites also with paired large yellow spots in posterolateral corners. Fore and mid legs yellow, femur for proximal 0.7 and tibia externally reddish, distal tarsal segment blackish; hind leg virtually entirely reddish brown, tarsus infuscate. Pterostigma brown, wings hyaline.

**Male.** Unknown.

**Remarks.** The possession of a long, backwardly curved, slender spine arising from the subalar prominence immediately distinguishes *talus* from all other Australian *Certonotus*. It appears to belong to the *humeralifer*-group but differs in having a more slender petiole with a much longer sternite. One specimen has asymmetric hind wings; the left wing has the distal abscessa of Cu1 incomplete, not joining Cu1 and cu-a, whilst in the right wing the vein is complete. This incomplete condition is found in *C. ixion* and *paluma* and we believe these are closely related species. All have similarly modified posterior gastric tergites, and rather small, oblique areollets. The petiole is more slender in these species than in other taxa in this group and the sternite is longer.

*C. talus* occurs in New South Wales and Victoria and has been collected in subtropical and temperate wet forest.

**Material examined**

Holotype ♀, **New South Wales**: Dorrigon Nat. Park, E. end of Blackbutt Track, 710 m, ii–iii.1980, in subtropical rainforest (*Newtown & Thayer*) (ANIC). Paratypes. **Victoria**: 2 ♀, Toolangi, xi.1982 (*Farrugia*) (BMNH). **New South Wales**: 1 ♀, Tubrabucca, i.1948 (*Burns*) (NMV).
Cortonotus tolangi sp. n.

(Fig. 60)

**Female.** Medium-sized species, fore wing length 6–7 mm. Labium with glossae un specialized. Lower face at narrowest point 1·1 times as broad as high; malar space 0·9–1·1 times as long as basal mandibular width. Occipital carina ventrally as long as basal mandibular width. Occipital carina ventrally as long as or slightly longer than abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, almost flat, in dorsal view parallel to mesoscutal margin; subalar prominence moderately convex. Scutellum sparsely punctate, transverse keel weak; metapleuron with shallow coarse close punctures; submetapleurale carina anteriorly expanded into a broad triangular lobe; metasternum with a weak tooth laterally. Propodeum quite short with anterior transverse carina complete; posterior transverse carina absent; lateromedian longitudinal carina vestigial, only present before anterior transverse carina; pleural carina present anteriorly; area superomedia undefined; area spiracularis incompletely defined internally; first and second lateral areae confluent, undefined laterally. Fore wing with 3r–m convergent towards 2r–m, joining Rs separately; 2m–cu joining M very near 3r–m. Hind wing with distal abscissa of Cu 1 absent. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 short and broad, the sternite 0·6 times as long as hind coxa, just reaching level of spiracle. Tergite 7 mediodorsally with indentation to 0·5 of length; tergite 8 posteriorly short and rounded; tergite 9 in dorsal view short and broad. Ovipositor projecting beyond apex of gaster by 4·0–4·5 times length of hind tibia.

Coloration. Very similarly coloured to *leeuwinensis* but differing in having the anterior two pairs of coxae entirely pale and the tibiae with at least proximal 0·5 whitish and mesoscutum centrally with a pair of short yellowish stripes.

**Male.** Unknown.

**Remarks.** *C. tolangi* belongs to the *leeuwinensis*-group. It is most readily distinguishable by its colour pattern. Structurally it is rather similar to *C. leeuwinensis* from which it may be distinguished by its shorter malar space and ovipositor. It is only known from the south-east of Australia, where it has been taken in wet sclerophyll forest.

**Material Examined**


Paratypes. Victoria: 2 ♀, Toolangi, xi.1982 (Farrugia) (BMNH); 1 ♀, Toolangi, xii.1982 (Farrugia & Gauld) (BMNH).

Cortonotus zebrus sp. n.

(Figs 51, 53, 59)

**Female.** Medium-sized species, fore wing length 7–8 mm. Labium with glossae unspecialized. Lower face at narrowest point 0·8–0·9 times as broad as high; malar space 0·8–0·9 times as long as basal mandibular width. Occipital carina ventrally weak, nearly twice as long as abscissa of hypostomal carina between it and mandibular base. Upper part of pronotum, slightly before posterior corner, very weakly convex, in dorsal view parallel with mesoscutal margin; subalar prominence strongly convex, centrally somewhat produced. Scutellum sparsely punctate, transverse crest quite weak; metapleuron anteriorly smooth, posteriorly with scattered punctures; submetapleurale carina anteriorly expanded into a broad rounded lobe; metasternum with a weak tooth opposite anterior end of lateral carina. Propodeum short with anterior transverse carina complete; posterior transverse carina absent; lateromedian longitudinal carina discernible as traces before anterior transverse carina; pleural carina incomplete posteriorly; area superomedia not delineated; area spiracularis virtually complete; and first and second lateral areae confluent, not defined laterally. Fore wing with 3r–m converging towards 2r–m, well separated at Rs; 2m–cu joining M 0·3 from 3r–m towards 2r–m. Hind wing with distal abscissa of Cu 1 absent. Hind tibia with posterior margin with one spine-like bristle. Gaster with segment 1 long, the sternite 0·6 times as long as hind coxa, just reaching level of spiracle. Tergite 7 mediodorsally with indentation to 0·5 its length; tergite 8 posteriorly short and rounded posteriorly. Ovipositor projecting beyond apex of gaster by 4 times length of hind tibia.

Coloration. A black species that sometimes has pale yellow-white marks on distal flagellar segments (except extreme apex of distal one); lower face entirely, orbits, most of pronotum, tegula, scutellum, postscutellum, subalar prominence, mesopleural stripe, most of mesopleuron and propodeum laterally and posteriorly, base of petiole, posterior and lateral margins of gastral tergites whitish. Anterior two pairs of legs whitish, femora and tibiae centrally, tarsi partly brownish marked. Hind leg black. Pterostigma blackish, wings hyaline.
Male. Similar to female but with fore wing length 3 mm; malar space 0.7 times basal mandibular width; 3r-m present; gaster with segment 1 quite stout, the sternite 0.5 times as long as hind coxa; apex of gonosquama flattened slightly with scattered hairs. Similarly coloured to female but with flagellum entirely black as is most of mesopleuron and metapleuron.

Remarks. The holotype differs from the female paratype in having entirely black antennae. C. zebrus belongs to the *leeuwinensis*-group. It is the only species in the complex which is virtually entirely black and white. Structurally it is rather unremarkable but it has a more strongly raised subalar prominence than any other species in this group.

It is only known from tropical Queensland.

Material examined

Holotype ♀, Queensland: Baldy Mtn Road, via Atherton, vi.1981, ex Malaise trap (Brown) (QM).
Paratypes. Queensland: 1 ♂, 3 km N. by E. Mt Tip Tree (17-02S 145-37E), x.1980, at light (Cardale) (ANIC); 1 ♀, Windsor Tableland via Mt Carbine, xii.1980, ex Malaise trap (BMNH).

**Ceretonotus** sp. A

(Figs 48, 50)

Female. Medium-sized species, fore wing length 7 mm. Labium with glossae unspecialized. Lower face at narrowest point 1.3 times as broad as high; malar space 1.0 times as long as basal mandibular width. Occipital carina ventrally long, about 3 times length of abscissa of hypostomal carina between it and base of mandible. Upper part of pronotum, slightly before posterior corner, moderately convex, in dorsal view projecting beyond mesoscutal margin; subalar prominence weakly convex, rather sharp and ridge-like. Scutellum coarsely, closely punctate, transverse keel weak; metapleuron closely, coarsely punctate; submetapleural carina anteriorly expanded into a broad rounded flange, metanotum with a distinct tooth near anterior end of lateral carina. Propodeum moderately long with anterior transverse carina centrally strong; lateromedian longitudinal carina present anteriorly and weak between transverse carinae; pleural carina strong anteriorly, posteriorly obsolescent; area superomedia clearly discernible, hexagonal; area spiracularis complete; first and second lateral areae indistinctly delineated, confluent. Fore wing with 3r-m converging towards 2r-m, joining Rs separately; 2m-cu joining M opposite 3r-m. Hind wing with distal abscissa of Cu1 absent. Hind tibia with posterior margin without spine-like bristles. Gaster with segment 1 short, the sternite 0.2 times as long as hind coxa, not reaching level of spiracle. Tergite 7 mediodorsally with indentation on posterior margin; tergite 8 posteriorly very elongate and narrow; tergite 9 in dorsal view quadrate, rounded posteriorly. Ovipositor projecting beyond apex of gaster by 4 times length of hind tibia.

Coloration. Head blackish with lower face, genal and frontal orbits yellow; alitrum reddish brown, the tergites peripherally black and only tegula and subalar prominence yellow. Gaster with tergites 3+ with posterior and lateral margins very narrowly yellow. Legs reddish brown, anterior two pairs of coxae yellowish marked, hind coxa, trochanter, femur proximally and distally, and tarsus infuscate. Pterostigma blackish, wings hyaline.

Male. Unknown.

Remarks. *Ceretonotus* sp. A is easily recognized by its colour pattern and possession of very slender tergal processes. The area superomedia is almost regularly hexagonal and strongly delineated except for the weak posterolateral sides. Despite lacking any trace of a distal abscissa of Cu1 in the hind wing this species appears to be quite closely related to *C. ixion*, suggesting it belongs in the *humeralifer*-group rather than in the *leeuwinensis*-group.

It is known only from Western Australia.

Material examined

Western Australia: 1 ♀, Swan River (BMNH).

**Tribe POECILOCRYPHTINI**

This relatively small tribe is characterized by the lack of an occipital carina dorsally and the presence of a single bulla in vein 2m-cu in the fore wing. It is restricted to Australia where it is represented by three genera, *Alaothyris*, *Urancyla* and *Poecilocryptus*.

Very little is known about the biology of poecilocryptines, but the available records suggest the species all oviposit into nutritious plant tissue. It is possible that the larva is partially phytophagous, as it has rather massive mandibles (Short, 1978).
Key to genera of Poecilocryptini

1 Fore wing with areolet and 2r-m obliterated by fusion of Rs and M (Fig. 63); gaster strongly laterally compressed; ovipositor very long, at least 6-0 times length of hind tibia
   ALAOTHYRIS Gauld (p. 138)
   - Fore wing with areolet distinct, bounded internally by 2r-m (Fig. 5); gaster cylindrical or depressed; ovipositor less than 5-0 times length of hind tibia

2 Hind wing with distal abscissa of Cu1 present; propodeal carinae vestigial dorsally; ovipositor strongly decurved (Fig. 64) .......................................................... URANCYLA Gauld (p. 141)
   - Hind wing with distal abscissa of Cu1 absent; propodeum with at least some carinae dorsally; ovipositor more or less straight ........................................ POECILOCRYPTUS Cameron (p. 139)

ALAOTHYRIS Gauld

Genus A; Gauld, 1983: 169.


Medium-sized species, fore wing length 6 mm; clypeus small, flat, truncate; labrum moderately large, exposed; mandible quite short, tapered, twisted about 20 times, almost evenly bidentate; malar space slightly less than basal mandibular width. Occipital carina absent on dorsal part of head, ventrally joining hypostomal carina above base of mandible. Antenna long, not tapered. Mesoscutum polished, almost smooth; notaulus deep on anterior 0-2 of scutum, notaular crest occluding extreme anterior end; scutellum weakly convex, not laterally carinate; propodeum long, evenly rounded without carinae dorsally; propodeal spiracles circular; gaster inserted at end of short propodeal neck, above and far behind coxal insertion. Fore tibia with a small tooth on outer side; mid and hind coxae very elongate; tarsal claws simple. Fore wing with cu-a proximal to base of Rs&M; 3r-m absent; Rs and M fused to obliterate areolet and 2r-m; 2m-cu with a single bulla. Hind wing with distal abscissa of Cu1 absent; basal cell slender; Sc bearing one hamulus. Gaster very long and slender, laterally compressed; tergite 1 slender, with spiracles a little behind centre; sternite 1 reaching far behind level of spiracles; tergites 2-3 with laterotergites folded under. Ovipositor very long and slender, projecting beyond apex of gaster by more than 6-0 times length of hind tibia; apex cylindrical.

REMARKS. A very distinctive genus easily recognized by its slender facies and characteristic venation. The systematic position of this genus is questionable. The mandible and elongate structure suggest a relationship with the Labenini, but the position of the petiolar spiracle, venation and shape of propodeum suggest that it is perhaps more closely related to the Poecilocryptini, especially Poecilocryptus. Unlike the Labenini, Alaothyris does not have fine, file-like teeth on the ovipositor apex, nor apparently does it have a lobe at the base of the ovipositor sheath. A single species is known.

Alaothyris elongissimus Gauld

(Fig. 63)

Alaothyris elongissimus Gauld, 1984: 94. Holotype ♀, QUEENSLAND (ANIC) [examined].

Female. Lower face slightly elongate, with a pronounced central tubercle; eye surface finely pubescent; ocelli arranged in an equilateral triangle; flagellum with about 28 segments. Mesoscutum polished, impunctate; mesopleuron and metapleuron similarly smooth, epicnemial carina dorsally obsolescent; submetapleural carina broad anteriorly. Gaster highly polished.

Coloration. Predominantly orange-brown species with flagellum, hind leg and gaster darker brown. Pterostigma brown, wings hyaline.

Male. Similar to female.

REMARKS. The holotype and paratype emerged from the seeds of Araucaria cunninghamii. What their host was is not known. Probably it will be found to be some seed-feeding beetle, but the possibility (given the semi-phytophagous tendencies of some labenines) that this is partially a seed-feeding ichneumonid cannot be ruled out.

MATERIAL EXAMINED

1 ♂ (paratype), same data as holotype.
POECILOCRYPTUS Cameron

Poecilocryptus Cameron, 1901: 527. Type-species: Poecilocryptus nigromaculatus Cameron, by monotypy.

Poecilopimpla Morley, 1914: 35, 36. [Unnecessary replacement name for Poecilocryptus Cameron.] [Homonym of Poecilopimpla Cameron, 1903.]

Medium-sized species, fore wing length 6–10 mm; clypeus rather small, apically very thin, truncate; labrum small, exposed; mandible short, slightly twisted, strongly narrowed, bidentate; malar space shorter than basal mandibular width. Occipital carina dorsally absent; eye with a weak indentation opposite antennal socket. Antenna moderately long, clavate. Mesoscutum polished, virtually impunctate; notauli deep on anterior 0·2 of scutum, notaular crests strong. Propodeum abruptly rounded with spiracle oval; area superomedia large, quadrate, often confluent with area petiolaris; area externa not usually defined laterally; gaster inserted well above level of hind coxae. Fore tibia simple, its apex not bearing a long spine; tarsal claws large, simple, or in some species those of the anterior two pairs of legs basally lobate. Fore wing with cu-a slightly proximal to base of Rs&M; 3r-m complete, enclosing a large, transverse pentagonal areolet; 2m-cu with a single bulla, straight but inclivous. Hind wing with distal abscissa of Cu1 absent; basal cell not exceptionally broad; 3c bearing about two hamuli. Gaster long, quite slender; tergite 1 slender, evenly broadened posteriorly with spiracles at or slightly behind centre, sternite reaching to spiracles, that of female bearing a pair of knob-like protuberances near anterior end. Ovipositor moderately long, projecting beyond apex of gaster by 2·8–3·3 times length of hind tibia, its apex cylindric, with lower valve partially enclosing the upper, with an indistinct matt area laterally, the upper valve with weak dorsal teeth.

REMARKS. Poecilocryptus is an endemic Australian genus with species widely distributed throughout the continent. They seem to be associated with a variety of galls on trees of the genera Eucalyptus and Acacia. Parrott (1954) recorded three species from Australia. In this work four species are recognized, two of which are described as new. One, P. galliphagus, has previously been incorrectly known as P. nigromaculatus. In fact nigromaculatus is a senior synonym of P. stramineus.

The relationships of the species. The four species may be placed in two species-groups, the nigromaculatus-group (containing nigromaculatus and galliphagus) which is characterized by having acute lobes on the claws of the anterior two pairs of legs, and the nigripectus-group (containing nigripectus and coloratus) which has the first lateral area very reduced in size.

Key to species of Poecilocryptus

1. Tergites 1 and 2 of gaster white; alitrunk predominantly black, only pronotum and anterior parts of mesoscutum and mesopleuron orange ................................................................. coloratus sp. n. (p. 139)
   - Tergites 1 and 2 of gaster bright yellow, sometimes with black marks; alitrunk predominantly bright yellow with profuse black spots ................................................................. 2

2. Propodeum with area superomedia delineated posteriorly by a strong carina (Fig. 56); flagellum with a subapical pale mark; sternite 1 of gaster with weak antero-ventral sublateral keels; tergite 2 entirely yellow ................................................................. nigripectus Turner & Waterston (p. 140)
   - Propodeum with area superomedia not delineated posteriorly (Fig. 57); flagellum entirely black; sternite 1 of gaster with strong antero-ventral sublateral tubercles; tergite 2 always black-marked ................................................................. 3

3. Distal apex of hind femur black; ovipositor projecting beyond apex of gaster by 2·0–2·3 times length of hind tibia ................................................................. galliphagus sp. n. (p. 140)
   - Distal apex of hind femur yellow; ovipositor projecting beyond apex of gaster by 2·8–3·3 times length of hind tibia ................................................................. nigromaculatus Cameron (p. 141)

Poecilocryptus coloratus sp. n.

Female. Unknown.

Male. Small species, fore wing length 4–5 mm. Hypostomal carina, above mandibular base, weakly raised. Metapleuron smooth and highly polished. Propodeal carinae quite weak; area superomedia not delineated by a carina posteriorly; lateral longitudinal carina present above spiracle; first lateral area quite small, less than the area of area dentipara. Fore wing with Rs between 2r-m and 3r-m distinctly shorter than length of 2r-m. Fore and mid tarsal claws simple. Gaster with sternite 1 simple.

Coloration. Face whitish, head, pronotum and anterior parts of mesothorax orange. Remainder of alitrunk black. Gaster with tergites 1 and 2 white, 3 white with a central black mark, 4+ black with posterior and lateral margins broadly white. Flagellum black. Fore leg orange; mid leg with femur and
proximal segments white, tibia and tarsus blackish; hind leg black, femur proximally and distally slightly reddish orange. Pterostigma blackish, wings infumate.

REMARKS. This small species is easily recognized by its atypical colour pattern. It is the only species in the genus that is not predominantly yellow. The propodeal carination is also quite distinctive. The simple tarsal claws and small first lateral area suggest *P. coloratus* may be related to *P. nigripictus*.

MATERIAL EXAMINED

*Holotype* ♂, Tasmania: Coles Bay, ii–iii.19– (TC).

Paratypes. Tasmania: 3 ♂, same data as holotype (BMNH, TC); 1 ♂, Mt Barrow, 700 m, ii.19– (TC).

Poecilocryptus gallaphagus sp. n.


**Female.** Medium-sized species, fore wing length 7–10 mm. Hypostomal carina, above mandibular base, moderately raised. Metapleuron smooth and highly polished. Propodeal carinae strong; area superomedia not delineated by a carina posteriorly; lateral longitudinal carina not complete above spiracle; first lateral area very large, more than twice the area of area dentipara. Fore wing with Rs between 2r-m and 3r-m about twice as long as length of 2r-m. Fore and mid tarsal claws with a well-developed acute basal lobe. Gaster with sternite 1 bearing a pair of antero-ventral sublateral tubercles. Ovipositor projecting beyond apex of gaster by 2-0–2-3 times length of hind tibia.

Coloration. A bright yellow species with black marks on interocellar area, vertex behind ocelli, three longitudinal stripes on mesoscutum, anterior propodeal areae, anterior margin of all abdominal tergites, hind femur centrally and hind tibia distally. Flagellum and ovipositor sheath black. Distal tarsal segments slightly infuscate. Pterostigma dark brown, wings hyaline.

**Male.** Similar to female though slightly more slender, often with sternal tubercles very weak.

REMARKS. This species is rather similar to *P. nigromaculatus*, with which it is frequently confused in collections. The two species may easily be separated by the characters given in the key.

HOST RECORDS. This species has been reared from galls on *Eucalyptus delegatensis* and *E. pauciflora*.

MATERIAL EXAMINED

*Holotype* ♀, Victoria: Wiseleigh via Bruthen, ix.1962, ex eucalypt gall (Hobb) (NMV).

Paratypes. Queensland: 1 ♀, no further data (Riek) (BMNH). New South Wales: 1 ♀, Dainer’s Gap, xi.1972 (ANIC); 1 ♀, Deer Vale, i.1931 (Burns) (NMV); 1 ♀, Mt Victoria, x.1930 (Burns) (NMV); 1 ♀, Sydney (Froggatt) (ANIC). Victoria: 2 ♀, Eildon area, ix.1959 (Irvine) (NMV); 2 ♀, Mt Pinniber, iv.1961 (Taylor) (ANIC); 1 ♀, Toolangi, xi.1982 (Farrugia) (BMNH); 3 ♀, Warrandyte, viii-x.1928 (Hill) (ANIC); 2 ♀, no further locality data (French) (BMNH). Tasmania: 3 ♀, Collinsvale, Fairy Glen, i-ii.1983 (Williams & Gauld) (BMNH).

Poecilocryptus nigripictus Turner & Waterston

(Fig. 56)

*Poecilocryptus nigripictus* Turner & Waterston, 1920: 24. Holotype ♀, Tasmania (BMNH) [examined].

**Female.** Medium-sized species, fore wing length 7–11 mm. Hypostomal carina, above mandibular base, strongly raised. Metapleuron with distinct longitudinal wrinkles, moderately polished. Propodeal carinae strong; area superomedia rectangular, delineated by a carina posteriorly; lateral longitudinal carina complete above spiracle; first lateral area not exceptionally large, of approximately the same area as area dentipara. Fore wing with Rs between 2r-m and 3r-m subequal to length of 2r-m. Fore and mid tarsal claws simple. Gaster with sternite 1 bearing a pair of weak antero-ventral sublateral keels. Ovipositor projecting beyond apex of gaster by 2-2-2-4 times length of hind tibia.

Coloration. Bright yellow species with interocellar area, vertex behind eyes, posterior part of mesoscutum, anterior part of propodeum and metapleuron, anterior 0-7 of tergite 1, and most of tergites 3 and 6 black. Legs yellow, hind femur broadly black centrally, distal hind tarsal segment infuscate. Flagellum black, with a broad subapical yellowish white band. Pterostigma dark brown, wings hyaline.

**Male.** Similar to female but slightly more slender and with gastric tergites more coarsely punctate.

REMARKS. This is a particularly characteristically patterned species. Structurally it is more similar to *P. coloratus* than it is to *P. nigromaculatus*, a species that it superficially resembles in ground-colour.
Host records. In the BMNH is a specimen reared from anthribid galls.

Material examined

Holotype ♀, Tasmania: Mt Wellington (Turner) (BMNH).

Queensland: 4 ♀, Brisbane, ii.1969 (Campbell) (QM); 1 ♂, Iron Range, v.1975 (Moulds) (AM); 1 ♀, no data (NMV). New South Wales: 1 ♂, Bateman’s Bay, x.1969 (Riek) (ANIC); 1 ♀ Bendigo (Froggatt) (ANIC). Australian Capital Territory: 2 ♀, Canberra, x.1930 (Bruce) (ANIC).

Poecilocryptus nigromaculatus Cameron

Poecilocryptus nigromaculatus Cameron, 1901: 528. LECTOTYPE ♀, AUSTRALIA (BMNH), here designated [examined].

Poeciloeryptus (sic) nigro-maculatus Cameron; Cameron, 1911: 335.

Poecilopimpla nigromaculata (Cameron) Morley, 1914: 36.


Poecilocryptus nigromaculatus Cameron; Townes et al., 1961: 117.

Female. Medium-sized species, fore wing length 6–10 mm. Hypostomal carina, above mandibular base, weakly raised. Metapleuron smooth and highly polished. Propodeal carinae strong; area superomedia not delineated by a carina posteriorly; lateral longitudinal carina absent above spiracle; first lateral area very large, more than twice the area of area dentipara. Fore wing with Rs between 2r-m and 3r-m about twice as long as length of 2r-m. Fore and mid tarsal claws with a well-developed acute basal lobe. Gaster with sternite 1 bearing a pair of antero-ventral sublateral tubercles. Ovipositor projecting beyond apex of gaster by 2.8–3.3 times length of hind tibia.

Coloration. A bright yellow species with black marks on interocellar area, vertex behind oceli, three longitudinal stripes on mesoscutum, anterior propodeal areae, anterior margin of all abdominal tergites and hind femur centrally. Flagellum and ovipositor sheath black. Distal hind tarsal segments strongly infuscate. Pterostigma dark brown, wings hyaline.

Male. Similar to female though slightly more slender, often with sternal tubercles very weak.

Remarks. In the BMNH are two specimens labelled as ‘Cameron types’ of nigromaculatus. They are conspecific and one has been labelled and is here designated as lectotype. Morley (1914) clearly referred to the female that was reared by Froggatt as the ‘typical’ specimen, and this must be construed as a valid type restriction (Art. 73(a)(i) of the Code). Parrott (1954) was incorrect to refer to the male in Froggatt’s collection as the holotype. The female holotype is a slightly undersized specimen, but clearly conspecific with nigromaculatus.

P. nigromaculatus appears to be the sister-species of P. galliphagus. Both species have a well-developed basal lobe on the fore and mid tarsal claws and have the first lateral area of the propodeum greatly enlarged. P. nigromaculatus may be recognized by its elongate ovipositor and entirely yellow hind tibia. We have examined the differences between this species and galliphagus tabulated by Parrott (1954) and have found that only the ovipositor character holds up. We failed to find any difference in the ratio of interocellar to orbital-ocellar distance, and the range of numbers of flagellar segments for both species is very similar. Small specimens of either species have fewer flagellar segments than large individuals. The extent of the black banding on third to fifth gastral tergites is quite variable in both species.

Host records. P. nigromaculatus has been reared from anthribid and chalcid galls on Acacia longifolia, and eriococcid galls on Eucalyptus.

Material examined

LECTOTYPE (nigromaculatus Cameron), ‘Australia’: no further data (BMNH). Paralektotype, 1 ♂, same data (BMNH). Holotype ♀ (nigromaculata var. straminea Morley), New South Wales: no further data (Froggatt) (BMNH).

‘Australia’: 1 ♀ (paralektotype of nigromaculatus) (BMNH). 38 ♀, 34 ♂, Queensland, New South Wales, Australian Capital Territory, Victoria, Tasmania (ANIC, BMNH, NMV).

URANCYLA Gauld

Genus U; Gauld, 1983: 169.


Medium-sized species; fore wing length 6 mm; clypeus flat, small, apically truncate with margin thin;
mandible strongly tapered, twisted and with upper tooth slightly the longer; malar space shorter than basal mandibular width. Occipital carina absent dorsally; ventrally joining hypostomal carina well above base of mandible. Antenna long, neither tapered nor clavate distally. Mesoscutum polished, punctate; notaulus present near front margin, with a small crest occluding extreme end; scutellum flat, without lateral carinæ; propodeum evenly rounded with vestiges of carinæ though areœa superomedia and petiolaris are not defined; gaster inserted low on propodeum, near level of hind coxae. Fore tibia with a small tooth on outer side, femur with a weak longitudinal ventral furrow; tarsal claws of female with a basal lobe. Fore wing with cu-a subopposite \( R_s&M; 3r-m \) present, weakly pigmented, enclosing a small pentagonal areœilet; \( 2m-cu \) with a single bulla. Hind wing with distal abscissa of \( Cu_1 \) present; first abscissa of \( Cu_1 \) shorter than \( cu-a \); basal cell moderately broad; \( Sc \) bearing one hamulus. Gaster moderately long, tergite 1 slender with spiracle slightly behind centre; tergites 2 and 3 with pendant laterotergites which are almost membranous. Ovipositor about as long as gaster, evenly decurved, apex simply acute with inconspicuous teeth and indistinct matt area laterally.

Male. Unknown.

Remarks. In Townes' (1969) key to Labiinae this genus runs to the tribe Clasini but it does not appear to be related to the genera in this group. Clasines have a nodus on the ovipositor apex, long, simple claws and two bullae in \( 2m-cu \). They also have no trace of a notaular crest. The twisted mandible and single bulla in \( 2m-cu \) are characters that \( Urancyla \) shares with \( Poecilocryptus \) and the two genera appear to be closely related.

**Urancyla fulva** Gauld

(Fig. 64)

*Urancyla fulva* Gauld, 1984: 95. Holotype \( \varphi \), QUEENSLAND (TC) [examined].

Female. Lower face elongate, regularly punctate; frons polished and finely punctate; ocelli arranged in an equilateral triangle. Flagellum with 30 segments. Mesoscutum polished, regularly and finely punctate; mesopleuron highly polished, smooth, almost impunctate; metapleuron polished with scattered fine punctures; submetapleural carina moderately wide, evenly tapered anteriorly. Gaster highly polished, finely punctate.

Coloration. Predominantly orange-brown species; face, upper orbits, genae, propleuron, anterior margin of pronotum, diagonal stripe across mesopleuron, fore coxa and trochanters and a stripe on mid coxa pale yellowish; flagellum, except centrally, scape and pedicel, frons centrally, vertex, interocellar area, occiput, mesoscutum and ovipositor sheath, pterostigma black.

Male. Unknown.

Remarks. This species is known only from the holotype.

Material examined

Holotype \( \varphi \), QUEENSLAND: Brisbane, xi.1972 (Sedlacek) (TC).

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—— 1911. On a collection of parasitic Hymenoptera (chiefly bred) made by W. W. Froggatt, in New South


Figs 1-14  1, 2, face of (1) Labium sp.; (2) Labena sp.  3, fore wing of Labena sp.  4, base of ovipositor sheath, Cerionotus nitidulus.  5, 6, fore wings of (5) Urancyla fulva; (6) Adelphion sp.  7, fore leg of Labena sp.  8-10, gonosquama of (8) Labena annulata; (9) L. keira; (10) L. pudenda.  11, 12, hind wings of (11) L. annulata; (12) L. keira.  13, 14, tergite 2 of (13) L. annulata; (14) L. chadwickii.
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Fig. 65 Cladogram showing putative phylogenetic relationship of Australian species of *Labena*. (Note. The holophyly of this grouping vis à vis the Neotropical species has not been established.) The apomorphic features supporting this cladogram are: 1, mesopleuron smooth; 2, ring of long hairs around apex of gonosquama; 3, apex of fore wing infumate; 4, apex of gonosquama indented; 5, apex of ovipositor with coarse teeth; 6, fore tibia slender; 7, vein *Cu*₁ incomplete in hind wing; 8, flagellum with apical white band; 9, gaster closely punctate; 10, mesoscutum striate.
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An introduction to the Ichneumonidae of Australia

I. D. Gauld

In the important field of biological and integrated control of pests the parasitic Hymenoptera are of particular significance, and this work considers one of the largest families of Parasitica, the Ichneumonidae. The group has received little attention in Australia – though it has already been utilized successfully in curtailing the ravages caused by accidentally introduced pests. For selective control programmes to be effective, however, a sound knowledge of the biology of both the pest and its parasites is essential – and a sound taxonomic base is vital for the development of such knowledge.

Ironically, considering the group's economic importance, the parasitic Hymenoptera are amongst the least studied of any group of living organisms, and taxonomic difficulties have presented major problems to many entomologists working with the Parasitica. An Introduction to the Ichneumonidae of Australia will go a long way towards rectifying this situation, being a taxonomic treatment, by genus, of the Australian ichneumonids, a comprehensive illustrated identification guide, and a summary of all available information on the group. It will also serve as an introduction to the biology and distribution of Australian ichneumonids, and provide a check-list of the described species and an index to their known hosts. It provides an important revision of ichneumonid nomenclature in order to bring the group into line with the generally accepted principles of zoological nomenclature.

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The tribe Pseudophloeini (Hemiptera: Coreidae) in the Old World tropics with a discussion on the distribution of the Pseudophloeinae

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Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The major morphological features of the Pseudophloeini are outlined and their bearing on the classification of the tribe is discussed. Twelve genera and 43 species are recognized in the tropical regions of Africa and Asia; descriptions and keys for their separation are provided. Four genera and 16 species are described as new. Three new synonymies are established at the genus-level and four at the species-level; 10 new combinations are established; two ‘forms’ are raised to the status of species and nine lectotypes are designated.

Introduction

Plant-feeding bugs of the family Coreidae are characteristic inhabitants of the herb and shrub layers of tropical and, to a lesser extent, of temperate ecosystems. They are frequently encountered in surveys of crop pests, since most of the world’s tropical crops are herbs or shrubs, and are usually represented in collections made during ecological studies in the tropics. Most of the literature available for the identification of Coreidae is out of date, fragmentary or lacks identification keys.

Pseudophloeinae may be recognized, with a little practice, by their general habitus and size, and by the absence of a dorsal sulcus on the tibiae; other groups of Coreoidea lacking tibial sulci
– Alydidae, Rhopalidae, Stenocephalidae and the coreid subfamily Hydariinae – are unlikely to be mistaken for Pseudophloeinae because they are all of characteristic appearance. Coreinae similar in size and build to Pseudophloeinae all have very distinct tibial sulci. Twenty-eight valid genera and 166 species of Pseudophloeinae have been described. Most of the species are 7–10 mm in length; a species of typical appearance is illustrated in Fig. 1.

The food plants of all species of the subfamily, where known, are herbaceous legumes (Fabaceae). Host plant records for the tropical Pseudophloeini are very scarce, as are other details of their biology. There is only a single, New World, species of the subfamily in which facultative brachyptery is known; all other species are fully macropterous. Flight, therefore, is probably important, yet there are very few records of them being caught in light traps, interception traps or yellow traps; presumably they fly only rarely and then not far. Most species have rather restricted ranges and only one is recorded from oceanic islands. Tropical-crop entomologists and collectors in Europe report them to move sluggishly even when disturbed and to be reluctant to fly. The typical habitats of Pseudophloeinae reflect those of their host plants: open woodlands and grasslands with scattered trees; a few species have penetrated drier grasslands on the one hand and forest clearings on the other, but deserts and dense forests, to judge from the distribution patterns of the tropical species, are impenetrable barriers to most of them. Several species are restricted to high altitudes, suggesting that low temperatures are not barriers to dispersal in the long term, a reasonable supposition in view of the richness of the Palaearctic pseudophloeine fauna.

The subfamily is represented in almost all parts of the major land masses except for non-tropical Australia. Recent revisions by Froeschner (1963), Dolling (1977) and Dolling & Yonke (1976) enable the Nearctic and Neotropical species to be identified. Most Palaearctic species are covered by the keys of Stichel (1960), which should be used in conjunction with the notes of Cherno (1979). The largest Palaearctic genus, Coriomeris Westwood, was revised by Chernova (1978). A new Palaearctic species of Microtelocerus Reuter was described from Sinai by Dolling (1979b) and a new genus with a single new species was added by Puchkov (1979). The tribe Clavigrallini, which is confined to the Old World tropics and contains a number of pest species, has been monographed by Dolling (1978: 1979a). The present revision covers all of the genera of Pseudophloeinae not treated in the above works.

**Diagnosis of Pseudophloeinae and its division into tribes**

Stål's original (1868: 535) diagnosis of Pseudophloeinae mentioned only the presence of an antevannal vein. Later (1873: 34–34), he mentioned also the broad cells at the base of the hemelytral membrane, the form of the metathoracic scent-gland auricle, the lack of a median dorsal impression on the head, the prominent and gently declivent tylus and juga, the prominent posterior angles of the seventh abdominal segment in both sexes, and the non-saculate tibiae. Dolling (1978: 282) gave a fuller diagnosis, adding mention of the outer apical processes of the antennifers and several features of the genitalia. The antevannal vein is not present in five genera: the Neotropical Vilga Stål; the Oriental Hoplolomia Stål and Indolomia gen. n., the Afrotropical Paramyla Linnaavouri and the Afro-Asian Risbecocoris Izzard. All five of these genera accord well with the revised diagnosis of the subfamily and there seems no reason to exclude them from it because of the absence of this single character; in fact, Stål (1873) included Hoplolomia in Pseudophloeinae, presumably on the basis of other features and in ignorance of the venation of the hind wing.

The tribe Clavigrallini was erected (as division Clavigrallaria) by Stål (1873: 81) in a key to the African and Asian genera of the subfamily. It was characterized by him as having the scutellum convex, the base of the posterior femur devoid of the small tubercle which is present in many genera of Pseudophloeinae, the body compressed laterally, the male genital capsule not bi-margined posteriorly, the propleuron emarginate on its posterior margin near the postero-dorsal angle, the second antennal segment equalling or exceeding the third in length and the prescutellar angles of the pronotum armed with a spine. The first couplet of Stål's key contrasted *Mevania* Stål, *Myla* Stål and *Hoplolomia* with the ‘Clavigrallarii’, uniting these three non-
Fig. 1 *Psilocromia pundaloyae*, dorsal view of male.
clavigralline genera on the basis of their common possession of a flat or almost flat scutellum, a tubercle at the base of the posterior femur, the posteriorly biemarginate genital capsule with the emargination filled by the apices of the parameres, the posterior tibia not or slightly shorter than the femur and the second antennal segment shorter than the third. Although Stål did not formally diagnose or name a 'division Pseudophloearia' to contrast with his 'Clavigrallaria', his recognition of the latter implies the existence of the nominate tribe. An additional feature, both universal among Clavigrallini and restricted to them, is the presence of a pair of small tubercles at the base of the mesoscutellum adjacent to the posterior margin of the pronotum. In a few Clavigrallini, the second antennal segment is shorter than the third, or the scutellum is flat, or the genital capsule is biemarginate posteriorly, or the posterior tibiae are subequal in length to the femora, or the body is depressed rather than compressed. The emargination of the propleuron, the absence of a femoral tubercle and the presence of the basal tubercles of the scutellum are constant features of the tribe, as is the presence of an antevannal vein. Among the non-clavigralline genera, the scutellum is occasionally convex and the propleuron emarginate (both conditions well developed in Vilga westwoodi (Kolenati)). The tubercle at the base of the femur is absent in Risbecocoris and Vilga.

No further tribes have been described, so the subfamily at present comprises the Clavigrallini and the nominate tribe, Pseudophloeini. The unique characters of the Clavigrallini are probably apomorphies within Pseudophloeinae while those of Pseudophloeini are, in general, plesiomorphies. Both the presence of the basal tubercle of the posterior femur and the presence of the antevannal vein of the metathoracic wing are probably apomorphies within the subfamily (though it is interesting to note that the genus Spathocera Stein, in the Coreinae, has an antevannal vein, and a group of genera including Riportus Stål, in the Alydinae, have a femoral tubercle). Pseudophloeinae can, therefore, be divided into four unequal groups (Table 1): Vilga and Risbecocoris, lacking both vein and tubercle; Paramyla, Hoplolomia and Indolomia, lacking the vein but possessing the tubercle; Clavigrallini, possessing the vein but lacking the tubercle; and all the remaining genera, possessing both vein and tubercle. Assuming that the lack of both vein and tubercle is primitive, a possible interpretation of the phylogeny of the Pseudophloeinae is that Clavigrallini and most Pseudophloeini are united by descent from a common ancestor that had no femoral tubercle but had acquired an antevannal vein; from this stock developed two lines: on the one hand Clavigrallini and on the other all those genera with both a femoral tubercle and an antevannal vein. On this interpretation, Paramyla, Hoplolomia and Indolomia would have acquired their femoral tubercles independently of most Pseudophloeini; alternatively, these three genera may have secondarily lost their antevannal veins. Recently, Štys (1978) suggested that the antevannal vein was primitively present in the common ancestor of all Coreidae. This interpretation is rejected here because it would involve recognition of a group comprising the genera Vilga, Risbecocoris, Paramyla, Hoplolomia and Indolomia sharing the apomorphy of the loss of this vein. This group, based on a loss character that unites these five morphologically diverse and geographically widely dispersed genera, is unlikely to have any phyletic validity.

A classification that reflected the most probable phylogeny of the subfamily would require the erection of two or three additional tribes to accommodate Vilga, Risbecocoris and, possibly, Paramyla plus Hoplolomia plus Indolomia. An assumption of independent acquisition of the antevannal vein by Clavigrallini and the main group of Pseudophloeini would require separate tribes for Vilga and Risbecocoris but not the other three of these genera. In the present work such new tribes are not erected. The subfamily Pseudophloeinae and the tribe Clavigrallini are both believed to be holophyletic in composition, leaving the nominate tribe paraphyletic.

Rejected genera

Four genera represented in the geographical area covered by the present revision were originally described in Pseudophloeinae or associated with genera that belong in the subfamily.

Brotheolus Bergroth (1908: 107) is a replacement name for the preoccupied Brotheus Distant
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(1902a: 248) which was placed by Distant (p. 246) in Pseudophloeinae. It was transferred to Coreinae: Gonocerini by Dolling (1979b: 97).

**Trallianus** Distant (1902b: 404–405) was originally placed in Pseudophloeinae but was transferred to Coreidae: Gonocerini by Dolling (1979b: 97).

**Cristovallia** Distant (1920: 149–150) was said by its author to have ‘affinity with the genera *Clavigralla* and *Cerealeptus*’ (both Pseudophloeinae). Brown (1958: 514) synonymized its type-species, *C. typica* Distant, with *Amblypelta bilineata* Stål in Coreinae: Dasynini.

**Austrocoris** Hsiao (1965: 426) was described in Pseudophloeinae. Later, Hsiao (1977: 253) synonymized it with *Chariesterus* Laporte but placed the latter genus in Pseudophloeinae. Its correct position is in Coreinae: Chariesterini.

**Abbreviations of depositories**

Specimens mentioned in the text are held in a number of different depositories; the addresses of 20 of these have been abbreviated as follows.

- **AMNH** American Museum of Natural History, New York, U.S.A.
- **BMNH** British Museum (Natural History), London, U.K.
- **BPBM** Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
- **CAS** California Academy of Sciences, San Francisco, U.S.A.
- **IAR** Institute of Agricultural Research, Samaru, Nigeria
- **IP** Institut für Pflanzenschutzforschung, Eberswalde, D.D.R.
- **IRSNB** Institut Royal des Sciences Naturelles, Brussels, Belgium
- **IZ** Institute of Zoology, Academy of Sciences, Leningrad, U.S.S.R.
- **IZPAN** Institut Zoologiczny, Polska Akademia Nauk, Warsaw, Poland
- **MNHN** Muséum National d'Histoire Naturelle, Paris, France
- **MNHU** Museum für Naturkunde der Humboldt-Universität, Berlin, D.D.R.
- **MRAC** Musée Royal de l'Afrique Centrale, Tervuren, Belgium
- **NMB** National Museum, Bulawayo, Zimbabwe
- **NMP** Natal Museum, Pietermaritzburg, South Africa
- **NMV** Naturhistorisches Museum, Vienna, Austria
- **NR** Naturhistoriska Riksmuseet, Stockholm, Sweden
- **TM** Transvaal Museum, Pretoria, South Africa
- **UG** University of Ghana, Legon, Ghana
- **UM** University Museum, Oxford, U.K.
- **ZMU** Zoological Museum of the University, Helsinki, Finland

**Terminology and measurements**

Antennal and rostral segments are numbered I to IV starting with the segment attached to the body. The term ‘rostral’ is used in preference to ‘labial’ because the base of the first segment of the labium is usually obscured; the first segment of the rostrum is arbitrarily taken to commence at the base of the labrum, which is almost always visible. Measurement of antennal segments excludes the narrow, unsculptured bases of segments I, II and III and the small ring-segment between III and IV. Ranges of measurements are given where this procedure seems useful (it is not used in the case of ratios of lengths of rostral and antennal segments, where it would be too cumbersome and would be of minimal use in identifying species). Means were calculated during the preparation of this revision but were discarded: because of the unequal representation of different populations in the samples available it was felt that they would be unhelpful and possibly misleading. Surprisingly often, means were found to fall almost exactly halfway between the extremes of the ranges cited. The reliability of the range of measurements of any species as a guide to what might be encountered by the reader in examining his own material will depend largely on the number of specimens examined by the author and the number of localities from which they were collected; this information is given under the heading ‘Material examined’ for each species. It should be borne in mind that the antennae of these insects are fragile and that the figures given for the ratios of the lengths of the antennal segments are in all likelihood based on progressively fewer specimens as one proceeds towards the distal end of the antenna. The
term ‘posterior’ as applied to angles and spines of the pronotum is avoided in favour of the unambiguous terms ‘posterolateral’ and ‘prescutellar’; the former usually project laterally or anterolaterally from the sides of the body while the latter are situated, if they are present at all, on the posterior margin of the pronotum close to the lateral angles of the scutellum and project posteriorly. Detailed descriptions of the body sculpture, pubescence and colour are usually given either under the description of the genus or under the description of one species of each genus that typifies the condition of these characters throughout the genus, and only deviations from this pattern, if they occur, are given for the other species. In descriptions of sculpture, the term ‘granule’ is applied to projections that are no higher than their width and ‘tubercle’ applies to projections longer than this; on the femora, there is a continuous gradation from granules through tubercles to small spines; all of these structures are probably derived from enlarged hair bases that, in the case of spines, have either lost the hair completely or have its insertion displaced from the apex of the setiferous tubercle.

Key to the genera of Pseudophloeini found in the Old World tropics

1 Posterior femur without tubercle adjacent to base of trochanter. Appearance characteristic (Fig. 2) ................................................................. RISBECOCORIS (p. 156)
   - Posterior femur with tubercle adjacent to base of trochanter, rarely obsolete and insect then of
general appearance of Fig. 1 ........................................................................... 2
2 Antennal segment II less than one-third as long as segment III .................. ARENOCORIS (p. 191)
   - Antennal segment II more than half as long as segment III .................. 3
3 Posterior margin of pronotum with a pair of spines projecting backwards over bases of clavi at
   rest (Figs 20, 25, 77) ................................................................................... 4
   - Posterior margin of pronotum smooth or at most with a few, low tubercles or granules. .... 5
4 Head dorsally and pronotum laterally with long spines; antennal segment I strongly clavate,
   with many long spines and tubercles (Fig. 77) ........................................ MEVANIDEA (p. 187)
   - Head, pronotum and antennae without spines ..................................... PARAMYLA (p. 165)
5 Main pubescence of body and hemelytra of short, decumbent, scale-like hairs (Figs 97, 98) ..... 6
   - Main pubescence of body and hemelytra of longer, erect or suberect, bristle-like hairs .... 8
6 Male with apical tooth of paramere upcurved, apex of paramere not filling posterior emargina-
   tion of genital capsule (Fig. 96). (Africa) ..................................................... MYLA (p. 193)
   - Male with parameres club-shaped, apical tooth short and not curved, apex of paramere filling
   posterior emargination of genital capsule (as in Fig. 21). (Asia) .................. 7
7 Pronotum with posterolateral angles strongly produced anterolaterally (Figs 63, 64).
   - Pronotum with posterolateral angles slightly prominent (Fig. 58) ........... PUNGRA (p. 179)
8 Abdominal sternites III to VII with posterolateral angles right-angled or acute, not projecting
   as triangular teeth (maximum degree of serration as in Fig. 42) ................ PSILOLOMIA (p. 168)
   - Abdominal sternites III to VII produced into triangular teeth, making outline of abdomen
   coarsely serrate (Figs 13, 19) ............................................................... 9
9 Antevannal vein present in metathoracic wing. (Africa) ............................... 10
   - Antevannal vein absent from metathoracic wing. (Asia) ...................... 11
10 Scutellum terminating apically in a small, elevated, white blob ........................ MEVANIOMOPHRA (p. 185)
   - Scutellar apex pointed, neither elevated nor white ............................. NEOMEVANIOMOPHRA (p. 183)
11 Pronotum (Fig. 12) coarsely granulate-tuberculate, posterolateral spines arising abruptly
   from posterolateral angles ................................................................. HOPLOLOMIA (p. 161)
   - Pronotum (Fig. 18) finely granulate-tuberculate, posterolateral angles tapering smoothly into
   posterolateral spines ........................................................................... INDOLOMIA (p. 163)

RISBECOCORIS Izzard

Risbecocoris Izzard, 1949: 478-479. Type-species: Risbecocoris tomentosus Izzard, by original designation.

Body rather elongate, about 2.5-3.0 times as long as broad, strongly depressed. Connexivum moderately expanded.

Head about as long as pronotum, strongly convex; eyes small, prominent; ocelli dorsally obscured by
pads of tomentose pubescence; dorsum of head strongly granulate and, at level of base of antennifers, with
a pair of prominent setiferous tubercles; each antennifer laterally with two or three similar tubercles and a
broad, weakly deflexed and ventrally incurved apical process. Antennal segment I varying in length from about four-fifths to almost equal to head width including eyes, with long, outstanding tubercles, cylindrical through most of its length but narrowed gradually towards base in proximal one-quarter; segments II and III distinctly more slender than I, tuberculate, II shorter than I, III longest of all; IV shortest, slightly thicker than II or III, elongate fusiform, specialized sensory area occupying its apical two-thirds. Bucculae occupying about one-half of ventral midline of head. Rostrum at rest reaching to posterior margin of mesosternum, segments I and II subequal, III about half as long as I and IV about two-thirds as long as I. Posterior half of head with two rows of tubercles flanking rostrum, in line with bucculae.

Pronotum shallowly declivent, granulate, posterior margin straight, prescutellar spines absent, postero-lateral angles weakly elevated, lateral margins almost straight, with five long, laterally directed spines. Scutellum about 1-2 times as long as its basal width, almost flat, apex pointed. Mesosternum deeply sulcate longitudinally. Metasternum convex with fine, median, longitudinal groove. Metathoracic scent-gland peritreme with dorsal ridge modified into a short, spout-like structure, circular in outline and completely surrounding orifice (Fig. 4). Corium with costal margin convex, apical margin weakly convex, all veins very strongly prominent; membrane of hemelytron with venation reticulate, prominent. Metathoracic wing (Fig. 5) with subcosta free in apical two-thirds, antevannal vein absent. Femora and tibiae with rows of prominent tubercules or granules; posterior femur without subapical spines but with one or two small tubercles in this position and no apical series; base of femur adjacent to trochanter lacking a tubercle.

Abdominal sternites III–VII with postero-lateral angles produced into progressively longer spines, lateral margins of sternites and spines bearing prominent granules and tubercles. Abdominal spiracles situated very close to lateral margins of sternites, prominent. Male genital capsule (Figs 9–11) broadly emarginate posteriorly, emargination filled by apices of parameres. Phallotheca with a ventral sclerite, produced dorsolaterally, and two rather broad dorsal longitudinal sclerites. Conjunctive with median dorsal and ventral lobes, distal and apical lobes various. Vesica short, not protected by any basal sclerites, wings of ejaculatory reservoir complex articulating with broad, distal dorsolateral sclerites. Spermathecal duct short, almost straight except for one sharp bend; bulb narrowly lunate. Anus of female directed ventrally.

Dense, off-white, tomentose pubescence present on head, pronotum, scutellum, clavus, corium, connexivum, underside, antennae up to and including base of segment IV and legs up to and including bases of tibiae. Erect hairs of body and of first one or two antennal segments very long and curved, remaining parts of antennae and other appendages with shorter, straight, erect hairs.

REMARKS. All species of this genus have a very distinctive appearance (Fig. 2) by virtue of their long, dense pubescence and long, lateral pronotal spines. Reticulate venation of the forewing membrane is characteristic of ground-dwelling Coreidae. The distally free subcosta in the metathoracic wing is unique in the family. The features that give the insects of this genus their remarkable appearance have probably arisen in response to the demands of what is, for a coreid, an unusually arid habitat.

DISTRIBUTION. All records come from a belt of semi-arid terrain stretching across Africa from Senegal to Kenya and thence into the Indian Desert.

Key to species

1 Larger, length of male 7.2 mm or more, of female 7.7 mm or more; antennal segment III about 1-3 times as long as segment I. (Sudan, Nigeria, Kenya, Chad) .................. numidianus (p. 160)
   - Smaller, length of male 7.1 mm or less, of female 7.6 mm or less; antennal segment III between 1-1 and 1-2 times as long as segment I ................. 2

2 Posterior femur with low granules on dorsal surface. (Niger) .................................. airensis (p. 159)
   - Posterior femur with outstanding tubercles on dorsal surface .................................. 3

3 Spines of postero-lateral angles of abdominal segments with weak sigmoid curvature, those of segment VII apically divergent. (Pakistan) .................................. quadrocephalus (p. 161)
   - Spines of postero-lateral angles of abdominal segments with stronger sigmoid curvature, those of segment VII apically convergent .................................. 4

4 Larger, length of male 6.7–7.1 mm, of female 7.1–7.6 mm. (Senegal) .................. tomentosus (p. 157)
   - Smaller, length of female 6.4–6.7 mm, male unknown. (India) ................................. delhiensis (p. 160)

Risbecocoris tomentosus Izzard

(Figs 5–11)

Risbecocoris tomentosus Izzard, 1949: 479–480, pl. 7. Holotype ♂, SENEGAL (BMNH) [examined].
Figs 2–11 Risbecocoris species. 2, 3, numidianus: (2) dorsal view; (3) apical view of conjunctiva and vesica. 4, quadrocepalus, left metapleuron and surrounding area, showing scent-gland peritreme. 5–11, tomentosus: (5) metathoracic wing; (6) dorsal view of conjunctiva and vesica; (7) apical view of same; (8) ventral view of same; (9) posterior view of male genital capsule with parameres; (10) dorsal view of same; (11) lateral view of same.
Length: $\sigma$, 6.7–7.1 mm; $\varphi$, 7.1–7.6 mm.

Head quadrate, its dorsal spine-like tubercle shorter than diameter of eye; tubercles on lateral margin of antennifer about 4 in number, conspicuous, 2–4 times as long as wide. Antenna with first segment about 0.95 times as long as width of head including eyes; ratio of lengths of segments about 1·00:0·93:1·11:0·56. Tubercles of segment I about twice as long as wide, those of segment II about 1·5 times as long as wide. Ratio of lengths of rostral segments about 1·00:0·90:0·43:0·67. Apex of corium at rest reaching to basal quarter or basal third of laterotergite VI. Width across hemelytra at rest about 0·72 times abdominal width (excluding spines and tubercles) in male, 0·77 times in female; abdominal width about 0·38 times total body length. Posterolateral spines of abdominal sternites with strong sigmoid curvature, those of segment VII apically slightly convergent. Tubercles on margins of abdominal sternites 1·50–2·25 times as long as wide, absent from segments I–IV, absent or single on segment V, one or two (rarely absent) on segment VI, one or two on segment VII. All femora dorsally with two rows of short tubercles.

Conjunctiva (Figs 6–8) with low, M-shaped dorsomedian lobe; large, membranous, paired distal dorsolateral lobes; globose, membranous apical dorsal lobes, small, membranous, digitiform apical ventral lobes, globose, membranous distal ventrolateral lobes and a small, median, apically bifid ventromedian lobe. Distal ventrolateral lobes each supported by a slender sclerite along its distal wall, this sclerite projecting anteriad as a narrowly triangular appendage, probably representing the totally sclerotized mesal lobe of the bilobed distal ventrolateral lobe. Distal dorsolateral lobes each with a strong, heavily sclerotized appendage arising near its base, adjacent to the apex of the respective wing of the ejaculatory reservoir complex, these sclerotized appendages not expanded apically.

Overall coloration appearing pale grey-brown to the naked eye. Colour of integument mid-brown; corium between veins, tibiae except for basal and apical annuli and spines of head yellow; lateral spines of pronotum yellow with apices black; apices of abdominal spines black. Forewing membrane slightly milky hyaline, veins white with occasional brown markings.

Remarks. This species differs from R. numidianus in its smaller body size and less elongated antennal segments III and IV, as well as in the form of the sclerotized distal appendages of the conjunctiva; the other known African species, R. airensis, has the tubercles of the femora reduced to granules only about as high as wide on the anterior two pairs of legs and obsolete on the posterior pair, whereas in tomentosus these tubercles are distinctly longer than wide.

Distribution. Known only from the type-locality in Senegal.

Material examined

Senegal: 1 $\sigma$ (holotype), Bambey, 26.ix.1942 (J. Risbec) (BMNH).

Senegal: 5 $\sigma$, 7 $\varphi$ (paratypes), Bambey, 26.ix.1942 [Izzard, 1949, gives dates as ix.1940, 26.xii.1943 and 1946.] (BMNH).

Risbecocoris airensis Villiers

Risbecocoris airensis Villiers, 1950a: 323–324. Holotype $\varphi$, Niger (MNHN) [examined].

Length: $\sigma$, unknown; $\varphi$, 7.2 mm.

Very similar to R. tomentosus. First antennal segment as long as head. Ratio of lengths of antennal segments as 1·00:0·96:1·18:0·68. Tubercles on lateral margin of antennifer short, hidden among the pubescence. Dorsal spine-like tubercle of head much shorter than diameter of eye. Lateral spines of holotype all with apices broken (not short as stated in original description). Anterior and intermediate femora with two dorsal rows of hispid granules about as high as wide; posterior femora with granules obsolete. Apex of corium at rest just reaching base of laterotergite VI. Lateral margins of abdominal sternites I–V without long tubercles, VI with a tubercle on one side only, VII with a tubercle on both sides. Width of abdomen (excluding spines) 0·38 times body length; width across closed hemelytra 0·82 times abdominal width.

Remarks. This species can be distinguished from others of the genus by the obsolete granulation of the posterior femora. The male is unknown; the holotype, stated to be of this sex in the original description, is in fact a female and it remains the only known specimen.

Distribution. Air Mountains.

Material examined

Niger: 1 $\varphi$ (holotype), Air Sud, Agadez, 525 m, 1–5.viii.1947 (A. Villiers & L. Chopard) (MNHN).
Risbecocoris numidianus sp. n.
(Figs 2, 3)

Length: ♂, 7.2-8.0 mm; ♀, 7.7-8.3 mm.

Head quadrate, dorsal spine-like tubercles longer than diameter of eye; antennifers laterally with 4-6 conspicuous tubercles up to 5 times as long as wide. Antennae with segment I 0.89-0.95 times as long as width of head including eyes; ratio of lengths of segments about 1:00:0.90:1:34:0.72. Tubercles of antennal segment I twice as long as wide or more, those of II up to twice as long as wide, those of III and base of IV about as long as wide. Ratio of lengths of rostral segments about 1:00:0.90:0.43:0.52.

All femora dorsally with two rows of tubercles about 2.5 times as long as wide, tubercles of tibiae about 1.5 times as long as wide. Apex of corium at rest reaching one-third or one-half of the way along laterotergite VI. Spines of posterolateral angles of abdominal segments with weak sigmoid curvature, apices of spines of segment VII weakly divergent. Numbers of tubercles present on lateral margins of abdominal sternites (excluding those on the spines themselves) varying from none to three on segments III and IV, one to three on V and VI and three to five on VII.

Conjunctiva (Fig. 3) differing from that of tomentosus in that apical dorsal and apical ventral lobes are absent and sclerotized appendages of distal dorsolateral lobes are broadly expanded apically.

Overall coloration dark grey-brown; integument generally dark brown; forewing membrane milky hyaline, its veins white with some brown streaks; tibiae, except for basal and apical annuli, yellow-brown; corium and clawus between veins pale brown; tubercles of head, abdomen and appendages pale brown; lateral spines of pronotum and abdomen pale brown, black-tipped; antennal segment IV very dark red-brown.

Remarks. This is the largest species of the genus. It differs from all its relatives in the proportionately longer antennal segments III and IV and in the apically expanded distal scleritized appendages of the conjunctiva; a distinctive species in an otherwise structurally rather uniform genus.

Distribution. Widespread in the eastern Sahel.

Material examined

Holotype ♂, Sudan: Umm Berembeita [11°51’ N, 30°40’ E; spelt Umerumbeita on label], on ground, 22.iii.1931 (F. G. S. Whitehead) (BMNH).


Chad: 1 ♂, Bas-Chari, near Fort-Lamy, Farcha, Forest, 8.viii.1963 (J. Pericarti); 1 ♂, Bas-Chari, near Douggia, 13.viii.1963 (J. Pericarti) (both R. Linnavuori coll.).

Nigeria: 1 ♀, NW. State, Badeggi RRS, 19.iii.1972 (J. T. Medler) (University of Ibadan).


Risbecocoris delhiensis (Bose) comb. n.

Hoplolomia delhiensis Bose, 1946: 75-76. Holotype (sex unknown), INDIA: Delhi, ix.1937, at light (Kerr) (Institute of Agricultural Research, New Delhi) [not examined].

Length: ♂, unknown; ♀, 6.4-6.7 mm.

Very similar to R. tomentosus. Dorsal spine of head much shorter than diameter of eye; antennifers bearing four tubercules up to 3 times as long as wide on their lateral margins. Head slightly wider than long.

First segment of antennae distinctly shorter than head, about 0.85 times as long as head width including eyes; ratio of lengths of antennal segments about 1:00:0.85:1:14:0.71. Tubercles of antennal segment I at most twice as long as wide, of segment II about 1.5 times as long as wide, of segment III about as long as wide. Ratio of lengths of rostral segments about 1:00:0.87:0.54:0.71. Femora with two dorsal rows of tubercles about 1.5 times as long as wide, tibiae with granules about as high as wide. Abdominal sternites with posterolateral spines stout and with rather strong sigmoid curvature, those of segment VII slightly convergent. Abdominal margins between the spines (which themselves bear tubercles) with tubercles up to 3 times as long as wide, borne singly on segments V-VII. Male unknown.

Remarks. In the original description, the body length is given as 7 mm. This species is the smallest of the genus. The holotype, said to be in the Agricultural Research Institute at New Delhi, was not available for study; the paratype, allegedly deposited in the BMNH, was not found.
**TRIBE PSEUDOPHLOEINI**

**DISTRIBUTION.** Eastern fringes of the Indian Desert.

**MATERIAL EXAMINED**

**India:** 2 ♀, Rajasthan, Pilani, ix.1965 (S. C. Goel) (BMNH).

**Risbecocoris quadrocephalus** Ahmad & Shadab

(Fig. 4)

*Risbecocoris quadrocephalus* Ahmad & Shadab, 1969: 151–155. Holotype ♀, **Pakistan:** Karachi, Malir, on grass near lucerne field, 7.12.1967 (Fareed Ahmed) (Karachi University Natural History Museum) [not examined].

**Length:** ♀, 6-7 mm; ♂, 7-2–7-3 mm.

Similar to *R. delhiensis* but slightly larger and tubercles of body and appendages slightly longer. Length of antennal segment I divided by head width including eyes 0-88–0-92. Ratio of lengths of antennal segments I:II:III about 1-00:0-89:1-17; length of segment IV divided by that of segment I 0-66 (type) or 0-69 in female, 0-77 in male. Posterolateral spines of abdominal sternite VII slightly divergent apically. A full description of the female is given in the original description. Conjunctiva of male similar to that of *R. tomentosus* in all respects except that the membranous lobe of the distal ventrolateral lobes is smaller and the ventromedian lobe is somewhat larger.

**REMARKS.** The differences between the Asian species of *Risbecocoris* are very slight. Substantially more material would be required for a definitive treatment of these forms. The orientation of the spines of abdominal sternite VII can be seen in the figures given in the original descriptions of *delhiensis* and *quadrocephalus* and may be reliable characters for distinguishing these two species. The two described Asian species are structurally very similar to *tomentosus* and the Arabian specimen mentioned below.

**DISTRIBUTION.** Southern Pakistan.

**MATERIAL EXAMINED**

**Pakistan:** 1 ♂, 1 ♀, Sind, Mainiforest, grass, 7.xi.1975 (Ali Khan) [determined as *quadrocephalus* by Ahmad and Khan] (BMNH).

**Risbecocoris** sp.

A single damaged specimen is mentioned here because of its biogeographical interest. It is a male from the island of Kamaran in the People’s Democratic Republic of the Yemen (‘South Yemen’), collected by G. C. Champion and deposited in the BMNH. It is 6-5 mm long; the length of its first antennal segment is 0-90 times the width of the head including the eyes and the second antennal segment is 0-87 times as long as the first; the remaining antennal segments are missing. Structurally, it is identical in almost every detail to *R. tomentosus*, including the detailed structure of the conjunctiva. The only differences apparent are the more slender vesica, the slightly smaller size and the slightly paler colour. The presence of a *tomentosus*-like form on an island near the Arabian shore of the Red Sea suggests that similar forms were and perhaps still are present throughout the northern edge of the Afrotropical Region and it forms a link between the Senegalese and Indo-Pakistan species.

**HOPLOLOMIA** Stål

*Hoploloomia* Stål, 1873: 82, 84. Type-species: *Hoploloomia scabricula* Stål, by monotypy.

Body oblong, slightly depressed, connexivum greatly expanded, insect strongly spinose-tuberculate and hispid.

Head slightly longer than pronotum, tuberculate; eyes rather small. Antennifers strongly divergent, their outer apical processes directed obliquely forwards and downwards, slightly curved inwards apically. Antennal segment I clavate, tuberculate; segment III the longest, IV shortest, fusiform, specialized sensory area of IV occupying three-quarters of its length. Bucellae rather short, occupying somewhat less than one-third of ventral midline of head. Rostrum at rest reaching disc of metasternum; segments I and II subequal, IV shorter, III very short.

Pronotum (Fig. 12) moderately or weakly declivent, tuberculate; posterolateral angles somewhat produced, bearing spines; posterior margin almost straight, prescutellar spines absent. Scutellum equilateral, flat or weakly convex, apex slightly raised. Dorsal ridge of metathoracic peritreme reniform, prominent. Meso- and metasternum shallowly sulcate. Corium with costal margin shallowly concave,
apical margin straight, apex not produced. Metathoracic wing (Fig. 17) without antevannal vein. Femora and tibiae strongly granulate to tuberculate; posterior femur with small basal tubercle, distally (Fig. 14) with two major spines and an apical series of three or four.

Abdominal sternites with lateral margins tuberculate, posterolateral angles spinously produced (Fig. 13). Male genital capsule posteriorly emarginate, emargination filled by apices of parameres. Conjunctiva (Figs 15, 16) with ventral lobes denticulate. Spermatheca with bulb narrowly lunate, duct about twice as long as bulb, simply looped.

Remarks. This small genus is characterized by the presence of a basal tubercle on the posterior femur in conjunction with the absence of an antevannal vein in the metathoracic wing and the strongly tuberculate and hirsute body. *Hoplolomia delhiensis* Bose is transferred to *Risbecocoris* (p. 160).

Distribution. Oriental region.

Key to species

1. Scutellum flat. (India) ................................................................. *campbelli* (p. 163)
   - Scutellum distinctly convex. (Southeast Asia) ................................................................. *scabricula* (p. 162)

*Hoplolomia scabricula* Stål

(Figs 12–14)

*Hoplolomia scabricula* Stål, 1873: 84. Holotype ♀, ‘India’ (NR) [examined].

Length: ♂, ♀, 6–4 mm.

Length of antennal segment I about 0.93 times as long as width of head including eyes; ratio of lengths of antennal segments about 1:00:0.81:1:20:0.62 (female). Ratio of lengths of rostral segments about 1:00:0.96:0.38:0.67.

Pronotum (Fig. 12) moderately declivous, spines of posterolateral angles directed laterad and slightly anteriad, width across apices of spines divided by width of head including eyes 2.17–2.54. Scutellum weakly but distinctly convex.

Conjunctiva with dorsomedian lobe deeply cleft, appearing almost as a pair of membranous dorsolateral lobes; distal dorsomedian lobe small, conical, membranous; distal dorsolateral lobes rather globular, each with a finger-like, membranous lobe arising at junction with dorsomedian lobe and a short, curved, sclerotized appendage arising opposite apex of wing of ejaculatory reservoir apparatus and curving downwards; apical ventral lobes membranous, globular; distal ventrolateral lobes each divided into a slender, finger-like, membranous lobe adjacent to apical ventral lobe, a large, spreading membranous lobe and two small, membranous but minutely denticulate ventral lobes. Sclerotized parts of conjunctiva consisting of these denticles, appendages of distal dorsolateral lobes and cup-like sclerite protecting base of vesica. Vesica moderately long, its apex obliquely truncate. Ejaculatory reservoir apparatus with wings but without straps.

Head granulate, dorsally with some stout tubercles; antennae granulate, segment I also tuberculate. Pronotum punctate, granulate and tuberculate with a pair of large, somewhat irregular, whitish tubercles near midline between posterolateral angles. Scutellum granulate-punctate, margins tuberculate. Thoracic pleura granulate-punctate. Clavus and corium granulate and deeply punctate, costal margin of corium in basal half tuberculate. Femora and tibiae granulate and tuberculate. Connexivum granulate-punctate. Abdominal sterna granulate, lateral margins tuberculate.

Pubescence of body and appendages of moderate length, semidecumbent, with longer, suberect or erect hairs arising from larger tubercles of appendages and dorsal surface of body, hairs arising from the tubercles of head and pronotum particularly long and erect.

Colour rufous brown. Anterior midline of pronotum, margins of clavi adjacent to scutellum, distal veins of corium, abdominal spines, large areas of laterotergites IV and V and anterior and posterior margins of VI and VII and apical two-thirds of posterior femora conspicuously darker. Bases of femora, first segment of each tarsus, tibiae except for basal and apical annuli, most of clavus and basal half of corium and spots on darker parts of femora stramineous. Hemelytral membrane fuscous hyaline, some groups of somewhat reticulate veins dirty white, veins of anal angle conspicuously white, the membrane surrounding them not infuscate.

Remarks. The type-locality is cited only as ‘India Orientalis’; it is assumed here that it was in South East Asia rather than in the Indian subcontinent on the basis of the distribution of the other material seen.
DISTRIBUTION. South East Asia. Hsiao (1964: 252) records this species from Yunnan, China.

MATERIAL EXAMINED
South East Asia ‘India orientalis’: 1 ♀ (holotype) (Stevens) (NR).

Hoplolomia campbelli sp. n.
(Figs 15–17)

Length: ♂, 5.7–5.8 mm; ♀, 6.7 mm.
Very similar to H. scabricula in size, form and colouring, including in the structure of the conjunctiva (Figs 15, 16) but body slightly more depressed and slightly narrower. Length of antennal segment I divided by width of head including eyes 0.85–0.93; ratio of lengths of antennal segments about 1:00:0.83:1.22:0.72. Pronotum shallowly declivent, width across apices of posterolateral spines divided by width of head including eyes 2.03–2.11. Scutellum flat.

REMARKS. Very similar to H. scabricula, this species is distinguished from it by the slightly more dorsoventrally flattened body, this difference being most apparent in the shallower slope of the pronotal disc and the flat, not convex, scutellum.

DISTRIBUTION. Southern India.

MATERIAL EXAMINED
Holotype ♂, India: Chikaballapura, iii.1915 (T. V. Campbell) (BMNH).
Paratypes. India: 1 ♂, Chikaballapura (Campbell), ii.1918; 1 ♀, Chikaballapura 11.i.1918 (BMNH).

INDOLOMIA gen. n.

Type-species: Indolomia conculata sp. n.

Body robust, connexivum widely expanded.
Head slightly longer than pronotum, with uniform, low granulation. Antennifers weakly divergent, outer apical processes triangular, apically curved inwards. Antennal segment I weakly clavate, slightly but distinctly shorter than head; segment III slightly shorter than I, II slightly shorter than III, IV shortest. Bucculae short, occupying only one-quarter of length of ventral midline of head. Rostrum with segment I reaching posteriorly almost to level of posterior margin of eye; segment II slightly shorter than I, III half as long as II, IV two-thirds as long as II.

Pronotum strongly declivent, its posterolateral angles strongly produced anterolaterally, posterolateral margin straight, without prescutellar spines; mostly rather weakly and uniformly granulate, with a pair of short, oblique ridges near midline between posterolateral angles, anterior and anterolateral margins and anterior half of midline with some larger and more prominent granules. Scutellum equilateral, convex, its apex slightly produced and swollen. Meso- and metasternum strongly sulcate longitudinally. Dorsal ridge of metathoracic peritreme shortly reniform. Corium with costal margin weakly concave and apical margin weakly convex, apex not produced. Metathoracic wing without antevannal vein. Anterior and intermediate femora each with a small subapical spine beneath; posterior femur with two or three major subapical spines and an apical series of tubercles and with a prominent basal tubercle. Posterior coxae separated by a space equal to about two-thirds of the width of a coxa.

Abdominal sternum III–VII with posterolateral angles triangularly produced, lateral margins with very obsolete granulation. Male genital capsule posteriorly emarginate, emargination filled by apices of parameres. Phallotheca with a broad ventral sclerite, produced laterally, and two thin, longitudinal dorsal sclerites. Phallotheca, conjunctiva and vesica subequal in length. Conjunctiva with sclerotized, ventrally directed distal dorsolateral appendages and a pair of sclerites protecting coiled base of vesica, otherwise completely membranous; dorsomedian lobe low, distal dorsomedian lobe conical, apical ventral lobes paired, weakly developed, distal ventrolateral lobes trilobed. Ejaculatory reservoir complex with wings well developed, straps absent.

REMARKS. This genus resembles Hoplolomia in that it lacks an antevannal vein in the metathoracic wing and has a basal tubercle on the hind femur. Because of the shape of the pronotum, the short pubescence and the absence of prominent tubercles from most of the body surface and appendages, it superficially
Figs 12–19 12–14, *Hoplolomia scabricula*: (12) dorsal view of pronotum; (13) ventral view of abdominal margin; (14) dorsal view of apical half of posterior femur. 15–17, *H. campbelli*: (15) dorsal view of conjunctiva and vesica; (16) ventral view of same; (17) metathoracic wing. 18, 19, *Indolomia conculata*: (18) dorsal view of pronotum; (19) ventral view of abdominal margin.

resembles some *Myla* species but the differences in the form of the male genitalia show that the two genera are not closely related.

**DISTRIBUTION.** A single species, in southern India.

**Indolomia conculata** sp. n.

(Figs 18, 19)

Length: ♂, 7.8 mm; ♀ unknown.

Head as long as its width including eyes. Length of antennal segment I divided by head width including eyes 0.89. Ratio of lengths of antennal segments as 1.00:0.89:0.94:0.83. Specialized sensory setae
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occupying about nine-tenths of length of segment IV. Antennae without prominent granules or tubercles. Rostral segment I 0.66 times as long as width of head including eyes; ratio of lengths of rostral segments as 1:0:0.89:0.45:0.64.

Pronotum (Fig. 18) with posterolateral angles terminating in short spines; width across apices of spines 2.43 times width of head including eyes. Legs moderately long, posterior tibia 0.96 times as long as posterior femur. Left femur of holotype with three major spines, the second half as long as the third and twice as long as the first, right femur with only two major spines, similar to second and third of left femur; an apical series of three spines present on both femora, one tubercle and two granules present between last and penultimate spines; a few granules present on rest of apical half of ventral surface of both femora. Scutellum, claval and corium strongly punctate and weakly granulate throughout. Abdominal sterna with posterolateral angles triangularly produced but not drawn out into spines (Fig. 19). Pubescence of body, antennal segment I and most of femora short, semidecumbent; that of rest of antennae, of tibiae and tarsi and parts of femora short or rather short, suberect; front of head and some large granules of pronotum with a few longer, erect hairs.

Colour various shades of brown. Head with midline and a U-shaped stripe adjacent to eyes and interrupted by ocelli conspicuously paler. Pronotum with midline and posterior disc conspicuously darker, the two oblique ridges of posterior disc conspicuously paler. Femora piceous with stramineous spots. Tibiae stramineous with basal and apical annuli piceous. Tarsi piceous, first segment dorsally stramineous. Connexivum banded pale and dark brown, abdominal dorsum rufous brown, anteriorly and anterolaterally piceous. Thoracic sterna piceous. Abdominal sterna mottled pale brown and piceous, piceous markings tending to form five longitudinal stripes. Hemelytral membrane fuscous hyaline; veins darker brown, interrupted by milky spots; anal angle of membrane, including veins, milky.

REMARKS. Only the holotype, which is complete but slightly crushed, is known.

MATERIAL EXAMINED

Holotype ♂, India: Anaimalai Hills, Cinchuna, 3500 ft [1067 m], v.1976 (T. Nathan) (BMNH).

PARAMYLA Linnavuori stat. n.


Body depressed, narrowly ovate, not conspicuously tuberculate or hispid, connexivum moderately expanded.

Head slightly shorter than pronotum, slightly longer than antennal segment I, dorsally granulate with two conspicuous, smooth, non-granulate lines arising between ocelli and diverging anteriorly, reaching half-way to antennifers, and a shorter, smooth line along outer margin of each ocelus. Antennifers divergent, outer apical processes of antennifers short, porrect. Antennal segment I longest, weakly but rather abruptly clavate, II shortest, III next shortest; I–III densely granulate, granules of I larger; IV with specialized sensory area occupying between two-thirds and four-fifths of its length. Bucculae occupying about one-quarter of ventral midline of head. Rostrum with segment I distinctly longest, II longer than IV, III shortest, apex of rostrum at rest reaching to disc of mesosternum.

Pronotum shallowly declivent, posterolateral angles scarcely prominent, bearing a short, triangular tooth, lateral margins granulate, disc granulate to tuberculate, posterior margin weakly convex, prescutellar spines well developed. Scutellum flat, equilateral, apex slightly or strongly elevated. Mesosternum sulcate, metasternum convex with slight longitudinal groove in anterior one-third. Dorsal ridge of metathoracic peritreme reniform. Metathoracic wing without antevannal vein. All femora granulate, anterior two pairs with or without a subapical spine beneath, posterior femur with a moderately well-developed basal tubercle and with two or three major subapical spines with only granules between them and an apical series of two to four tubercles. Posterior tibiae more than 0.90 times length of posterior femora.

Abdominal sternites with their posterolateral angles not produced, their densely granulate lateral margins forming a single, smooth curve. Genital capsule (Fig. 21) short, posteriorly emarginate, emargination filled by apices of parameres (Fig. 22).

REMARKS. Members of this genus are readily recognized among tropical Pseudophloeinae by their strongly depressed and largely non-tuberculate body. They have more the appearance of some Palearctic genera, but differ from these in the absence of an antevannal vein in the metathoracic wing. Linnavuori (1971) included Myla niokoensis Schouteden in his new subgenus Paramyla but the male genitalia of niokoensis are typical of the genus Myla and the resemblances between niokoensis and suspecta are confined to the
Paramyla species. 20, *australis*, dorsal view of body with hemelytra at rest and posterior femur and tibia. 21–26, *suspecta*: (21) posterior view of male genital capsule with parameres; (22) dorsomedial view of left paramere; (23) lateral view of phallotheca, conjunctiva and vesica; (24) ventral view of same; (25) dorsal view of head and pronotum; (26) dorsal view of posterior femur.

Superficial characters of a lack of abdominal spines, very short pronotal spines and very short pubescence.

**DISTRIBUTION.** Mountainous regions of central Africa and South Africa.

**Key to species**

1. Pronotum with prescutellar spines broad, triangular; hairs of pubescence longer than distance between adjacent hair insertions. (Mountains of central Africa) ............... *suspecta* (p. 166)
   - Pronotum with prescutellar spines slender; hairs of pubescence shorter than distance between adjacent insertions. (South Africa) ........................................... *australis* (p. 167)

**Paramyla suspecta** (Schouteden) comb. n.

(Figs 21–26)

*Myla suspecta* Schouteden, 1938: 294. Holotype ♂, ZAIRE (MRAC) [examined].
*Myla (Paramyla) suspecta* (Schouteden); Linnavuori, 1971: 177–178.

Length: ♂, 7.4–7.6 mm; ♀, 7.7–8.0 mm.
Antennal segment I with two different sizes of granulation, its length approximately equal (0.89–1.01 times) to width of head including eyes; ratio of lengths of antennal segments about 1.00:0.67:0.81:0.85;
specialized sensory area of segment IV occupying about four-fifths of its length. Ratio of lengths of rostral segments about 1·00:0·80:0·45:0·70.

Pronotum (Fig. 25) with disc granulate; lateral margins shallowly concave; posterolateral angles scarcely elevated above general level of posterior disc, width across apices of blunt posterolateral spines 1·73–1·82 times width of head including eyes; prescutellar angles with triangular spines. Scutellum with apex slightly elevated. Anterior and intermediate femora without subapical spines or tubercles, posterior femur (Fig. 26) with two major spines, the proximal one about half as long as the other, with only granules between them, and an apical series of two or three tubercles. Corium with costal margin markedly convex.

Male with phallosome short, consisting of a single ventral sclerite extending laterally almost to meet two rather less well-sclerotized dorsal sclerites. Conjunctiva (Figs 23, 24) with dorsomedian lobe large, its lateral angles prominent, distal dorsomedian lobe low, scarcely developed, distal dorsolateral lobes finger-like, wholly membranous and without sclerotized appendages, apical ventral lobes absent, distal ventrolateral lobes each divided into three: a dorsal, wholly membranous part, a ventral, largely sclerotized part, denticate along its anterior edge, and a narrow, denticate lobe situated anterior and medial to the two larger parts. Vesica stout, rather long, protected at base by a pair of sclerites. Ejaculatory reservoir complex with wings long, L-shaped, straps absent.

Head granulate throughout, granules larger along midline of tylus, gular region punctate. Antennal segment I with small, densely packed granules and some larger, outstanding granules, segments II–III with very small granules. Pronotal disc punctate, with scattered granules, anterior half with some larger granules or low tubercles, lateral margins with larger granules; scutellum weakly granulate-punctate; thoracic sterna and pleura punctate; femora and tibiae minutely granulate. Clavus and corium punctate throughout, punctures of clavus larger, of apex of corium smaller than average size of those on disc of corium, veins of clavus and corium granulate. Abdominal sternites and laterotergites minutely granulate, laterotergites also minutely punctate.

Insect clothed in short, semidecumbent pubescence, the hairs longer than the distances between their insertions; tubercles and larger granules of head and pronotum with longer, erect hairs.

Colour largely mid-brown. Membrane of hemelytra infuscate between veins, veins brown, with short, paler interruptions. Antennal segment IV, femora, especially posterior pair, and mesosternum dark brown to black; tibiae, except for basal and apical annuli, paler brown.

Remarks. This species seems to be one of the tropical Pseudophloeinae most highly adapted for life on the ground. The unusual form of the conjunctiva, lacking apical ventral lobes and sclerotized appendages to the distal dorsolateral lobes and with very strongly developed distal ventrolateral lobes, is presumably characteristic for the genus, and sets it somewhat apart from other genera.

Distribution. Highlands of central Africa.

Material examined

**Zaire**: 1 ♂ (holotype), Ituri, Nioka, vii.1934 (J. V. Leroy) (MRAC).

Zaire: 4 ♂, 4 ♀, data as holotype except that one male and two females have fuller date: 7.vii.1934 (probably all paratypes); 1 ♂, Ituri, de Buba à Petro (Nizi), 23.iii.1929 (A. Collart) (paratype); 1 ♀, Kibali-Ituri, Nioka, xii.1952 (J. Hecq) (MRAC). **Malawi**: 1 ♂, Masuku Mts, 6000–7000 ft [1800–2100 m], vii.1896 (A. Whyte) (BMNH).

**Paramyla australis** sp. n.

(Fig. 20)

Length: ♂, unknown; ♀, 7·5 mm.

Antennae with segment I proportionately longer and segment IV much shorter than in *P. spectata*, ratio of lengths of segments as 1·00:0·71:0·87:0·65; granulation of segment I uniform, segment IV with junction of specialized sensory area and area of normal pubescence oblique, specialized area occupying between three-quarters and two-thirds of its length. Body form (Fig. 20) slightly narrower than that of *spectata*; width of pronotum (Fig. 20) across apices of the blunt, triangular posterolateral spines 1·72 times width of head including eyes; prescutellar spines slender; posterolateral angles rather strongly elevated above level of posterior disc; lateral margins strongly concave. Scutellum with apex strongly raised. Corium with costal margin only weakly convex. Intermediate femur with a small subapical spine beneath; posterior femur (Fig. 20) with three major spines, of which the first is very small and the second about three-quarters the length of the last, a single tubercle between these two biggest spines and an apical series of four tubercles.

Sculpture of body, especially pronotum, rather more pronounced than in *spectata*; pronotal disc tuberculate. Pubescence of body and appendages very short, semidecumbent, white, the hairs distinctly...
shorter than the distances between their insertions; tarsi and apices of tibiae with longer, suberect pubescence but body without longer, suberect hairs.

REMARKS. This species diverges less from the typical body form of the subfamily than does its congener; the body is less flattened and there are more femoral spines. In contrast, the pubescence is abnormally short in the new species.

DISTRIBUTION. Known only from the type-locality in South Africa.

MATERIAL EXAMINED


**PSILOLOMIA** Breddin


Body oblong, not depressed, connivum rather narrowly to moderately expanded, body not conspicuously spinose, tuberculate or hairy.

Head about as long as pronotum, dorsally granulate to rather weakly tuberculate. Antennifers divergent, their outer apical processes short, broad, porrect. Antennae with segment I very weakly clavate, granulate, without conspicuously outstanding granules or tubercules; segments II and III never of conspicuously unequal length, minutely granulate. Bucculae occupying about one-quarter of ventral midline of head. Rostrum with segment I much the longest, II to IV subequal in length, apex of IV reaching to meso-metasternal suture.

Pronotum moderately declivent, its posterolateral angles not or rather weakly elevated and not or rather weakly produced laterally, posterolateral spines short, blunt or acute and arising abruptly from the angles, directed laterally; posterior margin straight, without humeral spines; disc and lateral margins with large granules or tubercles. Scutellum flat or weakly convex, equilateral, anterior angles prominent, apex elevated as a minute, whitish blob. Mesosternum shallowly sulcate; metasternum almost flat to distinctly convex, anteriorly concavely emarginate. Metathoracic peritreme (Fig. 38) with dorsal ridge bilobed, the anterior lobe much the larger. Clavus and corium punctate throughout, corium less heavily so apically and with apex not produced. Antevannal vein present in metathoracic wing (Fig. 39) but sometimes weak. Anterior and intermediate femora with zero to two small subapical spines beneath, posterior femur with three major subapical spines, some smaller ones and an apical series; tubercle at base of posterior femur small, sometimes obsolete. Posterior coxae not approximated.

Abdominal sterna III–VII with posterolateral angles not or slightly produced (maximum development in *P. brunneofusca*, Fig. 42). Spermatheca with bulb lunate, duct short, not convoluted. Male genital capsule posteriorly emarginate, emargination filled by apices of parameres. Conjugativa with dorsomedian lobe large, distal dorsomedian lobe smaller, both membranous; distal dorsolateral lobes slender, their posterior faces supported for much or, usually, all of their length by sclerites continuous with or articulating with wings of ejaculatory reservoir, which lacks straps; no sclerites protecting base of vesica; apical ventral lobe obsolete or transverse, sometimes weakly bilobed but never divided into two globular lobes; distal ventrolateral lobes membranous; ventral wall of conjugativa with a pair of posteriorly diverging, toothed, sclerotized strips, these weakly developed or absent in the smallest three species.

Pronotum, scutellum and thoracic pleura granulate-punctate, veins of hemelytra with occasional small granules, femora, tibiae, abdominal sternites and laterotergites granulate. Pubescence colourless or amber, simple, mostly rather short, semidecumbent to suberect, some species with long, erect hairs on pronotum and dorsum of head; pubescence never scale-like or tomentose.

REMARKS. This, one of the largest genera of the tribe, lacks any striking distinguishing features. The type-species of *Psilolomia* and *Neohoplolomia* are synonymized here. *P. brevitibialis*, the type-species of *Psilolomia*, is unique in that its vesica is about twice as wide as those of the other species examined and the distal dorsolateral lobes of the conjugativa are sclerotized for only about half their length. It shares with only *P. parva* both the absence of ventral, toothed, sclerotized strips from the conjugativa and the possession of an antennal segment II that is shorter than segment III; these are the only two species in which some of the dorsal granules of the head are developed into tubercles that are higher than wide. The conjugativa of *P. amphysia*, the third small species, has very weakly developed ventral sclerotized strips and thus forms a link between the other two and the large species of the genus. These differences do not seem of sufficient value to warrant the separation of *P. brevitibialis* or of *P. brevitibialis* plus *P. parva* from...
the remaining species at the generic level. Linnavuori (1970) placed the two African species known to him in Mevanomorpha, which is undoubtedly close to Psilolomia and might be regarded as a derivative of it with more pronounced pronotal and abdominal spines.

DISTRIBUTION. Afrotropical and Oriental regions; wholly continental, with no insular records.

Key to species

1 Side of head above each antennifer with a large tubercle almost as large as an eye (Figs 36, 37). (India)........................................................................................................ dispar (p. 174) 2
- Head without such tubercles. ................................................................................................................................. 3

2 Posterolateral angles of pronotum bearing acute spines that are longer than their basal width (Figs 1, 27, 30, 31, 33) ........................................................................................................................................................................ 7
- Posterolateral angles of pronotum with usually blunt spines no longer than their basal width (Figs 28, 29, 32, 34, 35)
Larger insects: length of male 7-6 mm or more; length of female 7-9 mm or more. Antennal segment I as long as or longer than width of head including eyes. .................................................. 4
- Smaller insects: length of male 7-2 mm or less; length of female 7-6 mm or less. Antennal segment I not as long as width of head including eyes. .................................................. 5

4 Coloration ochreous yellow. (India, Sri Lanka) ............................................... pudaloyac (p. 177)
- Coloration ferruginous or fuscous brown. (S. China to Malaya)  
  bruneofusca (p. 177), clavipes (p. 178)

5 Antennal segment II longer than segment III. (Africa) ........................................ 6
- Antennal segment II shorter than segment III. (Asia) ......................................... 6

6 Pronotum (Fig. 31) with lateral margins distinctly concave; abdominal sternites V and VI with posterolateral angles produced into short, acute spines. (Laos, Thailand) .......... parva (p. 174)
- Pronotum (Fig. 30) with lateral margins almost straight; abdominal sternites V and VI with posterolateral angles right-angled. (India, Sri Lanka) ........................................... brevitiibialis (p. 172)

7 Pronotum with lateral margins (Figs 32, 34, 35) bearing coarser tubercles and granules and longer and straighter pubescence. (Asia) .................................................. 8
- Pronotum with lateral margins (Figs 28, 29) bearing finer tubercles and shorter, more curved pubescence. (Africa) .................................................. 10

8 Pronotum with lateral margins (Fig. 35) strongly concave just anterior to posterolateral angles. (Thailand) .................................................. lata (p. 179)
- Pronotum with lateral margins (Figs 32, 34) weakly concave .................................. 9

9 Antennal segment I longer than width of head including eyes. General coloration ferruginous brown. (Burma) .................................................. steeleae (p. 178)
- Antennal segment I shorter than width of head including eyes. General coloration ochreous yellow. (India, Sri Lanka) ........................................... vulgaris (p. 175)

10 Antennal segment I not longer than width of head including eyes. Pronotum with lateral margins (Fig. 28) almost straight. (Nigeria, Central African Republic) .......... nigeriensis (p. 171)
- Antennal segment I longer than width of head including eyes. Pronotum with lateral margins (Fig. 29) distinctly concave. .................................................. 11

11 Larger insects: length of male 9-9 mm. (Sudan) ............................................... ferruginea (p. 172)
- Smaller insects: length of male 9-0 mm; length of female 9-7 mm. (Guinea, Nigeria) lamottel (p. 171)

Psilolomia amphrysis (Linnavaori) comb. n.

(Figs 27, 49)


Length: ♂, 6-6-7-2 mm; ♀, 7-2-7-6 mm.

Head dorsally granulate. Antennifers distinctly but not strongly divergent. Length of antennal segment I divided by width of head including eyes 0-88-1-00. Ratio of lengths of antennal segments in male about 1-00:0-78:0-73:0-82, in female about 1-00:0-77:0-71:0-74. Ratio of lengths of rostral segments in male about 1-00:0-65:0-50:0-73, in female about 1-00:0-58:0-52:0-61.

Pronotum (Fig. 27) with lateral margins slightly concave, bearing small tubercles that are slightly longer than wide; posterolateral spines acute, longer than their basal width; width across apices of spines divided by width of head including eyes 1-80-2-07. Metasternum moderately convex. Anterior and intermediate femora with or without one small, subapical spine beneath, posterior femur with three major spines, three or four minor spines between the second and third and an apical series of four. Length of posterior tibia about 0-7 times length of posterior femur.

Abdominal sternites III–VII with posterolateral angles acute, slightly prominent. Conjunctiva with distal dorsolateral lobes (Fig. 49) short, sclerotized throughout their length; ventral sclerotized strips weakly developed.

Pubescence of most of body and of hemelytra short, curved, semidecumbent; that of antennae and legs straighter, suberect; head also with some longer, suberect hairs arising from tubercles and larger granules; declivent part of pronotum also with pubescence of erect hairs about as long as diameter of an eye.

Colour sordid yellow, apical half of posterior femur heavily marked piceous; scattered, small piceous markings of greater or less extent present elsewhere on body and appendages, especially abdominal laterotergites and sternites. Granules of appendages usually piceous.

Remarks. This is the smallest of the African species and the only one of them with long pronotal pubescence (about as long as diameter of an eye); its pronotal posterolateral spines are longer than those of
other African species. It differs from the two small Asian species in having the second antennal segment longer than the third, not shorter.

**Distribution.** West Africa and Zambia.

**Material examined.**

**Ivory Coast:** 1 ♂, Lamto, 3.iii.1967 (Gillon), 1 ♀, Lamto, 7–10.ii.1962 (Gillon) (R. Linnavaurou coll; paratypes); 6 ♂, Lamto, various dates 26.vi.1962 to 21.vii.1964 (Gillon) (BMNH). **Nigeria:** 1 ♂, Samaru, Zaria, in dry plant detritus, 30.i.1955 (M.G.E.); 1 ♂, 1 ♀, Ilorin, under dead leaf, 19.iii.1955 (M.G.E.); 3 ♀, Gombe, Matzoro Lakes, i.1929 (Lloyd) (BMNH). **Zambia:** 1 ♂, Chisinga Plateau, Kalungwisi District, 4500 ft (1350 m), 25.x.1908 (Neave) (UM).

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**Psilolomia nigeriensis** sp. n.

(Figs 28, 57)

Length: ♂, 7-9-9-3 mm; ♀, 8-7-9-1 mm.

Head dorsally granulate. Antennifers distinctly but not very abruptly divergent. Length of antennal segment I divided by width of head including eyes 0-86-1-00. Ratio of lengths of antennal segments in northern males about 1-00:0-89:0-78:0-93; in southern males about 1-00:0-93:0-80:0-82; in northern females about 1-00:0-93:0-82:0-86; in southern females about 1-00:0-93:0-82:0-82. Ratio of lengths of rostral segments about 1-00:0-57:0-58:0-55.

Pronotum (Fig. 28) with lateral margins very shallowly concave, almost straight, bearing small granules; posterolateral angles each with a short, triangular spine; width across apices of spines divided by width of head including eyes 1-94:2-02. Metasternum rather strongly convex. Anterior and intermediate femora each without or with one small, subapical spine beneath; posterior femur with three major spines, rarely with a small spine preceding them, three or four minor spines between the penultimate and last major spines and an apical series of four or five. Length of posterior tibia divided by length of posterior femur 0-82-0-92.

Abdominal sternites III–VII with posterolateral angles acute and slightly prominent. Conjunctiva with ventral toothed sclerotized strips well-developed, distal dorsolateral lobes (Fig. 57) sclerotized throughout their length but less strongly so apically and ventrally, dorsomedian lobe bearing a narrow, membranous, apically bifid, median process; vesica longer than in any other species of the genus.

Pubescence of most of body and of hemelytra short, curved, semidecumbent; of antennae and legs suberect, longer and more erect ventrally on femora; head with uniform, short, semidecumbent pubescence; declivent part of pronotum with longer, less curved, suberect pubescence distinctly shorter than diameter of eye.

Colour sordid yellow – ochreous, usually with a slight ferruginous tinge and with piceous markings along apical margin of corium, thoracic and abdominal sterna and laterotergites and apical half of posterior femur; all tibiae with basal and apical annulli fuscous.

**Remarks.** This species differs from the other African species in its almost straight lateral pronotal margins. It is very similar to the Asian *P. vulgaris* but lacks suberect pubescence along the midline of the head and differs in the shape of the sclerotized distal dorsolateral lobes of the conjunctiva.

**Distribution.** West Africa.

**Material examined.**

Holotype ♂, Nigeria: U.C. Ibadan, on leaf of Vigna unguiculata, 31.i.1955 (G. H. Caswell) (BMNH). Paratypes. Nigeria: 1 ♂, data as holotype (Ibadan University); 1 ♀, Enugu, 30.x.1955 (Bechyne, Exped. Mus. G. Frey); 1 ♂, 1 ♀, Zaria, Samaru, at light, 12.vii.1966 (J. Deeming); 1 ♂, 2 ♀, Samaru, Zaria, in dry plant detritus, dry grass and plant bases, 30.i.1955 (M.G.E.) (BMNH). **Central African Republic:** 1 ♂, Bambari, u.v., 1964 (G. Pierrard) (MRAC).

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**Psilolomia lamottei** (Villiers) comb. n.

(Figs 29, 54)

*Acanthomia lamottei* Villiers, 1950b: 654–655. Holotype ♂, GUINEA (MNHN) [examined].

Length: ♀, 9-0 mm; ♀, 9-7 mm.

Head dorsally granulate. Antennifers strongly divergent. Length of antennal segment I divided by width of head including eyes about 1-1. Ratio of lengths of antennal segments about 1-00:0-84:0-78:0-76. Ratio of lengths of rostral segments about 1-00:0-58:0-61:0-58.
Pronotum (Fig. 29) with anterolateral margins concave, granulate; posterolateral angles prominent, bearing broadly triangular posterolateral spines; width across apices of spines divided by width of head including eyes 2-05 in male, 1-93 in female. Metasternum rather strongly convex. Anterior femur with one, minute, subapical spine beneath, intermediate femur with one small spine, posterior femur with three major spines (preceded by a small spine in holotype) with three minor spines between the penultimate and last major spines and an apical series of four; tubercle at base of posterior femur obsolete. Length of posterior tibia divided by length of posterior femur 0-84–0-85.

Abdominal sternites V and VI with posterolateral angles slightly prominent, slightly more acute than right-angled; those of VII angled at about 85°, slightly prominent. Vesica long and slender; conjunctiva with ventral toothed strips well developed; distal dorsolateral lobes (Fig. 54) sclerotized throughout, not apically angled or expanded.

Pubescence rather short, suberect to semidecumbent, of uniform length, no erect hairs present even on dorsal midline of head.

Coloration of holotype from Guinea sordid yellow with slight rufous tinge, antennal segment IV, tubercles of all appendages, basal annulus of posterior tibia and, less conspicuously, of other tibiae, meso- and metasterna and extensive mottling on abdominal sternum, laterotergites and apical half of posterior femur piceous or black. Male from Nigeria generally ferruginous without black or piceous markings except for those of abdomen and thoracic sterna.

Remarks. There is a close resemblance in structure, though not in colour, between the two specimens examined. This species resembles *P. ferruginea* in having the first antennal segment longer than the width of the head across the eyes and in the prominent posterolateral angles of the pronotum, but it is smaller and has fewer minor spines on the posterior femur. The two species are evidently closely related.

Distribution. Uplands of West Africa.

Material examined

**Guinea:** 1 ♀ (holotype), Nimba, ii.vi.42 (*M. Lamotte*) (MNHN).


*Psilolomia ferruginea* (Linnavuori) comb. n.


Length: ♂, 9-9 mm; ♀, unknown.

Head dorsally granulate. Antennifers strongly divergent. Length of antennal segment I divided by width of head including eyes about 1-2. Ratio of lengths of antennal segments as 1-00:0-90:0-77:0-63. Ratio of lengths of rostral segments as 1-00:0-71:0-57:0-68.

Lateral margins of pronotum very distinctly concave, bearing granules about as high as wide; posterolateral angles prominent, bearing short, broad posterolateral spines. Metasternum rather strongly convex. Anterior and intermediate femora each with a strong subapical spine beneath; posterior femur with three major spines, four minor spines between the first pair, three or four between the middle and apical major spines and an apical series of five.

Abdominal sternites III–VII with posterolateral angles more acute than right-angled, slightly prominent.

Coloration generally ferruginous.

Remarks. This species is closely similar to *P. lamottei*. It is the largest species of the genus.

Distribution. Known only from the type-locality in the foothills of the Ethiopian massif.

Material examined

**Sudan:** 1 ♂ (holotype), Blue Nile, Ingessana Mts, 17–22.xi.1962 (*R. Linnavuori*) (R. Linnavuori coll.).

*Psilolomia brevitibialis* Breddin

(Figs 30, 44, 50)

*Psilolomia brevitibialis* Breddin, 1909: 293. LECTOTYPE ♀, SRI LANKA (IP), here designated [examined].

Length: ♂, 5.8–6.4 mm; ♀, 6.4–7.3 mm.

Head dorsally granulate, tuberculate throughout vertex and midline. Antennifers distinctly divergent. Length of antennal segment I divided by width of head including eyes 0.78–0.81. Ratio of lengths of antennal segments about 1:00:0.79:0.96:0.83. Ratio of lengths of rostral segments about 1:00:0.50:0.54:0.54. Head and pronotum together constituting less than 0.39 (male) or 0.35 (female) of total length.

Pronotum (Fig. 30) with lateral margins straight, tuberculate; posterolateral angles not prominent; posterolateral spines short, acute; width across apices of spines divided by width of head including eyes 1:82–1:92. Metasternum moderately convex. Anterior and intermediate femora each without or with one small subapical spine beneath; posterior femur with three major spines, the first about half as long as the others, one to three minor spines between the two large ones and an apical series of four. Length of posterior tibia divided by length of posterior femur about 0.74.

Abdominal sternites III–VII with posterolateral angles right-angled, not prominent. Male conjunctiva (Fig. 44) with apical ventral lobes obsolete and ventral sclerotized strips absent; distal dorsolateral lobes (Fig. 50) short, supported by sclerotizations for only about half their length. Vesica unusually broad.

Pubescence suberect, short; tubercles of head and pronotum bearing longer, erect hairs shorter than three-quarters of the diameter of an eye.

Colour ochreous yellow, often sprinkled with minute red dots. Granules of antennae, femora and sometimes of tibiae piceous; antennal segment IV often piceous; anterior midline of pronotum, apical and basal annuli of tibiae, apical halves of posterior femora and more or less extensive markings of connexivum, especially posterior halves of laterotergites IV–VI, of pleura, of thoracic and abdominal sterna and of corium, especially in two places on the apical margin, piceous.

**Remarks.** The short, broad vesica and only partially sclerotized distal dorsolateral conjunctival lobes of this species are unique for the genus. The lack of ventral sclerotized conjunctival strips, the small body size and the possession of an antennal segment II that is shorter than segment III are all shared with *P. parva*. The two species can be distinguished externally by the form of the posterolateral angles of the abdominal sternites, which are acute in *parva* but right-angled in *brevitibialis*.

![Figs 36-43 Psilolomia species. 36, 37, dispar: (36) dorsal view of head; (37) lateral view of head. 38, 39, vulgaris: (38) left metathoracic scent-gland aperture; (39) metathoracic wing. 40–43, ventral view of abdominal margin of (40) steeleae; (41) lata; (42) brunneofusca; (43) vulgaris.](image-url)
DISTRIBUTION. Southern India and Sri Lanka.

MATERIAL EXAMINED


India: 26 ♂, 31 ♀, data as holotype of N. typica (paralecotypes of typica) (BMNH); 1 ♀, Coimbatore, x.1953 (P. S. Nathan) (IRSNB). Sri Lanka: 1 ♂, Pundaloya (BMNH).

Psilolomia parva sp. n.

(Figs 31, 45, 51)

Length: ♂, 5.4–5.9 mm; ♀, 5.9–6.5 mm.

Head dorsally granulate, tuberculate on vertex and in midline. Antennifers distinctly but rather weakly divergent. Length of antennal segment I divided by width of head including eyes about 0:86. Ratio of lengths of antennal segments about 1:00:0:73:0:89:0:81. Ratio of lengths of rostral segments about 1:00:0:55:0:55:0:55. Head and pronotum together constituting more than 0:39 (male) or 0:35 (female) of total length.

Pronotum with lateral margins (Fig. 31) weakly concave, posterolateral angles scarcely prominent; posterolateral spines acute, at least 1:5 times as long as their basal width; width of pronotum across apices of spines divided by width of head including eyes 1:74–1:83. Metathoracic wing with antevannal vein weak, difficult to see. Metasternum rather strongly convex. Anterior and intermediate femora without or with a single subapical spine beneath; posterior femur with three major spines, the first about half as long as the other two, one to three minor spines between the two large spines and an apical series of four. Length of posterior tibia divided by length of posterior femur about 0:72.

Abdominal sternites III–VII with posterolateral angles acute, slightly but distinctly prominent. Male conjunctiva (Fig. 45) without ventral sclerotized strips, distal dorsolateral lobes (Fig. 51) short, supported by sclerotization throughout their length; vesica slender.

Pubescence short, semidecumbent on hemelytra and most of body, slightly longer and less decumbent on legs and antennae, tubercles of head and pronotum bearing longer, almost erect hairs about as long as two-thirds diameter of an eye.

Colour ochreous yellow; ground colour of clavus, corium and posterior half of pronotum pale cinereous, without yellow tinge. Grey or piceous markings of greater or lesser extent present on midline and posterior border of pronotum, on scutellum, on hemelytra, especially costal and apical areas of corium; on anterior and posterior borders of laterotergites, including more than posterior halves of laterotergites IV and V; on apical halves of femora, especially posterior pair; and on thoracic pleura and abdominal sterna. Mesosternum and metasternum entirely piceous. Tibiae with basal, apical and median annuli grey.

REMARKS. This is the smallest species of the genus. It differs from the African P. amphrysa in having the second antennal segment shorter than the third and from the Asian P. brevibtialis in having the posterolateral angles of the abdominal sternites acute. The antevannal vein is very indistinct, probably because it is functionally obsolete in such a small wing.

DISTRIBUTION. South-east Asia.

MATERIAL EXAMINED


Psilolomia dispar (Walker) comb. n.

(Figs 36, 37, 48)

Clavigralla dispar Walker, 1872: 6. Holotype ♂ (no locality cited) (BMNH) [examined]. [Clavigralla aliena (Walker); Distant, 1901: 426. Misidentification.]

Length: ♂, 8.4–9.0 mm; ♀, 8.9–9.9 mm.

Head (Figs 36, 37) dorsally granulate, with antennifers very short, slightly divergent, outer apical process obsolete; a large, granular tubercle, almost as large as the eye, present on side of head above each antennifer. Length of antennal segment I divided by width of head including eyes 0:81–0:90. Ratio of
lengths of antennal segments in male about 1·00:1·01:0·88:0·87, in female about 1·00:0·99:0·84:0·92. Ratio of lengths of rostral segments about 1·00:0·63:0·55:0·61.

Pronotum with lateral margins shallowly concave, granulate, posteralateral angles elevated but only weakly produced laterally, posteralateral spines acute, about 1·5 times as long as their basal width; width of pronotum across apices of spines divided by width of head including eyes 1·96–2·04. Metasternum weakly convex. Anterior femur with one small subapical spine beneath, intermediate femur with one small spine and one very small one, posterior femur with three major spines, the first pair with no minor spines between them, the second and last with three or four minor spines between them and with an apical series of four; holotype and some other specimens with a small spine preceding the three major spines.

Abdominal sternites III–VII with posteralateral angles slightly more acute than right-angled and slightly prominent. Conjunctiva (Fig. 48) with ventral, toothed sclerotized strips well developed, distal dorsolateral lobes sclerotized throughout, L-shaped.

Coloration generally ferruginous; dorsal midline of head with distinct, narrow, yellow stripe; antennal segments III–VII yellow with granulation piceous; segment IV ferruginous; pronotum with anteromedian macula and posteralateral spines brown; legs yellow but extensively covered with brown granules, tibiae with basal, apical and median annuli brown, femora extensively mottled brown or ferruginous, especially apically; thoracic sterna brown; abdominal sterna yellow with brown markings largely confined to two longitudinal bands; laterotergites yellow with brown markings medially and posteriorly; clavus and corium ferruginous, the latter with a few obscure spots on veins brown, membrane fuscous, veins spotted darker, apex of corium and membrane throughout with large, cream spots.

Pubescence rather short, semidecumbent to suberect; erect hairs about as long as two-thirds diameter of eye present rather densely on declivent part of pronotum and on ventral surfaces of femora; main pubescence of head consisting of short, almost decumbent hairs but larger granules, especially of dorsal midline, bearing short, suberect to erect hairs.

Remarks. This species is immediately recognizable by the presence of the large tubercles above the antennifers; these could be mistaken for the antennifers themselves in dorsal view. The first antennal segment is unusually short for one of the larger species of the genus. Walker’s original description refers to three longitudinal brown bands on the pronotum; the lateral ones are, in fact, shadows in the shallow troughs between the gently convex pronotal disc and the elevated posteralateral angles. Distant (1901: 426) redescribed the type-specimen of Clavigralla dispers Walker under the impression that it was the type of Cletus alienus Walker. The latter, which is now missing, was a female from New Guinea whereas the type of dispers was specified by Walker as a male without locality data donated by Saunders.

Distribution. India.

Material examined

1 ♂ (holotype), no data (Saunders) (BMNH).

India: 1 ♂, Pondicherry State, Karikal, vii.1963 (P. S. Nathan) (BMNH); 2 ♂, 1 ♀ ‘E. Ind.’ (Bacon); 1 ♂, ‘Bgl’ (Haw.); 1 ♀, no locality (Haw.) (all UM); 1 ♂, Pondicherry State, Karikal, 1.i.1959 (Nathan); 1 ♂, Karikal Terr., Kurumbaragum, vii.1953 (Nathan); 6 ♂, 2 ♀, Tranquebar, vii.1953 (Nathan) (J. A. Slater coll.).

Psilomolia vulgaris sp. n.

(Figs 32, 38, 39, 43, 55)

Length: ♂, 7·9–8·8 mm; ♀, 8·7–9·7 mm.

Head dorsally granulate. Antennifers abruptly divergent. Length of antennal segment I divided by width of head including eyes in male about 0·89, in female about 0·95. Ratio of lengths of antennal segments in male about 1·00:0·89:0·75:0·89, in female about 1·00:0·96:0·81:0·93. Ratio of lengths of rostral segments about 1·00:0·56:0·56:0·56.

Pronotum (Fig. 32) with lateral margins very shallowly concave, bearing large, conical tubercles about as high as wide; posteralateral spines short, blunt, not longer than wide; width across apices of spines divided by width of head including eyes 1·98–2·11. Metasternum moderately convex. Anterior and intermediate femora each without or with a single, small subapical spine beneath; posterior femur with three major spines, rarely preceded by an additional small spine, the first pair of large spines without or with a single minor spine between them, three or four minor spines between the middle and distal spines and an apical series of four. Length of posterior tibia divided by length of posterior femur 0·75–0·79. Metathoracic wing (Fig. 38) and peritreme (Fig. 39) typical of the genus.

Abdominal sternites III–VII with posteralateral angles slightly more acute than right-angled, very
weakly prominent (Fig. 43). Male conjunctiva with ventral sclerotized strips rather weakly developed, distal dorsolateral lobes fully sclerotized, strongly angled before their spatulately expanded apices (Fig. 55).

Antennal segments I–III with suberect pubescence shorter than width of segment; rostrum with short, suberect and decumbent pubescence; head with short, semidecumbent hairs and dorsally with longer, suberect hairs not confined to midline; pronotum with short, semidecumbent pubescence posteriorly and suberect pubescence on disc and anteriorly, interspersed except posteriorly with rather longer, erect hairs; legs with short to moderately long, suberect pubescence, femora with longer, erect hairs ventrally; clavus and corium with short, semidecumbent pubescence; thoracic pleura and sterna and abdominal sterna and laterotergites with slightly longer, semidecumbent pubescence.

Coloration generally pale yellowish brown; ocellar tubercles and granules of antennae, rostrum and legs brown. Pronotum with anteromedian macula, lateral granules and posterolateral spines in part brown; scattered markings on pleura, scutellum and corium, especially apical areas of corium, brown; thoracic sterna piceous; femora sparsely mottled with brown, apical half of posterior femur, especially on posterior face, reddish brown. Abdominal laterotergites and bands along abdominal sterna mottled dark brown. Membrane of hemelytra very palely infuscate, veins paler with interrupted brown streaks.

Figs 44–57 Psilolomia species. 44–46, dorsal view of conjunctiva and vesica of (44) brevitibialis; (45) parva; (46) brunneofusca. 47, 48, ventral view of conjunctiva and vesica of (47) brunneofusca; (48) dispar. 49–57, apical view of vesica, ejaculatory reservoir apparatus and distal dorsolateral lobes of conjunctiva of (49) amphrysus; (50) brevitibialis; (51) parva; (52) brunneofusca; (53) lata; (54) lamottei; (55) vulgaris; (56) pudaloyae; (57) nigeriensis.
REMARKS. This species closely resembles *P. pandaloyae* and the African *P. nigeriensis*; it differs from the former in the shorter pronotal postero-lateral spines, from the latter in the longer pubescence of the head and from both in the form of the distal dorsolateral lobes of the conjunctiva. The sexual dimorphism in the relative length of antennal segment I is unusual; the shortness of this segment in the female results in the length of segment IV divided by that of segment I being greater in the female than in the male, the reverse of the usual situation in the subfamily, where segment IV is relatively longer in the male.

**DISTRIBUTION.** Southern India, Sri Lanka.

**MATERIAL EXAMINED**

- **Holotype ♂, India:** Madras, Karikal, Kurumbagarum, xi.1953 (*P. S. Nathan*) (J. A. Slater coll.).
- **Paratypes. India:** 8 ♀, 1 ♂, Karikal Territory, Kurumbagarum, ix.1954 (*Nathan*) (IRSNB); 1 ♂, Karikal, v.1957 (*Nathan*); 1 ♂, Tranquebar, viii.1956 (*Nathan*) (BPBM); 1 ♂, 2 ♀, Pondicherry or Karikal, vii.1953 (*Nathan*) (BMNH); 9 specimens, Tranquebar, vii.1953 (*Nathan*); 36 specimens, Kurumbagarum, various dates vii–xi.1953 and viii.1954 (*Nathan*) (J. A. Slater coll.).

**Psilolomia pandaloyae** sp. n.

(Figs 1, 56)

Length: ♂, 8.2–8.8 mm; ♀, 9.1 mm.

Head dorsally granulate. Antennifers rather strongly divergent. Length of antennal segment I divided by width of head including eyes 1:00–1:05. Ratio of lengths of antennal segments about 1:00:0:92:0:75:0:80 (IV missing in female). Ratio of lengths of rostral segments about 1:00:0:58:0:49:0:56.

Pronotum (Fig. 1) with lateral margins shallowly concave, bearing short tubercles slightly longer than their basal width; postero-lateral spines longer than wide; width across apices of spines divided by width of head including eyes 2:00–2:12. Metasternum weakly convex, its anterior emargination extending posteriorly as a shallow sulcus for over half its length. Anterior femur with a minute subapical spine beneath, intermediate femur with none, posterior femur with three major subapical spines, one minor spine between the first two, three between second and third and an apical series of four. Length of posterior tibia divided by that of posterior femur about 0:82.

Abdominal sternites (Fig. 1) with postero-lateral angles distinctly acute and slightly prominent. Male conjunctiva with ventral, toothed, sclerotized strips well developed; distal dorsolateral lobes (Fig. 56) wholly sclerotized, not angled before the spatulate apex.

Pubescence rather short, suberect, tending to semidecumbent on ventral surface of body; longer, erect hairs throughout declivert part of pronotum and dorsal surface of head. Longest hairs of head and pronotum more than two-thirds as long as diameter of an eye.

Coloration pale yellowish brown with darker markings, as in *P. vulgaris*.

**REMARKS.** This species closely resembles *P. vulgaris* but differs in the longer and more slender postero-lateral pronotal spines and the longer pubescence.

**DISTRIBUTION.** India, Sri Lanka.

**MATERIAL EXAMINED**

- **Holotype ♀, Sri Lanka:** Pandaloya (*Green*) (BMNH).
- **Paratypes. India:** 1 ♂, Chikkaballapura, i.1915 (*Campbell*); 1 ♂, Kodai Kanal, v.1918 (*Campbell*) (BMNH).

**Psilolomia brunneofusca** sp. n.

(Figs 33, 42, 46, 47, 52)

Length: ♂, 7.6–8.8 mm; ♀, 7.9–8.5 mm.

Head dorsally granulate. Antennifers abruptly divergent. Length of antennal segment I divided by width of head including eyes 1:15–1:20. Ratio of lengths of antennal segments in male about 1:00:0:81:0:68:0:74, in female about 1:00:0:83:0:77:0:73. Ratio of lengths of rostral segments about 1:00:0:62:0:56:0:60.

Lateral margins of pronotum (Fig. 33) concave, bearing granules about as high as wide; postero-lateral spines acute, longer than their basal width and slightly curved posteriorly; width across apices of spines divided by width of head including eyes 2:11–2:14. Metasternum weakly convex. Anterior femur with a small, subapical spine beneath, sometimes with an incipient second one proximal to it; intermediate femur with two spines; posterior femur with three major spines and usually a fourth, smaller one proximal to the others, one to three minor spines between the first pair of large spines, three to four between the...
penultimate and last and an apical series of four or five. Length of posterior tibia divided by that of posterior femur 0·78–0·80.

Abdominal sternites III–VII (Fig. 42) with posterolateral angles acute and prominent. Male conjunctiva (Figs 46, 47) with ventral sclerotized strips well developed and distal dorsolateral lobes (Fig. 52) fully sclerotized, with slightly expanded apices.

Pubescence short, semidecumbent; rather longer and suberect on legs, antennae, declivent part of pronotum and dorsum of head; length of hairs of suberect pubescence equalling half to two-thirds diameter of an eye.

General colour dark ochreous brown to almost black. Antennae and legs yellow with all granulation dark brown, antennal segment IV strongly infuscate, apical halves of anterior and intermediate tibiae mottled with dark brown, apical half of posterior femur heavily mottled dark brown. Head, pronotum and scutellum ochreous with dark brown markings, the raised, white apex of the scutellum (universal in the genus) strongly contrasting. Thoracic pleura and abdominal sternae and laterotergites reddish yellow with more or less extensive dark brown markings; thoracic sternae piceous or black. Clavus and corium dark ochreous or grey-brown, main veins of corium spotted both darker and paler; membrane darkly infuscate, veins brown; membrane and apex of corium with more or less conspicuous whitish spots, those of membrane often interrupting darker colour of veins.

REMARKS. This is a widespread, dark brown species similar in build to the much paler, yellowish *P. vulgaris*. It may be synonymous with *P. clavipes*, from southern China, but specimens of the latter were not available for study. It may be that the abdominal sternites of *clavipes* lack the acutely produced posterolateral angles that are more developed in *P. brunneofusca* than in any other species of the genus. The Indian specimen examined differed from the south-east Asian specimens only in having slightly broader posterolateral pronotal spines. The specimen from peninsular Malaya reported below represents the most south-easterly record of any species of the tribe; only some Clavigrallini represent the subfamily in the Malay Archipelago and northern Australia.

**Distribution.** South-eastern India, Laos, Malaya.

**Material examined.**


Paratypes. *Laos*: 1 ♀, Wapikhamthong Prov., Khong Sedone, 18.ix.1965 (*native collector*) (BMNH); 1 ♀, Borikhone Prov., Pakkading, 100–200 m, 23.iv.1965 (J. L. Gressitt); 1 ♀, Vientiane Prov., Tha Ngone, 3.i.1965 (*native collector*) (BPBM); 1 ♀, Luang Prabang, Pak Leung, 5.iii.1920 (R. V. de Salvaza) (BMNH).

*India*: 1 ♀, Anamalai Hills, Cinchona, 3500 ft [1070 m], v.1957 (P. S. Nathan) (BMNH).

*Malaya*: 1 ♀, Perlis, Kaki Bukit, 27.v.74 (P. Roche) (BMNH).

**Psilocoris clavipes** (Hsiao) **comb. n.**


Length: ♀, unknown; ♀, 8·7 mm.

Length of antennal segment I about 1·5 times width of head including eyes. Ratio of lengths of antennal segments as 1·00:0·87:0·80:0·80. Ratio of lengths of rostral segments as 1·00:0·69:0·54:0·61. Pronotum with posterolateral angles not produced; posterolateral spines longer than their basal width.

General coloration 'dark ochraceous'.

REMARKS. The partial description given here is based on that of Hsiao (1964: 251–252, 259). No material was available for study. A photograph of this species is reproduced by Hsiao (1977: pl. 46, fig. 603). It looks very similar to *P. brunneofusca* and the two species may be synonymous.

**Distribution.** Southern China (Yunnan).

**Psilocoris steeleae** sp. n.

(Figs 34, 40)

Length: ♀, unknown; ♀, 8·3 mm.

Head dorsally granulate. Antennifers weakly divergent. Length of antennal segment I divided by width of head including eyes 1·03. Ratio of lengths of antennal segments as 1·00:0·86:0·76:0·79. Ratio of lengths of rostral segments as 1·00:0·64:0·54:0·68.

Pronotum (Fig. 34) with lateral margin distinctly concave, bearing tubercles slightly longer than their
basal width; posterolateral spines short, broadly triangular; width across apices of spines divided by width of head including eyes 1:91. Metasternum almost flat. Anterior and intermediate femora each with a small, subapical spine beneath; posterior femur with three major spines, the first half as long as the other two, no minor spines between this and the middle spine, two minor spines between the two large spines and an apical series of three. Posterior tibiae rather long, 0-88 times as long as posterior femur.

Abdominal sternites III–VII with posterolateral angles (Fig. 40) slightly more acute than right-angled, weakly prominent.

Pubescence short, semidecumbent; rather longer and suberect on legs, antennae, declivent part of pronotum and dorsum of head; length of hairs of suberect pubescence equalling half to two-thirds diameter of an eye.

Coloration paler than in P. bruneofusca but not as pale as in P. vulgaris; darker markings distributed as in vulgaris; membrane of hemelytra fuscos with traces of pale spotting.

REMARKS. This new species differs from P. vulgaris in the longer first antennal segment and darker colour, and from P. bruneofusca in its shorter pronotal and abdominal spines.

DISTRIBUTION. Known only from the type-locality in Burma.

MATERIAL EXAMINED

Holotype ♀, Burma: Mishmi Hills, Lohit River, 24.iii.1935 (M. Steele) (BMNH).

Psilolomia lata sp. n.

(Figs 35, 41, 53)

Length: ♂, 7-8–8-5 mm; ♀, 8-5–9-3 mm.

Head dorsally granulate. Antennifers rather strongly and often abruptly divergent. Length of antennal segment I divided by width of head including eyes 1:03–1:16. Ratio of lengths of antennal segments in male about 1:00:0:90:0:76:0:79, in female about 1:00:0:90:0:77:0:70. Ratio of lengths of rostral segments about 1:00:0:67:0:53:0:60.

Pronotum (Fig. 35) with lateral margins deeply concave, bearing tubercles slightly longer than their basal width; posterolateral spines short, triangular; width across apices of spines divided by width of head including eyes 1:96–2:09. Metasternum flat, midline broadly and very shallowly concave throughout. Anterior and intermediate femora each bearing a single subapical spine, rarely a second spine present on intermediate femur; posterior femur with three, rarely four, major spines, penultimate spine preceded by a single minor spine or not, succeeded by three or four minor spines; terminal series consisting of four, rarely five, spines. Posterior tibia rather long, its length divided by that of posterior femur 0:86–0:87.

Abdominal sternites III–VII with posterolateral angles (Fig. 41) slightly more acute than right-angled, not or very slightly prominent. Conjunctiva with ventral sclerotized strips well developed; distal dorso-lateral lobes (Fig. 53) supported by sclerotization right up to their apices, which are not expanded.

Pubescence short, semidecumbent; rather longer and suberect on legs, antennae, declivent part of pronotum and dorsal midline of head; length of hairs of suberect pubescence equalling half to two-thirds diameter of an eye.

General coloration ferruginous, dark markings distributed as in P. vulgaris; membrane of hemelytra slightly infuscate, veins brown, interrupted by paler stretches.

REMARKS. This broad-bodied, ferruginous species may be distinguished from all others of the genus by the very deeply concave pronotal lateral margins.

DISTRIBUTION. Thailand.

MATERIAL EXAMINED


Paratypes. Thailand: 4 ♂, data as holotype; 2 ♂, 2 ♀, Chiangmai, Doi Suthep, 1300 m, 8.vi.1965 (Ashlock) (BPBM; BMNH).

PUNGRA gen. n.

Type-species: Pungra angusta sp. n.

Body form rather narrowly oblong, slightly depressed, connexivum slightly widened.

Head longer than pronotum. Antennifers moderately divergent, outer apical processes porrect, broadly triangular. Antennal segment I about as long as head width across antennifers, abruptly but weakly...
clavate, slightly longer than II, distinctly shorter than III, IV equal to I in male, shorter in female. Bucculae occupying about one-quarter of length of ventral midline of head. Rostrum at rest reaching to anterior disc of metasternum, segment II subequal to I, IV much shorter, III shortest.

Pronotum gently declivent, much broader than long, with a pair of small, raised calli on posterior disc between posterolateral angles, posterolateral angles weakly produced, posterolateral spines small, lateral margins with four stout tubercles each, posterior margin weakly convex, prescutellar spines absent. Scutellum almost flat, equilateral, its apex scarcely raised. Mesosternum and metasternum deeply sulcate throughout. Dorsal ridge of metathoracic peritreme reniform. Metathoracic wing with antevannal vein. Anterior and intermediate femora without spines or tubercles, posterior femur with basal tubercle well developed, with two major subapical spines preceded by granules and with three or four spine-like tubercles between them and an apical series of four tubercles.

Abdominal sternites with posterolateral angles only slightly prominent, lateral margins not tuberculate. Male genital capsule emarginate, emargination filled by apices of parameres.

REMARKS. This rather undistinguished genus is probably close to *Pseudomyla*, which it resembles in the presence of stout tubercules on the lateral margins of the pronotum, but differs from it in the shape of the posterolateral pronotal angles.

**DISTRIBUTION.** India.

**Pungra angusta** sp. n.

*(Fig. 58)*

Length: ♂, 7.3–7.7 mm; ♀, 8.0–8.4 mm.

Length of antennal segment I 0.76–0.89 times width of head across eyes; ratio of lengths of segments about 1:00:0:96:1:28:1:00 (male) or 1:00:0:98:1:32:0:85 (female); specialized sensory area of segment IV occupying about five-sixths of its length. Ratio of lengths of rostral segments about 1:00:0:92:0:30:0:56.

Pronotum (Fig. 58) with lateral margins straight for much of their length, posterolateral angles abruptly but shortly produced, posterolateral spines short, width across apices of spines 1.63–1.68 times width of head across eyes. Calli of posterior disc granular, close together. Length of posterior tibia 0.84–0.86 times length of posterior femur.

Abdominal sternites with posterolateral angles acute, very slightly prominent. Aedeagus similar in all respects, including the unpaired apical ventral lobe, to that of *Pseudomyla spinicollis* except that distal dorsomedian lobe is broadly conical and lacks finger-like processes at the lateral angles.

Antennal segment I strongly, II and III weakly granulate. Head granulate, dorsally with a few larger granules and tubercles. Pronotum weakly granulate, densely punctate, with a few tubercles anteriorly in addition to the four stout tubercles on the lateral margins. Scutellum, abdominal sternites including their lateral margins and laterotergites weakly granulate, thoracic pleura moderately granulate-punctate, thoracic sterna weakly punctate. Clavus and corium strongly, seriately punctate except for impunctate area near middle of apical margin of corium. Femora rather weakly granulate.

Pubescence of antennae, head, thorax, femora and abdomen of short, crisped, semidecumbent, pale, rather flattened hairs. Femora, tibiae and tarsi with short, suberect, fine hairs. Tubercles of head and pronotum with short, erect, curved, flattened hairs.

Colour yellowish stramineous, ocellar tubercules dark brown, antennal segment I, sides of head, pronotum, pleura, thoracic and abdominal sterna with diffuse brown markings; apices of all femora, especially the posterior pair, with brown mottling, all tibiae with proximal and distal incomplete brown annuli, anterior tibiae also with incomplete median brown annuli. Membrane of hemelytra colourless, its veins white, veins of membrane and of corium with a few brown spots. Laterotergites with small brown patches at base, at apex and in middle of lateral margins.

**DISTRIBUTION.** India.

**MATERIAL EXAMINED**

Holotype ♂, **India:** Nagpur (BMNH).

Paratypes. **India:** 1 ♀, Bombay; 1 ♂, 1 ♀, Maharashtra, Jalna, 4 ix. 1971 (J. C. Deeming) (BMNH).

**PSEUDOMYLA** gen. n.

Type-species: *Merocoris spinicollis* Spinola.

Body rather narrowly oblong, not depressed, connexivum moderately widened.

Head shorter than pronotum; antennifers moderately divergent, outer apical processes of antennifers
about as long as broad, porrect. Antennal segment I abruptly but weakly clavate, as long as or slightly shorter than head; segments I–IV subequal in length; specialized sensory area occupying about eight-ninths of length of antennal segment IV. Bucculae occupying about one-quarter of ventral midline of head. Rostrum at rest reaching to anterior margin or disc of metasternum, segment II almost as long as I, IV about two-thirds as long and III about two-fifths as long as I.

Pronotum (Figs 63, 64) with posterolateral angles strongly produced and directed forwards, strongly declivent, posterior margin straight or very shallowly emarginate, without prescutellar spines, lateral margins each with three or four stout tubercles, disc between posterolateral angles with a pair of small, transverse, granular calli. Scutellum almost flat with apex and anterior angles slightly elevated. Mesosternum and metasternum sulcate. Dorsal ridge of metathoracic peritreme reniform. Metathoracic wing with antevannal vein present but feebly developed. Anterior and intermediate femora with or without a single subapical spine beneath; posterior femur with a well-developed basal tubercle, three major subapical spines of which the proximal one is about half as long as the others, two or three tubercles between the two largest spines and an apical series of three or four tubercles. Posterior tibia 0.8–0.9 times as long as femur.

Abdominal sternites III–VII with posterolateral angles produced into small spines (Fig. 62). Male genital capsule posteriorly emarginate, emargination filled by apices of parameres. Spermatheca with bulb gibbously lunate, bulb short.

Remarks. These reddish ochreous insects with strongly produced and anteriorly directed posterolateral pronotal angles have been placed in the African genus Myla on the basis of the wholly superficial similarities of body shape. The genitalia of the males are quite unlike the characteristic form encountered in that genus and the nearest relative of *Pseudomyla* may be *Pungra*, which it resembles in the presence of stout tubercles on the lateral margins of the pronotum and granular calli on its posterior disc; the form of the conjunctiva is very similar in the two genera.

Distribution. Oriental region.

Key to species

1 Pronotum (Fig. 63) with posterolateral margins behind the posterolateral spines weakly concave, almost straight. (Central and southern India, Sri Lanka) .................. spinicollis (p. 182)

- Pronotum (Fig. 64) with posterolateral margins behind the posterolateral angles distinctly convex. (S. China, Laos) .......................................................... cornuta (p. 182)
Pseudomyla spinicollis (Spinola) comb. n.

(Figs 59–63)

Merocoris spinicollis Spinola, 1837: 216–217. Syntype(s). INDIA: Bombay (Dupont) [lost].

Clavigralla concolor Dohrn, 1860: 403. LECTOTYPE ♂, SRI LANKA (IZPAN), here designated [examined]. Syn. n.

Myla concolor (Dohrn) Stål, 1873: 84.

Length: ♂, 6.75–7.1 mm; ♀ unknown.

Length of antennal segment I equal to width of head including eyes; ratio of lengths of antennal segments about 1:00:0:92:1:00:0:96. Ratio of lengths of rostral segments about 1:00:0:91:0:41:0:68.

Pronotum (Fig. 63) with posterolateral margins (extending backwards from posterolateral spines) very weakly concave, almost straight. Metasternum moderately convex, shallowly sulcate throughout. Anterior and intermediate femora each with a single, small (Sri Lanka) or obsolete (Bombay) subapical spine.

Conjunctiva (Figs 59–61) with M-shaped dorsomedian lobe with pronounced dorsal angles; low, broad distal dorsomedian lobe with two anteriorly projecting finger-like appendages; distal dorsolateral lobes descending, supported throughout their ventral faces by a sclerotized strip articulating with apices of wings of ejaculatory reservoir complex; apical ventral lobe single, weakly sclerotized; distal ventrolateral lobes membranous except for a pair of toothed strips in ventral wall, which project at their anterior ends on very small, free lobes. Vesica slender, protected at base by a single, asymmetrical sclerite; ejaculatory reservoir asymmetrical but with wings symmetrical, strips absent.

Granulation of antennal segment I dense, uniform, that of segments II and III sparser and smaller; head granulate, pronotum and all pleura strongly punctate and rather weakly granulate, scutellum moderately granulate-punctate, thoracic and abdominal sterna weakly granulate, laterotergites weakly granulate-punctate, clavus and corium densely and strongly serially punctate except for impunctate area near middle of apical margin of corium, femora and tibiae sparsely and weakly granulate.

Semidecumbent, short, white pubescence of flattened hairs present on antennal segments I–III, head, thorax, clavus, corium and femora; hairs of thoracic pleura, pronotum and scutellum confused, those of other areas lying more uniformly parallel, femora, tibiae and tarsi with rather longer, fine, colourless, semi-erect pubescence.

Entire insect ochreous red except for black meso- and metasterna, diffuse blackish markings on ventral surfaces of head, pronotum and abdomen and colourless hemelytral membrane with veins marked white and brown; tibiae paler red than rest of insect.

REMARKS. Spinola’s type-material of Merocoris spinicollis, sent him by Dupont from Bombay, could not be found in Spinola’s collection by Prof. Dott. Carlo Vidano, of Turin, who kindly searched for it on my behalf, nor is it catalogued by Casale (1981). The genus is of such distinctive appearance that there can be no doubt that spinicollis belongs here. Spinola’s description is clear and the length given (3 French lines: equal to 7 mm) is within the measured range of specimens available. The slight difference in the size of the spines of the anterior and intermediate femora of the specimens from Bombay and those from Sri Lanka does not seem sufficient to warrant a division of the material into two species, particularly in view of the small number of specimens available. If it should prove that the Sri Lanka specimens are specifically distinct from the Bombay ones, Dohrn’s name concolor is available for the species.

DISTRIBUTION. India and Sri Lanka. Hsiao’s (1964: 252) record of Myla concolor from China refers to the material upon which he later (Hsiao, 1965: 427) founded the following species.

MATERIAL EXAMINED

Sri Lanka: 1 ♂ (lectotype of concolor), (Nietner) (IZPAN).

Sri Lanka: 1 ♂, Pandaloya (BMNH); 1 ♂, Pandaloya (Atkinson) (UM). India: 2 ♂, Bombay (Dixon), 1 ♂, Bombay (BMNH).

Pseudomyla cornuta (Hsiao) comb. n.

(Fig. 64)


Length: ♂, 7.0 mm (fide Hsiao, 1965); ♀, 6.5–7.2 mm.

Length of antennal segment I 0.94 times width of head including eyes; ratio of lengths of antennal segments about 1:00:0:90:1:06:0:88. Ratio of lengths of rostral segments about 1:00:0:95:0:41:0:68.
Pronotal margins behind posterolateral spines gently but distinctly convex (Fig. 64). Metasternum moderately convex, rather deeply sulcate throughout. Anterior and intermediate femora unarmed (*fide* Hsiao) or with a single, small subapical spine beneath. Posterior femur with three major spines, the most proximal less than one-third as long as the others, between which are two to four tubercles and beyond which is an apical series of four tubercles. Coloration, especially of clavus and corium, more ochreous than that of *P. spinicollis*.

**REMARKS.** Type-material was not available but the material examined agrees rather closely with the original description, and the locality from which it was obtained is near to the type-locality.

**DISTRIBUTION.** China: Yunnan (type-locality) and Laos.

**MATERIAL EXAMINED**


**NEOMEVANIOMORPHA gen. n.**

Type-species: *Mevaniomorpha annulipes rodhaini* Schouteden, 1938: 296.

Body oblong, neither compressed nor depressed, connexivum broad.

Head about as long as pronotum; eyes small, prominent. Antennifers divergent, outer apical process about as long as broad, porrect. Antennal segments subeual in length, segment I weakly clavate, granulate to tuberculate, distinctly shorter than head, segments II and III slender, very weakly granulate, IV elongate fusiform with specialized sensory area occupying about seven-eighths of its length. Bucculae occupying about one-quarter of ventral midline of head. Rostrum at rest reaching disc of metasternum; segment III the shortest, II and IV subequal, slightly shorter than I.

Pronotum (Fig. 65) rather strongly declivent, granulate-tuberculate, lateral margins bearing several short tubercules, posterolateral angles strongly produced anterolaterally, tapering to terminal spine; posterior margin weakly convex, with a few granules, prescutellar spines absent. Scutellum almost flat, equilateral, apex not elevated or swollen. Mesosternum and metasternum strongly sulcate throughout. Dorsal ridge of metathoracic peritreme bilobed, anterior lobe much the larger. Corium with apical margin straight. Metathoracic wing with antevannal vein present. Anterior and intermediate femora with subapical spines beneath, posterior femur with three major subapical spines and some minor ones and with basal tubercle well developed. Posterior coxae separated by about half the width of a coxa.

Abdominal sterna III–VII produced into broad, triangular spines, lateral margins almost smooth. Spermatheca (Fig. 72) with bulb lunate, duct long and tightly convoluted. Sclerites of wall of gynarium triradiate, with three arms of comparable length, one arm rising to meet upper ends of rami, one descending almost to meet base of second valvula and one extending horizontally posteriorly. Ovipositor with valvulae longer and more slender than in related genera. Male genital capsule (Fig. 69) short, posteriorly emarginate, emargination filled by apices of the short parameres (Figs 70, 71). Aedeagus (Figs 66, 67, 68) showing phallotheca of form typical in the tribe; conjunctiva with dorsomedian lobe M-shaped, membranous, distal dorsomedian lobe membranous, small, rounded–conical; distal dorsolateral lobes small, weakly sclerotized, apical ventral lobes paired, membranous, subglobular, distal ventrolateral lobes large, membranous, bilobed; ventral wall of conjunctiva with two longitudinal tracts of denticles that extend anterolaterally up sides of conjunctiva; vesica protected at base by a dorsal, cup-like sclerite; ejaculatory reservoir with long wings that extend inside the distal dorsolateral lobes to their apices, without straps.

**REMARKS.** The anterolaterally directed pronotal angles are shared with the African genus *Myla* and the Oriental *Psilocyma*, both of which have decumbent, scale-like pubescence in contrast to the suberect to erect hairs of *Neomevaniomorpha*. The raised, white tip of the scutellum that is characteristic of *Psilocyma, Mevaniomorpha* and *Mevanidea* is not found in this genus; it is least well developed in *Psilocyma* but the form of the conjunctiva is dissimilar. Probably the closest relatives of the genus *Neomevaniomorpha* are *Mevaniomorpha* and *Mevanidea*.

**DISTRIBUTION.** Central Afrotropical region.

*Neomevaniomorpha rodhaini* (Schouteden) comb. n., stat. n.

(Figs 65–72)

*Mevaniomorpha annulipes rodhaini* Schouteden, 1938: 296. LECTOTYPE ♀, ZAIRE (MRAC), here designated [examined].
Length: $\delta^\prime$, 7.4–7.7 mm; $\varphi$, 7.9–9.0 mm.

Antennal segment I about equal to width of head across antennifers, bearing some granules about as high as wide or, in one male paralectotype, with a few tubercles slightly higher than wide among the granules. Ratio of lengths of antennal segments about 1.00:0.96:1.08:0.96. Ratio of lengths of rostral segments about 1.00:0.92:0.64:0.87.

Shape of pronotum as in Fig. 65. Corium with apex reaching or almost reaching suture between laterotergites V and VI. Sulcus of mesosternum and metasternum very broad. Anterior and intermediate femora each with a single subapical spine beneath; posterior femur with first major spine less than half as long as the other two, followed by about three very small minor spines, space between the two larger spines with two or three minor spines and an apical series of four minor spines present. Length of posterior tibia divided by length of posterior femur 0.80–0.84.

Abdominal sternites III–VII with their posterolateral angles drawn out into spines equal in length at most to one-third of the width of their respective laterotergites. Spermatheca and male genitalia as in Figs 66–72 (see description of genus for discussion of salient features).

Head granulate; gular region punctate; vertex, frons, tylus and juga shortly tuberculate. Pronotum granulate-punctate, declivent area and lateral margins tuberculate, pleura granulate-punctate, sterna granulate, scutellum granulate-punctate with the granules on its lateral margins prominent. Hemelytra with clavus and corium punctate throughout, veins anteriorly, especially costal margin of corium, strongly granulate. Legs, especially femora, abdominal sternites and laterotergites granulate.

Pubescence of moderate to rather short, suberect hairs; dorsum of head and declivent part of pronotum with long, erect hairs.

Coloration generally mid-brown; ventral midline of thorax and of abdomen piceous. Membrane of hemelytra fuscous, the veins darker with occasional small, white spots; posterior basal angle white, appearing as a conspicuous, white triangle just behind end of claval commissure when hemelytra are at rest.

REMARKS. This is the only species of the genus. It seems strange that Schouteden could have described this insect as a form of *Mevaniomorpha annulipes*, from which it differs strikingly in the shape of the pronotum and in coloration.
DISTRIBUTION. Zaire and adjacent part of Zambia.

MATERIAL EXAMINED
Zaire: 1 ♂ (lectotype), Sankisia, 1911 (Dr Rodhain) (MRAC).
Zaire: 1 ♂, Lulua, Kapanga, viii.1932 (F. G. Overlaet); 1 ♀, Lulua, Kapanga, ix.1932 (F. G. Overlaet) (both paralectotypes; 2 ♂, Sankuru, M’Pemba Zeo (Gandajika), 28.ix.1958 (R. Maréchal); 1 ♂, Tshupa, Lukolela (De Guide); 1 ♀, Lulua, Kapanga, i.1933 (F. Overlaet); 1 ♀, Wombali, viii.1913 (P. Vanderijst) (labelled ‘allotypus’) (MRAC). Zambia: 1 ♀, Upper Kalungwisi Valley, 4200 ft [1260 m], 11.ix.1908 (S. A. Neave) (UM).

MEVANIONOMORPHA Reuter


Body oblong, slightly depressed; connivium broad.

Head about as long as pronotum, granulate-tuberculate. Antennifers strongly divergent, outer apical process present. Antennal segment I weakly clavate, granulate or granulate-tuberculate, longer or shorter than head; III longer than II, both slender, granulate, IV shortest, narrowly fusiform, specialized sensory area occupying four-fifths to five-sixths of its length. Bucculae occupying about one-quarter of ventral midline of head. Rostrum at rest reaching to disc of metasternum, its first two segments subequal in length, fourth shorter, third shortest of all.

Pronotum rather shallowly declivent, granulate-tuberculate and punctate, its posterolateral angles moderately produced laterally with posterolateral spines arising abruptly from them or greatly produced laterally and tapering gradually into the laterally-directed spines; lateral margins with several outstanding tubercles; posterior margin straight, smooth in front of scutellum, granulate further towards sides of body, prescutellar spines absent but granules present in their usual position on each side. Scutellum equalivent, its apex elevated into a small, white swelling occupying about one-fifth of its length. Mesosternum and metasternum longitudinally sulcate throughout. Metathoracic scent-gland peritreme with dorsal ridge bilobed, anterior lobe much the larger, constriction between lobes shallow, sometimes obsolete. Corium with costal and apical margins slightly convex. Metathoracic wing with antevannal vein. Anterior and intermediate femora with one or more small subapical spines beneath; posterior femur with three major subapical spines, some minor ones and a basal tubercle. Posterior tibia slightly more than four-fifths as long as femur. Posterior coxae separated by rather less than width of one coxa.

Abdominal sternites III–VII with posterolateral angles projecting as broad, triangular teeth, lateral margins almost smooth. Spermatheca with bulb lunate, duct tightly convoluted within concavity of bulb. Sclerites of wall of gynatrium L-shaped. Male genital capsule posteriorly emarginate, emargination filled by apices of parameres. Phallotheca with ventral sclerite short ventrally, strongly produced posterolaterally, dorsal sclerites very weakly sclerotized. Conjunctiva with flat-topped dorsomedian lobe, conical distal dorsomedian lobe, short distal dorsolateral lobes, broad apical ventral lobes, large distal dorsoventral lobes, all of them membranous; two strips of denticles present in ventral wall of conjunctiva; coiled base of vesica protected by two sclerites of which the left sclerite is twice as long as the right one.

REMARKS. This genus differs from Psilolomia in the greater projection of the posterolateral angles of the abdominal sternites and the presence of sclerites at the base of the vesica. The head and first antennal segment are not nearly so spiny as in Mevanidea.

DISTRIBUTION. Tropical Africa.

Key to species
1. Antennal segment I shorter than width of head including eyes; posterolateral spines of pronotum arising abruptly from the posterolateral angles; width across apices of spines less than 2-5 times width of head including eyes. (Widespread in tropical Africa) ...... annulipes (p. 185)
   - Antennal segment I longer than width of head including eyes; posterolateral angles of pronotum tapering gradually into spines; width across apices of spines more than 2-5 times width of head including eyes. (Forests of Central and West Africa) ................................................................. picta (p. 187)

Mevaniomorpha annulipes Reuter
(Figs 73, 75, 76)
[Clavigralla elevator (Fabricius) sensu Dallas, 1852: 511. Misidentification; not Coreus elevator Fabricius, 1803: 194.]
Meaniomorpha annulipes Reuter, 1883: 13-14. Holotype ♀, Ghana (ZMU) [examined].

Length: ♂, 7-2-8-2 mm; ♀, 7-8-9-9 mm.

Antennal segment I about as long as width of head across antennifers. Ratio of lengths of antennal segments in male about 1:00:1:04:1:08:0:88, in female about 1:00:1:04:1:12:0:84; total length of antenna less than 3-7 times width of head including eyes. Ratio of lengths of rostral segments about 1:00:0:92:0:54:0:78.

Posteralateral angles of pronotum (Fig. 73) prominent, posteralateral spines arising abruptly from them, directed laterally; width across apices of spines divided by width of head including eyes 2-2-2-4.

Aedeagus as in Figs 75, 76 (see description under genus).

Head dorsally granulate-tuberculate, laterally granulate, ventrally punctate. Pronotum granulate throughout, tuberculate anteriorly, punctuate posteriorly; scutellum and pleura punctate-granulate; thoracic and abdominal sterna and laterotergites weakly granulate. Clavus and corium punctate throughout, veins sparsely and weakly granulate; femora granulate.

Pubescence of rather short, suberect hairs, almost decumbent on head and pleura; longer, erect hairs present on dorsum of head and pronotum.

Colour pattern of medium brown and piceous markings on a paler, yellow ground. The most prominent dark markings is a stripe along anterior midline of pronotum, a pair of spines in front of anterolateral angles of pronotum, apical margin of corium, spot in apical part of disc of corium usually separate from dark apical margin, posterior two-thirds of laterotergites III-V, posterior margins of laterotergites V and VI, anterior margins of laterotergites III-VII and extensive motting on apices of posterior femora.

REMARKS. Some specimens in the north-eastern part of the range have shorter posteraleral pronotal and abdominal spines than the main population; such specimens were referred to the variety picta Schouteden by Linnaviuori (1970: 43-45); picta in fact has longer spines than true annulipes and appears to be a good species.

DISTRIBUTION. Widespread in tropical Africa.

MATERIAL EXAMINED

Ghana: 1 ♂ (holotype), Addah (Reitter) (ZMU).

Guinea: 1 ♂, Nimba, Yalanzou, ‘ii.vi.42’ (Lamotte), 1 ♂, Nimba, Kouleu, ‘ii.vi.42’ (Lamotte) (MNHN). Sierra Leone: 1 ♀ (leg. Morgan fide Dallas, 1852: 511) (labelled ‘425a’ and ‘Clavigralla elevator,’); 1 ♂, Mopeille, 1.vi.1926 (Hargreaves) (BMNH). Ivory Coast: 1 ♀, Tai, 12.xi.1979 (Couturier) (MNHN); 1 ♂, Bingerville, xii.1963 (Décèle); 1 ♀, Korea, au sud de Dalao, ix.1961 (Décèle) (MRAC).

Nigeria: 1 ♂, Calabar, 9.xi.1955 (Bechyné, Exp. Mus. G. Frey); 1 ♂, Akpasha Udi, 27.x.1955 (Bechyné, Exp. Mus. G. Frey); 1 ♂, near Bida, between Dabba and Kutiwenji, 20.xi.1970 (Deeming); 1 ♀, Gombe, Matzoro Lakes, i.1929 (Lloyd) (BMNH). Cameroun: 2 ♂, Batouri District, 3°45’N, 13°45’E, 750 m, 1.v–6.vi.1935 (Merfield) (BMNH); 1 ♀, Baigom, rég. Bamoun (MNHN). Zaïre: 1 ♂, Gamangui, ii.1910 (Lang & Chapin) (AMNH); 1 ♂, Haut-Uele, Manda, 18.iii.1925 (Schouteden); 1 ♂, Sankuru, M’Pemba Zeo (Gandajika), 1960 (Maréchal); 1 ♂, Kivu, Mulungu, 1939 (Hendrickx); 1 ♂, Kivu, Mulungu-Tshibinda, xi.1951 (Leffevre); 1 ♂, Kivu, Mwenga, Kitutu, rive de l’Elia, 650 m, forêt marécageuse primaire, humus, iv.1958 (Leleup); 1 ♂, Katanga, Luembe, viii–ix.1956 (de Caters); 1 ♀, Lulu, Kafakumba, xii.1932 (Overlaet); 1 ♀, Maulema, Wamaza, iii–iv.1957 (Cotonco); 1 ♀, Gandajika, iv.1959 (Decelle); 1 ♂, Bas-Congo, Thysville, 1959–1963 (Michaux); 1 ♀, Bas-Congo, Mayidi, 1942 (van Eyen); 1 ♂, Kivu, Mulungu, 1938 (Hendrickx); 1 ♀, Kivu, Mulungu, Tshibinda, xi.1951 (Leffevre); 1 ♀, Kivu, Iblanda, 1952 (Vandelannoite) (MRAC). Uganda: 1 ♂, Mutunda, 1.vi.1911 (Marshall); 1 ♂, Western Ankole, 4500–5000 ft (1350–1500 m), 10–14.x.1911 (Neave) (BMNH). Kenya: 1 ♂, Embu, 12.x.1914 (Browne); 1 ♀, N. slopes of Mt Kenya, on Embu-Meru road, 4500–5000 ft (1350–1500 m), 13–14.ii.1911 (Neave); 1 ♀, Nong, v.1926 (Gedye); 1 ♂, 1 ♀, Kaimosi, iii–iv.1932 (Turner); 1 ♀, Chuyu Hills, 5200 ft (1600 m), iv.1938 (Coriodyon Mus. Exped.) (BMNH). Zambia: 1 ♂, Lake Bangweulu, N’Sumba Island, 25.xi.1946, beaten from climbers (Steele); 1 ♂, Lake Bangweulu, Kapola, N. of Kapata, 27.x.1946 (Steele); 2 ♂, 1 ♀, Lake Bangweulu district, N’Salushi Island, 13.xi.1946 (Steele); 4 ♂, Upper Luanga River, 27.vii–13.viii.1910 (Neave); 1 ♂, Luanga to Petauke, 14–17.x.1910 (Neave) (BMNH); 1 ♂. Lower Kalungwisi valley, 3500 ft (1050 m), dense forest, 12–13.iii.1908 (Neave) (UM). Malawi: 1 ♂, Ruo valley, 1000–2000 ft (300–600 m), 21–25.iv.1910 (Neave) (BMNH). South Africa: 1 ♀, Transvaal, Louis Trichard, 20–30.xii.1956 (Capener) (J. A. Slater coll.); 1 ♀, Natal, ‘P. town’ (?=Pinetown), Gramin (BMNH).
MEVANIOMORPHA Schouteden stat. n.

(Me vanityomorpha plecta) Schouteden, 1938: 296. LECTOTYPE ♂, Zaire (MRAC), here designated [examined].

Length: ♂, 8.1–8.4 mm; ♀, 8.6–9.3 mm.

Antennal segment I longer than width of head including eyes; ratio of lengths of antennal segments about 1.00:0.91:0.96:0.71; total length of antennae more than 4.1 times width of head including eyes. Ratio of lengths of rostral segments about 1.00:0.93:0.55:0.79.

Pronotum (Fig. 74) with posterolateral angles merging gradually into posterolateral spines, width across apices of spines 2.6–3.0 times width of head including eyes; tubercles of disc and margins long.

Male genitalia similar to those of M. annulipes but ejaculatory reservoir complex with wings rather longer.

Pubescence as in M. annulipes; granulation and tuberculation more pronounced. Colour pattern very similar to that of annulipes but all elements of pattern darker; antennae rather dark brown throughout.

REMARKS. This species differs from M. annulipes in the longer appendages, more pronounced posterolateral spines of the pronotum and darker colour. Linnavuori (1970: 43–45), presumably basing his identification on coloration, referred dark specimens of true annulipes to this taxon; these specimens in fact had slightly shorter spines and appendages than typical annulipes. After the above description was completed, Dr V. van Zeijst showed me two males of picta from the Tai forest in the Ivory Coast; these specimens had very long, slender pronotal spines and were almost black; superficially, they closely resembled the unrelated Clavigralla hystricis Dallas, which occurred in the same forest.

DISTRIBUTION. Rain forests of Central and West Africa.

MATERIAL EXAMINED

Zaire: 1 ♂ (lectotype), Sankuru, Komi, iv.1930 (J. Ghesquière) (MRAC).

Zaire: 1 ♂, Sankuru, Komi, 2.v.1930 (Ghesquière); 1 ♂, Stanleyville (= Kisangani), 20.xii.1929 (Collart); 1 ♀, Uele, Dingila, ix.1933 (Brédo); 1 ♂, Lomani, Kambaye, vii.1930 (Quarré) (paralectotypes) (MRAC); 1 ♀, Yangambi, xi.1937 (Henrard) (MRAC). Cameroun: 1 ♀, Batouri (MNHN).

MEVANIDEA Reuter

Me vanitya Stål, 1866: 110. Type-species: Clavigralla spiniceps Signoret, by monotypy. [Homonym of Mevania Walker, 1854: 442–443.]


Mevanida Bergroth, 1907: 146. [Replacement name for Mevania Stål.] Syn. n.

Body not depressed, conivexum moderately expanded. Aspect, especially of head and pronotum, spinose (Fig. 77).

Head slightly shorter than pronotum, dorsally with numerous, long, spine-like tubercles. Eyes small, prominent. Antennifers moderately divergent, external apical processes porrect and directed slightly downwards. Antennal segment I strongly clavate, bearing numerous spine-like tubercles on its expanded apical part. Antennal segments I and IV subequal in length, IV fusiform; II subequal to or rather longer than I, III much the longest; II–IV almost smooth, bearing hairs about as long as width of segments II and III. Bucculae occupying about one-quarter of ventral midline of head. Rostrum at rest reaching to anterior margin or disc of metasternum; segment II slightly and IV distinctly shorter than I, III obviously shortest.

Pronotum strongly declivent, posterior margin straight or slightly convex, prescutellar spines well developed, tubercles present between them and posterolateral angles, along lateral margins and on disc, including some on posterior part. Posterolateral angles of pronotum slightly produced, posterolateral spines arising abruptly from them, directed laterally and slightly anteriorly. Scutellum equilaterally, slightly convex, its apical one-third conspicuously swollen, china-white. Mesosternum deeply sulcate throughout; metasternum sulcate for half or all of its length. Metathoracic peritreme with its dorsal ridge simple or unequally bilobed, the anterior lobe in the latter case much the larger. Metathoracic wing with antevannal vein. Anterior and intermediate femora with two rows of tubercles and granules beneath. Posterior femur with basal tubercle and beneath with three major subapical spines, the first spine two-thirds as long as the others; usually three minor spines between the two biggest ones and an apical series of four. Posterior tibia short, two-thirds to three-quarters as long as femur and conspicuously curved near base.

Abdominal sternites III–VI with posterolateral angles produced into broad, triangular spines, lateral
Fig 73-78 73, *Mevaniomorpha annulipes*, dorsal view of head, pronotum, scutellum and first antennal segment. 74, *M. picta*, dorsal view of head, pronotum and first antennal segment. 75, 76, *M. annulipes*: (75) ventral view of conjunctiva and vesica; (76) dorsal view of phallotheca, conjunctiva and vesica. 77, *Mevanidea hystrix*, dorsal view omitting legs and last three antennal segments. 78, *Arenocoris intermedius*, antenna.

Margins of sterna granulate. Spermatheca with bulb very narrow, duct three to four times as long as bulb, convoluted. Male conjunctiva with dorsomedian lobe M-shaped, membranous, distal dorsomedian lobe of similar size, also membranous, distal dorsolateral lobes obsolete, distal ventrolateral lobes large, bifid, weakly sclerotized on their posterior faces, apical ventral lobes membranous, paired, ventral wall of conjunctiva with or without a pair of toothed, sclerotized strips; basal, coiled part of vesica protected by two subequal sclerites.
Remarks. The appearance of the two species of this genus is very characteristic (Fig. 77), the spiny head and first antennal segment being particularly notable. The genus is probably derived from a *Mevaniomorpha*-like form.

Distribution. Africa and Madagascar.

Key to species

1 Membrane of forewing with an irregular, opaque, piceous or dark brown spot occupying about half of its area. (Africa) ................................................................. **hystrix** (p. 189)
– Membrane of forewing translucent, with some darker markings along veins and sometimes with dark amber shading of area between veins, but never with an opaque spot. (Madagascar) **spiniceps** (p. 190)

**Mevanidea hystrix** (Gerstaecker)

(Fig. 77)

*Mevania hystrix* Gerstaecker, 1873: 408–409. Holotype ♀, KENYA (MNHU) [examined].


*Mevanidea kilimana* Schouteden, 1910: 157. [Nomen nudum.]

*Mevaniera kilimana* Schouteden, 1912: 55. LECTOTYPE ♀, KENYA (NR), here designated [examined].

[Synonymized by Schouteden, 1938: 295.]

*Mevanidea hystrix* (Gerstaecker) Schouteden, 1938: 295.

Length: ♀, 5.7–6.8 mm; ♂, 6.2–7.6 mm.

Ratio of lengths of antennal segments in male about 1:00:1:02:1:30:1:02, in female about 1:00:1:14:1:41:1:00. Ratio of lengths of rostral segments in male about 1:00:0:97:0:55:0:79, in female about 1:00:0:97:0:50:0:75. Head dorsally with numerous granules and tubercles of various lengths, most noticeably a pair of spine-like tubercles close together between eyes with a third immediately behind them, a long, spine-like tubercle on each side of vertex just posterior to inner basal angles of antennifers, a staggered row of long tubercles all along tylius and others, rather shorter, on juga; sides and ventral surface of head punctate-granulate.

Pronotum with lateral margins almost straight, bearing three or four long tubercles, lateral angles suddenly prominent; prescutellar spines long, slender, sinuous; centre of disc with a widely spaced pair of conical tubercles, two groups of partially fused, blunt granules behind them but less widely spaced and a row of three similar clusters of granules between these and posterior margin in addition to more generally distributed granules and tubercles. Scutellum and thoracic pleura and sterna punctate-granulate. Hemelytra with clavus and corium, except for smooth area in middle of its apical part, punctate, veins anteriorly and basally granulate. Femora strongly granulate, shortly tuberculate dorsally and ventrally, with one or two subapical tubercles of the anterior and intermediate femora enlarged and occupying the usual positions of subapical spines; posterior femur with three major subapical spines beneath, one to four minor spines in the space between the first two and three or four in the space between the middle and last, with an apical series of three or four. Posterio tibia about two-thirds as long as femur.

Ventral wall of conjunctiva of aedeagus with a pair of apically divergent, toothed, sclerotized strips; vesica short, about as long as either of the wings of the ejaculatory reservoir complex.

Pubescence throughout of moderate to short, suberect hairs with some long, erect hairs on pronotum.

Colour pattern as in Fig. 77; the pale areas being stramineous and the dark areas varying from dark brown to dark red in different specimens. The most striking features of the colour pattern are the china-white, swollen apex of the scutellum, an irregular, opaque, dark brown blotch in the middle of the membrane of the hemelytra and a dark brown (never red) transverse spot near middle of corium edged proximally with white; laterotergites III to VI largely dark with a pale band anteriorly, VII largely pale.

Remarks. I can trace no earlier synonymy of *granulifera* with *hystrix* than that of Linnavuori (1978: 36); however, the synonymy is not indicated as new in that publication. The holotype of *M. hystrix* Gerstaecker is a small (6.0 mm) and very red male from Mombasa (Kenya) and that of *M. granulifera* Reuter a large (7.1 mm) blackish brown female from ‘Addah’ (i.e. Ada, Ghana). The great distance (4500 km) between the type-localities and the striking difference between specimens at the extremes of the range of colour variation have led earlier workers to recognize two species on the African continent. The reddish coloration is in general more pronounced in specimens from eastern and southern Africa and the brownish
coloration more pronounced in those from western Africa. The dark brown blotch in the middle of the membrane of the hemelytra is variable in extent but not in colour. The egg of this species is illustrated by Cobben (1968: 97, fig. 84).

**Distribution.** Widespread in subsaharan Africa.

**Material examined**


**Mevanidea spiniceps** (Signoret) comb. n.

*Clavigralla spiniceps* Signoret, 1861: 944. LECTOTYPE ♀, MADAGASCAR (NMV), here designated [examined].

*Mevania spiniceps* (Signoret) Stål, 1866: 110–111.

*Mevaniella spiniceps* (Signoret) Bergroth, 1907: 146.

Length: ♂, 6.8–7.8 mm; ♀, 7.3–8.2 mm.

Ratio of lengths of antennal segments in male about 1:00:1:30:1:55:1:15, in female about 1:00:1:14:1:48:1:04. Ratio of lengths of rostral segments in male about 1:00:0:92:0:54:0:87, in female about 1:00:0:92:0:55:0:78. Head strongly spiny-tuberculate but with fewer tubercles and granules than *M. hysterix*; the pair of long tubercles on vertex between eyes without a tubercle behind them. Posterior tibia about three-quarters as long as femur.

Aedeagus with no ventral sclerotized, toothed strips on conjunctiva and with vesica about twice as long as either wing of ejaculatory reservoir.

Colour pattern of dark to pale, often somewhat rufous (but never strongly reddish) brown areas and stramineous areas; membrane of hemelytra without opaque, brown blotch though with some brown markings along veins and occasionally with some dark amber shading of membrane between veins. Laterotergites III to V largely dark, each with a pale band anteriorly, VI and VII largely pale.

**Remarks.** This species resembles *M. hysterix* in general appearance. The main differences are in the aedeagus, where the longer vesica of *spiniceps* is presumably plesiomorphic and the absence of ventral sclerotized strips in the conjunctival wall apomorphic, and the absence of the dark brown blotch on the hemelytral membrane. The presence of only two spines, rather than three, on the vertex between the eyes is constant in all the specimens examined. *M. spiniceps* and a few species of *Clavigralla* (tribe *Clavigrallini*) are the only Pseudophloeinae known from Madagascar.

**Distribution.** Madagascar.

**Material examined**

Madagascar: 1 ♀ (lectotype) (NMV).

Madagascar: 1 ♀, Tulear Province, Tongobory, 200 m, 27.iii.1968 (*K.M.G. & P.D.*) (BMNH); 4 ♂, 2 ♀, no data; 1 ♀, Région de Sud-est, Fort-Dauphin, i.1901 (*Alluaud*); 1 ♂, Nossi-Bé, 5.vii.1900 (*Alluaud*); 1 ♂,
Ammocoris

Arenocoris conspicuously fusiform,

Boudicca Loukoube, Fanjahira, Ivondro, position;

descending midline.

auriculate, of

[Unnecessary synonymy INCLUDED genera eastern DISTRIBUTION.

1829), Blanchard, Head Pronotum additional, venation cooler parts of Europe and another into Ethiopia and Chad.

of


[Atractus Laporte sensu Curtis, 1834: legend to pl. 500. Misidentification.]


Ammocoris Agassiz, 1848: 48, 94. [Unjustified emendation of Arenocoris Hahn.]

Psammocoris Marshall, 1868: 281. [Unjustified emendation of Arenocoris Hahn.]

Boudicca Kirkaldy, 1909: 30. [Unnecessary replacement name for Pseudophloeus Burmeister.]

Body strongly depressed, ovate; connexivum considerably expanded in middle. Body and appendages conspicuously granulate-tuberculate.

Head distinctly longer than pronotum. Antennifers divergent with outer apical process either porrect or deflexed. Antennae with segment I much shorter than width of head, strongly incrassate except for basal one-eighth; segments II and III slender, II much shorter than I, III about 4 times as long as II, IV short, fusiform, intermediate in thickness between I and II. Bucculœ occupying about two-fifths of ventral length of head. Rostrum at rest reaching to posterior margin of mesosternum.

Pronotum weakly declivous, abruptly widenedit posteriorly; posterolateral angles truncate, sometimes auriculate, not pointed and not bearing posterolateral spines; posterior margin almost straight, weakly developed prescutellar lobes (not spines) present. Scutellum equilateral, lateral margins elevated anterio-

rly, apex elevated and bilobed. Mesosternum throughout and metasternum anteriorly deeply sulcate in midline. Metathoracic scent-gland peritreme with dorsal lobe entire, its dorsal margin evenly rounded, descending anteriorly and posteriorly to enclose orifice in at least its dorsal half. Membrane of hemelytron with venation reticulate. Metathoracic wing with antevannal vein well developed. Anterior and intermediate femora without subapical spines beneath, sometimes with a very slightly enlarged tubercle in this position; posterior femur with a single, large tubercle or blunt spine subapically beneath, very rarely with an additional, slightly enlarged tubercle distad of this; base of posterior femur with a prominent tubercle adjacent to trochanter.

Abdominal margin evenly rounded, posterolateral angles of sternites obtuse or right-angled, not prominent. Male genitalic capsule short with tongue triangular, lip obtusely angled in middle; parameres broad, flat, their apices filling posterior emargination of capsule. Phallotheca comprising two slender, dorsal sclerites and a slightly shorter, broad, ventral sclerite. Conjunctiva with dorsomedian lobe broad, membranous; distal dorsolateral lobes very long, their posteroventral sides supported by sclerotized extensions of wings of ejaculatory reservoir apparatus; vesica not protected basally by sclerites; apical ventral lobes small, membranous; distal ventrolateral lobes large, bilobed, the lower lobe sclerotized on its posterior face; ventral wall of conjunctiva with two slender, parallel sclerites; ejaculatory reservoir complex with wings long, straps absent. Ovispositor with second valvulae emarginate at apex. Sclerites of dorsal wall of gynaerum short, each comprising a narrow, longitudinally elongate, vertical, mesal plate supporting a thin, sclerotized ring and a narrow, horizontal, transverse, anterior plate articulating laterally with second valvifer and its ramus. Spermatheca with bulb lunate or half-moon shaped, duct about 1.5 times as long as bulb, slightly undulate but not convoluted.

INCLUDED SPECIES. Stichel (1962: 194–195) lists six species: egenus (Horvath, 1917), falleni (Schilling, 1829), gestroi (Bergevin, 1930), intermedius (Yakovlev, 1883), laissimus Seidenstücker, 1960 and waltli (Herrich-Schaeffer, 1834). Chernova (1979: 579) established the synonymy of egenus with falleni, and the synonymy of gestroi with intermedius is established below.

REMARKS. This is essentially a Palæartic genus, with a single eremic species intrusive into the north-eastern part of the Afrotropical region. Within the tropical fauna it is readily distinguished from other genera of Pseudophloeineae by the very short antennal segments I and II.

DISTRIBUTION. Europe, North Africa, Canary Islands, western Asia; mostly eremic but two species extend into cooler parts of Europe and another into Ethiopia and Chad.
Key to species

1. Outer apical process of antennifer deflexed .......................................................... 2
   - Outer apical process of antennifer porrect .......................................................... 3

2. Antennal segment I longer, length of incrassate part 0.46 or more times width of head including eyes. 
   (Spain, Portugal, western Asia and northern Africa southwards to Chad and Ethiopia) .......... \textit{intermedius} (p. 192)
   - Antennal segment I shorter, length of incrassate part less than 0.46 times width of head including eyes. 
     (Europe, western Asia, North Africa from Morocco to Libya) .................. \textit{falleni} (Schilling)

3. Head shorter, its length equal to its width including eyes. 
   (Europe, Canary Islands, coastal countries of North Africa, western Asia, Central Asia)   \textit{waltii} (Herrich-Schaeffer)
   - Head longer, its length about 1.2 times its width including eyes. 
     (Turkey and adjacent areas of U.S.S.R.) ...................................................... \textit{latissimus} Seidenstucker

\textbf{Arenocoris intermedius} (Yakovlev)

(Fig. 78)


\textit{Arenocoris intermedius} (Yakovlev) Kirichenko, 1952: 165.

Length: ♂ 6.0–7.2 mm, ♀ 5.6–7.4 mm.

Head granulate-tuberculate. Length of head equal to its width inclusive of eyes; antennifers strongly divergent, their outer apical processes deflexed. Antennae (Fig. 78) with segment I abruptly incrassate from a slender base, incrassate part tuberculate; segments II and III slender, weakly and densely granulate; IV shortly ovate-fusiform, nearly as thick as I and with apical sensory area occupying about one-half of its length. Length of antennal segment I (excluding slender basal part) divided by width of head including eyes 0.47–0.61. Ratio of lengths of segments (again excluding slender base of I) in male about 1.00:0.58:2.34:0.80, in female about 1.00:0.57:2.25:0.83. Ratio of lengths of rostral segments about 1.00:0.98:0.52:0.72.

Pronotum granulate-tuberculate, lateral margins each bearing three or four prominent tubercles, disc with two longitudinal rows of semiglobular granules, most of these in contact with the neighbouring ones, not standing separately; anterolateral margins distinctly but rather shallowly concave. Scutellum, pleura, femora and veins of corium granulate. Abdomen with laterotergites granulate.

Colour pale yellowish brown, usually with darker brown mottling, to piceous with paler markings. Antennal segments I to III usually pale yellowish brown throughout, infuscate in darkest specimens, III never darkened at apex, intercalary segment and segment IV always black. Membrane of hemelytra colourless, veins white with short, piceous streaks.

Remarks. \textit{Pseudophloeus gestroi} was described from a single male taken at the oasis of Jarabub (Giarabub) in Libya by Confalonieri. In his original description, Bergevin (1930: 32–33) compared it with \textit{falleni} and \textit{waltti} but not with \textit{intermedius}, which suggests that he was not familiar with this last species. His description agrees well with \textit{intermedius}, especially in the ‘almost smooth’ antennal segment III and in the shape of the pronotum, which is usually less abruptly widened posteriorly in this species than in most specimens of \textit{falleni}. In \textit{falleni}, antennal segments II and III are distinctly more strongly granulate. Bergevin did not mention the length of antennal segment I in relation to the width of the head, which is greater in \textit{intermedius} than in \textit{falleni}. A drawing of the holotype of \textit{P. gestroi}, kindly supplied by Dr R. Poggi, confirms that this species is synonymous with the former rather than the latter. I have seen specimens of \textit{falleni} from several localities each in Britain, Spain and Greece and from single localities in Austria, Gibraltar and Tunisia (Sbeïtla). The specimen of \textit{intermedius} listed below from Ethiopia has shorter appendages than the others examined. Its antennal segment I was found to be almost as short as in \textit{falleni}. It appears to have suffered some damage to one posterior leg and to the abdominal apex during development, which suggests that it may not be typical of the species in Ethiopia. Dr I. M. Kerzhner (pers. comm.) reports two specimens from Addis Ababa in IZ.

Distribution. Eremic. Spain and Portugal but no other countries in Europe to the north of the
Mediterranean Sea; North Africa south to Chad and Ethiopia; Sinai; Iraq; Iran; Turkey; Turkmenia (in part *fide* Stichel, 1962: 194).

**Material examined**

**Egypt:** 1 ♀, (holotype of *angustus*), Sinai, Aioun Mousa, ii.1899 (*Atruan*) (*data fide* Reuter, 1891) (ZMU).

**Chad:** 2 ♀, Kanem District, N’Gouri, viii.1958, x–xi.1958 (*Renoud*) (MRAC). **Sudan:** 1 ♂, Um Enderaba, 2.x.1927, at light (*Johnston*) (BMNH). **Ethiopia:** 1 ♂, Simien, Ras Degien, below the pass, over 4300 m, swept from *Senecio farinaceus* and Helichrysum citrinum, 11.xii.1952 (*Scott*) (BMNH).

**Extralimital material.** **Spain:** 4 ♀, Cangas (*Champion*). **Algeria:** 3 ♀, 2 ♀, Biskra (*Champion*). **Tunisia:** 1 ♀, Tozeur (*Champion*); 2 ♀, Gafsa (*Champion*); 2 ♀, Sfax (*de Vauloger*). **Libya:** 1 ♂, Cyrenaica, xi.1942. **Palestine:** 1 ♂, 1 ♀, Gaza district, Deir El-Belah, 10.v.1917, 14.v.1917 (*Austen*). **Iraq:** 1 ♂, 2 ♀, Baghdad, xii.1918, 27.xi.1918 (*Harwood*). **Iran:** 2 ♀, Shiraz, Bushire, 1–2.v.1927 (*Siyazov*). **U.S.S.R.:** 1 ♂, 2 ♀, Uzbekistan, Termez, 24.v.1912, 5.v.1912; 25.v.1912 (*Kirichenko*); 2 ♂, 1 ♀, Tadjikistan, Molotovabad (= Pyandzh), 5–7.iii.1944 (*Kirichenko*). (All BMNH.)

**MYLA** Stål

*Myla* Stål, 1866: 111. Type-species: *Myla nigrispina* Stål, by monotypy.

Body form parallel-sided, length about 3 times breadth, sometimes broader (*M. lata*), sometimes somewhat depressed (*M. niokensis*), connexivum narrow to broad.

Head about as long as broad, weakly granulate. Antennifers weakly divergent, their outer apical processes prorect. Antennae with segment I varying in length from about 0.50–1.25 times width of head including eyes, almost isodiametric throughout its length, weakly granulate; segment III about 1.25 times as long as II, both segments slender and weakly granulate; segment IV elongate, cylindrical, variable in length between the species so that in some it is the longest and in others the shortest segment, its specialized sensory area occupying nine-tenths of its length or more. Bucculae occupying about one-third of ventral length of head. Rostrum at rest reaching posteriorly to base of metasternum.

Pronotum strongly declivent anteriorly, disc weakly or very weakly granulate; lateral margins with many small granules or a few large granules or tubercles; posterolateral angles scarcely to very strongly produced anterolaterally or laterally, bearing obsolete to long, slender and acute posterolateral spines; posterior margin weakly convex, smoothly rounded, sometimes appearing slightly trilobed but without distinct emarginations or projections. Scutellum equilaterally or slightly elongate, its apex slightly elevated above clavi at rest, usually white; lateral margins, especially anteriorly, slightly elevated; disc flat, weakly granulate-punctate. Mesosternum sulcate throughout. Metasternum strongly convex, sulcate only anteriorly. Metathoracic scent-gland peritreme with dorsal ridge reniform. Corium with distal margin weakly or very weakly concave, its apex reaching to level of suture between laterotergites V and VI when at rest. Metathoracic wing with antevannal vein present. Anterior and intermediate femora usually with a single, prominent, subapical granule or tubercle beneath; posterior femur with well-developed basal tubercle and subapically beneath with three major spines, of which the first (proximal) one is very small, two to four small granules or tubercles between the two larger spines and an apical series of four tubercles. Posterior coxae separated by a distance equal to approximately half the width of a coxa.

Abdominal sterna III to VII with posterolateral angles acute, weakly to strongly produced, lateral margins of these sternites finely or obsolescently granulate. Male genital capsule posteriorly emarginate, the emargination with a central cusp; parameres with blades flat, their apices not occluding emargination of capsule (Fig. 96), proximal tooth of paramere simple, apical tooth long, upcurved. Phallotheca (Figs 111–113) comprising a single dorsal and a single ventral sclerite, both broad, each with a narrow, median, posterior projection, ventral sclerite proximally produced dorsad on each side to meet dorsal sclerite. Conjugctica (Figs 111–114) with dorsomedian lobe membranous, transverse, its lateral angles prominent; distal dorsolateral lobes membranous, arising close together over ejaculatory reservoir, finger-like, reflexed anteriad; apical ventral lobes large, membranous, paired; distal ventrolateral lobes deeply bifid, wings of ejaculatory reservoir complex extending into the dorsal, descending arm of each lobe, ventral, anteriorly directed arm of each lobe membranous and without sclerotized support; ventral lobes lightly sclerotized, wide apart, narrow, anteriorly directed and slightly upcurved; base of vesica without protective sclerites. Sclerites of wall of gymnoturn in female each comprising a curved plate parallel to rami bearing a longer, ventral, mesal and a shorter, dorsal, lateral process, both directed posteriorly. Spermatheca (Figs 115, 116) with bulb lunate, duct adjacent to bulb tightly convoluted, connected with gymnoturn by an S-shaped portion of the duct.

Main pubescence of body, hemelytra, femora and first antennal segment consisting of short, semidecum-
bent to adpressed, white, flattened, scale-like hairs. Coloration, probably of all species, variable, basically grey-brown with more or less of a yellowish or reddish suffusion.

Remarks. This genus differs from all others in the tribe in the form of the parameres, of which the distal tooth is long and sharply upcurved at right angles to the blade and the apices do not fill the posterior emargination of the genital capsule. The form of the phallotheca is also unique within the tribe. The scale-like pubescence is sufficient to distinguish Myla species from all other African Pseudophloeinae except Paramyla australis. Myla species are sometimes mistaken for members of the tribe Clavigrallini which, however, lack the tubercle that is present in Myla at the base of the posterior femur. Eleven species, all African, are accepted here as members of the genus. For M. concolor Dohrn and M. cornuta Hsiao, see Pseudomyla; for M. suspecta Schouteden, see Paramyla. M. schnelli Villiers was transferred to Clavigralla by Dolling (1979a: 34).

Distribution. Africa south of the Sahara, including Ethiopia. Not so far recorded from any islands or from Arabia.

Key to species

1 Length of antennal segment I divided by width of head including eyes 0·84 or less; in doubtful cases width of pronotum across apices of posterolateral spines divided by width of head 2·22 or less. ................................................................. 2
   - Length of antennal segment I divided by width of head including eyes 0·85 or more; in doubtful cases width of pronotum across apices of posterolateral spines divided by width of head more than 2·30. ................................................................. 4

2 Length of antennal segment I divided by width of head less than 0·54. (East Africa, rare) dispar (p. 198)
   - Length of antennal segment I divided by width of head more than 0·54. ................................................................. 3

3 Pronotum (Fig. 85) with posterolateral spines very short. (Mountains of East Africa) niokensis (p. 201)
   - Pronotum (Fig. 80) with posterolateral spines longer. (Cameroun) onceroma (p. 203)

4 Pronotum (Fig. 89) with posterolateral spines short, laterally directed; tibiae (Fig. 95) with alternate dark and light annuli. (East Africa, rare) lata (p. 200)
   - Pronotum (Figs 79, 81–84, 86–88) with posterolateral spines longer, directed anterolaterally; tibiae stramineous, unicolorous ................................................................. 5

5 Pubescence of body (Fig. 98) long, individual scale-like hairs of thorax longer than distance between their insertions. (West and Central Africa) gracilis (p. 204)
   - Pubescence of body (Fig. 97) short, individual scale-like hairs of thorax shorter than distance between their insertions ................................................................. 6

6 Ocelli (Fig. 81) very large, distance between ocellus and eye less than half diameter of ocellus. (East Africa) somalica (p. 200)
   - Ocelli (Figs 79, 82) smaller, distance between ocellus and eye equal to or greater than diameter of ocellus ................................................................. 7

7 Head (Fig. 82) elongate, apically acute, its midline fuscous; eyes small. (Widespread in Africa) microphthalmal (p. 202)
   - Head (Fig. 79) short, apically obtuse, its midline not fuscous; eyes larger ................................................................. 8

8 Lateral margins of pronotum (Fig. 86) bearing large, prominent granules. (Southern Africa, rare) granula (p. 198)
   - Lateral margins of pronotum (Figs 79, 84, 87, 88) with smaller granules ................................................................. 9

9 Posterolateral angles of pronotum and abdominal sternites (Fig. 92) less prominent. (Ethiopia) abyssinica (p. 197)
   - Posterolateral angles of pronotum (Figs 79, 84, 87, 88) and abdominal sternites (Fig. 91) more prominent. ................................................................. 10

10 Paramere (Figs 99, 100) with apical tooth projecting beyond apex of shaft; second valvula (Fig. 119) apically rounded. (West and Central Africa) hoploxyx (p. 194)
   - Paramere (Fig. 104) with apical tooth not projecting beyond apex of shaft; second valvula (Fig. 120) obliquely truncate, with apex acute. (Central, eastern and southern Africa) calida (p. 197)

Myla hoploxyx (Dallas)
(Figs 79, 84, 91, 96, 99, 100, 119)

Clavigralla? hoploxyx Dallas, 1852: 515. Holotype ♀, Gambia (BMNH) [examined].
Figs 79–94  Myla species. 79–82, dorsal view of head and pronotum of (79) hoploxys; (80) onceroma; (81) somalica; (82) microphthalma. 83–89, dorsal view of pronotum of (83) gracilis, lectotype; (84) hoploxys; (85) niokensis; (86) granula; (87) calida from Zaire: Mpese; (88) calida, holotype from Uganda; (89) lata, holotype. 90–94, ventral view of abdominal margin of (90) niokensis; (91) hoploxys; (92) abyssinica; (93) lata, holotype; (94) gracilis.
Myla nigrispina Stål, 1866: 111. Lectotype ♀, ‘Guinea’ (NMV), here designated [examined]. Syn. n.
Myla hoploxys (Dallas) Stål, 1873: 84.
Myla hoploxys nigrispina Stål; Linnavauri, 1971: 176.

Length: ♂, 9.8–11.7 mm; ♀, 9.7–12.0 mm.

Head (Fig. 79) slightly longer than wide, broadly rounded anteriorly. Length of antennal segment I divided by width of head including eyes in male 0.88–1.16, in female 0.89–1.09. Ratio of lengths of antennal segments in male about 1.00:0.80:1.03:0.96, in female about 1.00:0.84:1.04:0.85. Length of rostral segment I divided by width of head including eyes in both sexes 0.69–0.81, ratio of lengths of rostral segments about 1.00:0.84:0.43:0.64.

Pronotum (Figs 79, 84) with posterolateral angles produced anterolaterally and terminating in short spines, lateral margins very weakly granulate. Width across apices of posterolateral spines divided by width of head including eyes in male 2.14–2.84, in female 2.20–2.92. Length of posterior tibia divided by that of posterior femur 0.89–1.06.

Abdomen rather narrow, its lateral margin (Fig. 91) weakly convex, posterolateral angles of sternites III–VII projecting as fairly short, narrow, posteriorly directed spines; abdominal laterotergites narrow, laterotergite V usually at least twice as long as wide, rarely slightly less. Paramere (Figs 96, 99, 100) with apical tooth long, upcurved, its posterior margin projecting distinctly beyond apex of shaft. Aedeagus very similar in all respects to that of M. calida, q.v. Female with second valva of ovipositor (Fig. 119) terminating in an apically rounded lobe.

Pubescence of head, all exposed parts of thorax, abdominal laterotergites, antennal segment I, femora, claval and corium composed of short, flattened, scale-like, decumbent or adpressed, white hairs, each hair much shorter than the distance between its own insertion and that of its nearest neighbour, each insertion borne on a large granule on the head and a small granule elsewhere, granules of thoracic pleurites, posterior lobe of pronotum, scutellum and hemelytra each positioned on the anterior (or proximal on hemelytra) border of a large puncture. Pubescence of disc of abdominal venter suberect, not scale-like, grading laterally into white, scale-like type. Pubescence of antennal segments II to IV, tibiae and tarsi suberect, rather short, not scale-like.

General coloration of body and appendages greyish yellow, more or less heavily suffused red. Antennal segments II and III, tibiae and tarsi stramineous. Apex of rostral segment IV, posterolateral angles and spines of pronotum and often a line along lateral margins of pronotum piceous. Membrane of hemelytra whitish hyaline, its veins brown with frequent whitish hyaline interruptions. Elevated apex of scutellum and dorsal ridge of metathoracic peritreme white, the latter often margined piceous.

Remarks. This and the next four species form a group of closely related taxa which are probably all rather variable in pronotum shape, size and coloration. Examination of the genitalia is the only completely reliable way of distinguishing between this species and M. calida, with which it is partly sympatric. Although the genitalia of the female lectotype of M. nigrispina were not dissected out, the specimen corresponds in every other way with the West African species recognized here as M. hoploxys. No other species of this complex was detected in the area of the type-locality of M. nigrispina (‘Guinea’, = West Africa). There is no justification for Linnavauri’s (1971: 175, 176) recognition of two, largely sympatric subspecies distinguished by size, colour and some slight, probably allometric structural features. Large, red individuals with long posterolateral pronotal spines predominate in the western part of the range of the species and are rare in the eastern part. This species includes cowpea (Vigna) in its diet and, according to Professor A. E. Akingbohunbe (pers. comm.), it is approaching the pest status of the Clavigralla species on this crop.


Material examined

**Gambia**: 1 ♂ (holotype of hoploxys), (no other data) (BMNH). ‘Guinea’: 1 ♀ (lectotype of nigrispina) (coll. Signoret), (NMV).

**Gambia**: 1 ♂ (no further locality data; pin and locality label identical with those of holotype of C. hoploxys but also with label: ‘Saunders Coll.’): 1 ♀, 3.iii.1911 (Simpson) (BMNH). **Senegal**: 1 ♂, Bambe, 6.v.1943 (Risbec) (BMNH); 1 ♂, 2 ♀, M’Bambe, 28.x–6.xi.1939 (Risbec) (MRAC). **Ivory Coast**: 4 ♂, Lamto, 7.v.1963, 14.v.1963, 28.v.1963, 18.i.1963; 3 ♀, Lamto (Toumodi), 18.i.1964, 24.vii.1964; 1 ♀, Bouaké, 21.vii.1962 (probably all leg. Gillon) (BMNH); 2 ♂, Bouaké, ii.1968 (Schmitz) (MRAC).

**Ghana**: 1 ♀, Tafo, 8.xi.1965 (Leston); 1 ♂, Labadi, 12.x.1965 (Leston) (BMNH); 1 ♂, Namgua, 30.ii.1964, on cowpeas; 1 ♂, 1 ♀, Sokode, 7.xi.1967 (Leston); 1 ♀, (locality illegible), 8.xii.1965 (Leston); 1 ♀, Legon, 22.ix.1968, in u.v. trap (Kumar); 1 ♀, Abouadi, 7.xi.1967 (Leston) (UG).

**Mali**: 1 ♂, 40 miles
Myla abyssinica Linnauvori
(Figs 92, 97, 102)


Length: ♂, 9-9-10-1 mm; ♀ unknown.
Very similar to M. hoploxyx. Length of antennal segment I divided by width of head including eyes 0-88-0-93. Ratio of lengths of antennal segments about 1:00-0:80-1:05-1:04. Length of rostral segment I divided by width of head including eyes 0:69-0:75. Ratio of lengths of rostral segments about 1:00-0:84-0:45-0:64. Pronotum with posterolateral spines as short as in the shortest-spined examples of M. hoploxyx; width across apices of spines divided by width of head including eyes 2:16-2:21. Connexivum narrow, laterotergite V about 2.5 times as long as wide. Posterolateral spines of sternites III to VII short (Fig. 92). Length of posterior tibia divided by length of posterior femur 0:96. Paramere (Fig. 102) with apical tooth relatively shorter than that of M. hoploxyx.

Remarks. This species was described by Linnauvori (1971: 175) in a dichotomous key. Subsequently, the same author (Linnauvori, 1978: 21, 36, 103, figs 16f, 16g, 69d) provided a fuller description, with figures, suggesting at the same time that it might be only a race of M. hoploxyx. In his 1978 publication, he designated his unique specimen as holotype. As he already validly described the species in 1971, without designating a type-specimen, his 1978 action must be regarded as a lectotype designation. In view of the small differences separating species in this genus it seems appropriate to accord full specific status to this taxon, especially as the two specimens examined here are very similar to the one described by Linnauvori. The strong reddish suffusion noted by Linnauvori (1978) in the type-specimen is not apparent in the two specimens I have seen.

Distribution. Endemic to Ethiopia on the available evidence.

Material examined
ETHIOPIA: 1 ♂, Djoudjou Abayi, Didessa R., Goma, 2000 ft (600 m), 10.v.1905 (Zaphiro) (BMNH); 1 ♂, Gemu-Gofa Prov., 45 km N. of Demika, near Jinka road, 1460 m, 30.iv.1974 (de Rougemont) (MRAC).

Myla calida sp. n.
(Figs 87, 88, 101, 111-114, 120)

Length: ♂, 9-0-10-6 mm; ♀, 9-0-10-3 mm.
Very similar to M. hoploxyx. Length of antennal segment I divided by width of head including eyes in male and female 0-92-1-05. Ratio of lengths of antennal segments in male about 1:00-0:75:0:95-0:94, in female about 1:00-0:80-0:95-0:82. Length of rostral segment I divided by width of head including eyes in male 0-66-0-75, in female 0-69-0-79. Ratio of lengths of rostral segments in male about 1:00-0:85:0:43-0:64, in female about 1:00-0:85-0:42:0-61.

Pronotal shape variable (Figs 87, 88), posterolateral spines on average more strongly divergent than those of M. hoploxyx; width across apices of posterolateral spines divided by width of head including eyes in male 2:30-2:85, in female 2:31-2:62. Granulation of lateral margins of pronotum slightly more pronounced than in M. hoploxyx. Length of posterior tibia divided by length of posterior femur 0:89-0:95.

Connexivum and abdominal spines as in M. hoploxyx. Paramere (Fig. 101) with apical tooth shorter than that of M. hoploxyx, its posterior margin not or scarcely projecting posteriad of apex of shaft. Aedeagus
(Figs 111–114) of the form usual in the genus. Ovipositor with second valvula (Fig. 120) obliquely truncate, apex acute and slightly upturned.

Coloration on average more yellowish than greyish, never as deeply suffused red as the most extreme examples of *M. hoploxyx*.

**Remarks.** The second valvula of this species is very distinctive. The shape of the paramere is rather variable but it is never so long as that of *M. hoploxyx*, nor is its apical tooth so long or so prominent. The shape of the pronotum is also variable (compare Figs 87, 88), as is the colour. In many individuals there is a conspicuous black line along the lateral margins of the pronotum.

**Distribution.** Eastern, central and southern Africa. Absent from West Africa. Northern limit unknown.

**Material Examined**

Holotype ♀, Uganda: W. shores of Vic. Nyanza, Buddu, 3700 ft (1100 m), 19–25.IX.1911 (S. A. Neave) (BMNH).

Paratypes. Zaire: 1 ♂, 1 ♀, Ngowa, 5.VI.1939, 16.VI.1939 (Mertens); 1 ♂, Kwango, Ngowa, 3.X.1937 (Mertens); 1 ♂, 1 ♀, Ngowa–Kwango, no date and 17.II.1938 (Mertens); 1 ♂, Kibangula, 1957 (Henry); 1 ♂, 2 ♀, Mpese, 7–26.VI.1937 (Cooreman) (IRSNB); 1 ♂, Sankuru, M’Pemba Zéo (Gandajika), 17.VII.1958 (Marechal); 1 ♂, Kwango, Popokabaka, v.1952 (Pierquin); 1 ♂, Kasai, Ilebo (Théry); 1 ♂, Bokala, 20.V.1915 (Mayné); 1 ♂, Tolo, early XII.1913 (Maes); 1 ♂, Kivu, Kavimvira (Uvira), vi.1955, at light (Marlier); 1 ♂, Kinshasa (Tynant); 1 ♂, Lita, 25.V.1912 (Christy); 1 ♂, ‘Dans le belon. Post Telegraphiq au dessous de Block river, 22 Mai 1909. Herbes et arbustes à 3–4 au dessus du fleuve, endroit non boisé, 1 à 17 heures’ (Voyage de S.A.R. le Prince Albert); 1 ♀, Kisantu, 1925 (Varderijst); 2 ♀, Luluwa, Kapanga, i.1933, v.1933 (Overlaet); 1 ♀, Sankuru, M’Pemba Zéo (Gandajika), 28.IV.1960 (Maréchal); 1 ♀, Mayidi, 1942 (van Eyen); 1. without abdomen, Bas-congo, Lemfu, vi.1945 (de Beir) (MRAC); 6 ♂, 13 ♀, Faradje, 29°40’E, 3°40’N (Lang, Chapin) (AMNH). Zambia: 1 ♂, 1 ♀, High Plateau, L. Tanganyika, 4500 ft (1350 m), 18–21. VIII.1908 (Neave) (UM). Angola: 1 ♂ (other data illegible) (BMNH). Zimbabwe: 1 ♂, Salisbury, v.1963 (NMB); 1 ♂, Umtali (BMNH). South Africa: 1 ♂, Durban, 1902 (Muir) (BMNH).

**Myla dispa** sp. n. (Fig. 104)

Length: ♀, 9.6 mm; ♂, unknown.

Resembles *M. hoploxyx* in most respects, including the shape of the paramere (Fig. 104), which distinguishes it from *M. calida*. Lateral margins of pronotum rather more strongly granulate than those of *M. calida*; and posterolateral spines of pronotum short. Length of antennal segment I divided by width of head including eyes 0.53. Ratio of lengths of antennal segments as 1:00:0:82:1:06:1:18. Width of pronotum across apices of posterolateral spines divided by width of head including eyes 2:22. Length of posterior tibia divided by that of posterior femur 0:92.

**Remarks.** Perhaps this is an outlying representative of *M. hoploxyx* but it differs from that species and from *M. calida* in the relative lengths of the antennal segments, of which I and II are very short and III and IV longer with respect to I.

**Distribution.** Zambia.

**Material Examined**

Holotype ♀, Zambia: L. Bangweolo, Chirui Island, 3800 ft (1140 m), 5–7.VII.1908 (Neave) (UM).

**Myla granula** sp. n. (Figs 86, 121)

Length: ♀, unknown; ♂, 10.2–10.4 mm.

Resembles *M. hoploxyx* and *M. calida* in general form. Length of antennal segment I divided by width of head including eyes 0.85–0.93. Ratio of lengths of antennal segments in holotype as 1:00:0:84:1:00:0:95, in paratype as 1:00:0:82:0:92:0:91. Length of rostral segment I divided by width of head including eyes 0:66–0:69. Ratio of lengths of rostral segments in holotype as 1:00:0:87:0:40:0:60, in paratype as 1:00:0:94:0:44:0:67. Pronotum (Fig. 86) with posterolateral angles produced laterally almost perpendicular to axis of body, posterolateral spines very short, width across apices of spines divided by width of head including eyes 2:34–2:37; lateral margins bearing very large granules. Length of posterior tibia divided by
Figs 95–110  Myla species. 95, lata, posterior tibia. 96, hoploxyx, posterior view of male genital capsule with parameres. 97, 98, detail of pubescence of left metapleuron of (97) abyssinica; (98) gracilis. 99, hoploxyx, dorsomedial view of left paramere. 100, hoploxyx, lateral view of same. 101, 102, dorsomedial view of left paramere of (101) calida; (102) abyssinica. 103, somalica, dorsomedial view of right paramere, 104–110, dorsomedial view of left paramere of (104) dispar; (105) microphthalmia; (106) nioensis; (107) lata; (108) gracilis from Zaire: Ngowa; (109, 110) gracilis, two specimens from Zaire: Faradje.
length of posterior femur 0.95–0.99. Ovipositor with second valvula (Fig. 121) symmetrically tapering towards narrowly rounded apex.

**Remarks.** This species differs from *M. hoplopyx* and *M. calida* mainly in the shape and granulosity of pronotum. The second valvulae of the ovipositor are characteristic; males are unknown.

**Distribution.** South Africa.

**Material examined**


*Myla somalica* Linnavuori

(Figs 81, 103)


Length: ♀, 10.5–11.5 mm; ♀ unknown.

An elongate species related to *M. calida*. Ocelli very large (Fig. 81). Length of antennal segment I divided by width of head including eyes 0.85–0.99. Ratio of lengths of antennal segments about 1:00:0.82:0.97:1.08. Length of rostral segment I divided by width of head including eyes 0.70–0.71. Ratio of lengths of rostral segments about 1:00:0.87:0.42:0.66.

Pronotum (Fig. 81) with posterolateral angles shortly produced laterally, with slight anteriad inclination; width across apices of posterolateral spines divided by width of head including eyes 2.31–2.44. Posterior tibia long, its length divided by that of posterior femur 0.96–1.03.

Paramere (Fig. 103) with shaft long, as in *M. hoplopyx*, teeth of blade short, as in *M. calida*.

**Remarks.** This species is readily distinguished from all others of the genus by its enormous ocelli. The paratype was received after the above measurements were taken. It is 9.8 mm long, its first antennal segment is 0.90 times the width of the head and the antennal ratio is 1:00:0.79:1:07:1:08. The paramere is indistinguishable from that of the inland specimens with which it seems to be conspecific despite the difference in habitat.

**Distribution.** Highlands of eastern central Africa to the Somali coast.

**Material examined**


*Myla lata* sp. n.

(Figs 89, 93, 95, 107)

Length: ♂, 9.8–10.8 mm; ♀ unknown.

A very broad-bodied species. Length of antennal segment I divided by width of head including eyes in holotype 0.88. Remainder of antennae in holotype and whole of antennae in paratype missing. Length of rostral segment I divided by width of head including eyes in paratype 0.70; ratio of lengths of its rostral segments as 1:00:0.80:0.45:0.63; rostrum not visible in holotype mount.

Pronotum (Fig. 89) very broad, lateral margins strongly granulate, posterolateral angles weakly produced, terminating in small, laterally directed spines; width across apices of posterolateral spines divided by width of head including eyes 2.52–2.56.

Abdomen broad, its lateral margins (Fig. 93) strongly convex, posterolateral angles of sternites III to VII produced into broad, triangular spines. Connexivum broad, laterotergite V about five-sixths as broad as long. Paramere (Fig. 107) with both teeth of blade on a common stem.

Coloration ferruginous; all tibiae stramineous with basal, median and apical annuli piceous (Fig. 95).

**Remarks.** This species is very distinctive by reason of its great breadth. It is the only species of the genus in which the tibiae are conspicuously bicolourous.
Distribution. Central Africa.

Material Examined

Holotype $\sigma^0$, Zambia: N. Lake Bangweolo, 4200 ft [1260 m], Luwingu, 21.vii.1908 (Neave) (UM).
Paratype. Zaire: 1 $\sigma^0$, Katanga, Lufira River, 3500 ft [1050 m], 10.ix.1907 (Neave) (BMNH).

Mylia niokensis Schouteden

(Figs 85, 90, 106)

Mylia niokensis Schouteden, 1938: 294. LECTOTYPE $\sigma^0$, Zaire (MRAC), here designated [examined].
Myla (Paramyla) niokensis Schouteden; Linnavuori, 1971: 178.

Length: $\sigma^0$, 8.2-9.3 mm; $\varphi$, 8.7-9.7 mm.

Head similar in shape to that of Myla hoploxy. Antennae, especially segment I, short. Length of antennal segment I divided by width of head including eyes in male 0.56-0.74, in female 0.55-0.69. Ratio of lengths of antennal segments in male about 1:00:0:95:1:14:1:48, in female about 1:00:1:04:1:09:1:33. Length of rostral segment I divided by width of head including eyes in both sexes 0.64-0.75. Ratio of lengths of rostral segments about 1:00:0:85:0:44:0:64.

Pronotum (Fig. 85) with posterolateral angles produced forward, their apices directed laterally but very weakly produced in that direction, terminating in very short spines, margins behind the produced angles concave, diverging posteriorly so that in most cases greatest width of pronotum is not across apices of posterolateral spines but across posterior lobe; width across apices of posterolateral spines divided by width of head including eyes in male 1:88-2:16, in female 2:00-2:22. Length of posterior tibia divided by length of posterior femur in both sexes 0:94-1:06.

Abdomen with lateral margin (Fig. 90) moderately convex; posterolateral angles of sternites III to VI weakly prominent. Connexivum moderately broad, laterotergite V about 1:7 times as long as wide. Paramere (Fig. 106) very similar to that of Myla hoploxy.

Colour yellow-brown with punctures of pronotum and hemelytra and often parts of underside and posterior femora piceous or black; body and appendages often with a reddish tinge. The darkest species of the genus. Pubescence as in Myla hoploxy. Granules of lateral margins of pronotum about as prominent as those of Myla hoploxy.

Remarks. This species may easily be recognized by the form of the pronotum, except that it might be confused with Myla abyssinica from which it differs in that its antennal segment I is much shorter and segment IV is very long compared with I. Specimens from Zaire have the apical tooth of the paramere slightly shorter than it is in those from Ethiopia and Kenya. Ethiopian specimens differ from the others in having a slightly longer rostral segment IV. Antennal segment I is shortest, both in proportion to head width and in proportion to the other segments, in Kenyan specimens and longest in those from Zaire. The numbers of specimens available are too low for it to be certain that these distinctions are not artefacts of sampling.

Distribution. Records suggest that the species occurs at high altitudes in three separate areas: Ethiopia; near Nairobi in Kenya; and on the common borders of Zaire, Uganda, Tanzania and Rwanda.

Material Examined

Zaire: 1 $\sigma^0$ (lectotype), Ituri, Nioka, 7.viii.1934 (Leroy) (labelled: ‘holotypus’) (MRAC).

Ethiopia: 1 $\sigma^0$, Mt Chilálo, forest, ca 8500 ft (2550 m), 24.xi.1926 (Scott); 1 $\sigma^0$, Gojjam, Fasilo Bahr Dar, scrub, 2.viii.1965 (Kütching); 1 $\sigma^0$, Addis Ababa, Filoá, vii.1941 (Menegetti); 1 $\varphi$, Simien, Atchegas Ghiyorgis, ca 10,900 ft (3270 m), 4.xii.1952, arable land (Scott); 1 $\varphi$, Urgessa R., Jimu, 2300 ft (690 m), 3.v.1905 (Zaphiro); 1 $\varphi$, Mt Zuqála, in crater, ca 9000 ft (2700 m), 26.x.1926 (Omer Cooper) (BMNH).

Zaire: 3 $\varphi$ (paralectotypes), Ituri, Nioka, vii.1934 (Leroy); 1 $\varphi$ (paralectotype), Ituri, Nioka, vii.1934 (Leroy).

Nioka, vii.1934 (Leroy); 1 $\sigma^0$, Tshamgussa, 8-15.viii.1934 (de Witte); 1 $\varphi$, Parc Nat. Albert, Lac Gando, 2600 m, Mt Tamira, 11.iii.1935 (de Witte); 1 $\sigma^0$, Kivu, Mulungu-Tshibinda, xi.1951 (Lefèvre) (MRAC); 1 $\varphi$, Ituri Forest, 40 miles (64 km) NNE. of Beni, 3000 ft (900 m), 10-12.ix.1959, indigeneous forest with cultivated patches (Cambridge Expedition); 1 $\varphi$, Butembo-Beni road, 29°30'E, 0°25'N, 4000 ft (1200 m), 11.x.1959, agricultural district (Cambridge Expedition) (BMNH).

Uganda: 1 $\sigma^0$, Kasinga Channel, Katunguru, 1931 (Worthington) (BMNH).

Kenya: 1 $\sigma^0$, Limuru, 10.iii.1911 (Anderson); 1 $\sigma^0$, Kinangop, iii.1930 (Turner); 2 $\sigma^0$, W. Aberdares, above 9000 ft (2700 m), 3-12.ii.1911 (Neave) (BMNH).

Rwanda: 1 $\sigma^0$, Rubengeria, 1900 m, terr. Kibuye, 12.ii.1953 (Basilinsky) (MRAC).

Tanzania: 1 $\varphi$, Mt Meru, Olkokola, facing NW., 2800 m, 24.vi-1.viii.1957 (Basilinsky, Lefére) (MRAC). No data: 1 $\sigma^0$ (ex coll. Schouteden) (MRAC).
Myla microphthalmal Linnavuori
(Figs 82, 105, 115, 117)


Length: \( \sigma \), 8.3–9.7 mm; \( \varphi \), 8.6–9.9 mm.

Head (Fig. 82) more elongated and more acutely pointed anteriorly than is usual in the genus, eyes small. Length of antennal segment I divided by width of head including eyes in males from the type-locality (Ivory Coast) 0.91–0.97, in females from type-locality 0.90–0.97, in males and females from elsewhere respectively 0.76–0.93 and 0.76–0.91. Ratio of lengths of antennal segments in males and females from Ivory Coast respectively about 1.00:0.86:1.05:0.98 and 1.00:0.88:1.04:0.85; in males and females from elsewhere respectively about 1.00:0.88:1.05:1.17 and 1.00:0.90:1.05:1.03. Length of rostral segment I divided by width of head including eyes in both sexes 0.72–0.84; ratio of lengths of rostral segments about 1.00:0.85:0.44:0.67.

Pronotum (Fig. 82) with posterolateral angles rather strongly produced anterolaterally and lateral margins finely granulate with a few larger granules; width of pronotum across apices of posterolateral spines divided by width of head including eyes 2.15–2.65, not differing significantly between the sexes.

Length of posterior tibia divided by length of posterior femur 0.89–0.98.

Abdomen with posterolateral angles of sternites III to VII produced as short, acute spines. Paramere (Fig. 105) with blade broad, distal margin of apical tooth evenly curved, apical tooth rather longer than basal tooth. Spermatheca (Fig. 115) with bulb short, duct tightly convoluted. Second valvula of ovipositor (Fig. 117) apically narrow, elongate, parallel-sided.

Coloration reddish or greyish brown, dorsal midline of head always with median fuscous stripe; pronotum with anterolateral margins, posterolateral spines and anterior half of midline fuscous. Colour pattern otherwise and pubescence as in M. hoploxyss.

Remarks. The fuscous midline of the head distinguishes this species from all others in the genus. The series from the type-locality (Ivory Coast: Lamto, Toumodi) was found to differ from the rest of the material examined in several biometric ratios, as indicated above. A particularly striking difference was found in the ratio of the lengths of antennal segments I and IV. The length of segment IV divided by that of segment I in five males and two females from the Ivory Coast was, respectively, 0.91–1.00 and 0.84–0.86; in 12 males and six females from the rest of Africa this value was, respectively, 1.02–1.30 and 1.00–1.10. Although the Ivory Coast sample size is small, the measurements of this ratio fall completely outside the range determined for specimens from the rest of Africa. It may be that the Ivory Coast population has been isolated from the remainder for a considerable period. Perhaps an ancestral population of this species was isolated in mountain refugia in east Central Africa and Guinea and has re-invaded the lower-lying areas from these two centres. One male is omitted from the description above because of its even more elongate head and its aberrant measurements. It is from Zaire: Mongende; its length is 9.0 mm; the width of its pronotum, length of antennal segment I and length of rostral segment I, all divided by the width of the head, are respectively 2.82, 1.03 and 0.84. The lengths of the four antennal segments are in the ratio of 1.00:0.84:0.97:1.00.

Distribution. The species is known from the following areas: (1) Ivory Coast and (2) Southern Africa, avoiding desert and dense forest and extending northwards to 4°S in the west and 2°N in the equatorial mountains of the east.

Material examined

Ivory Coast: 6 \( \sigma \), 3 \( \varphi \), Lamto (Toumodi), 5.vi.1962, 12.vi.1962, 10.vii.1962, 4.vi.1963, 11.vi.1963, 27.viii.1963, 21.vii.1964 (Gillon); 1 \( \varphi \), Bouaké, 21.vii.1962 (Gillon) (BMNH). Kenya: 1 \( \sigma \), Kaimosi, iii–iv.1932 (Turner) (BMNH). Rwanda: 1 \( \sigma \) (paratype), Kibungu, 1500 m, 2.ii.1953 (Basilewsky) (MRAC). Urundi: 1 \( \sigma \)' (paratype – locality but not date cited in original description), Kitega, xi.1935 (Lefèvre); 1 \( \varphi \) (paratype), Kitega, vii.1935 (Lefèvre); 2 \( \varphi \) (paratypes), Usumbura, 1934 (Lefèvre) (MRAC). Zaire: 1 \( \varphi \), Uele, Wango, 29.vii.1931 (Brédo); 1 \( \sigma \), Ituri, Nioka, vii.1934 (Leroy); 1 \( \sigma \), Kivu, Mulungu, 1938 (Hendricks); 1 \( \sigma \), Mayidi, 1942 (van Eyen); 1 \( \sigma \), Kisantu, 1919 (Vanderijst) (all paratypes); 1 \( \sigma \), Tshambi, xii.1934 (de Witte); 1 \( \varphi \), Rég. Thysville (Bas-Congo), 1959–1963 (Michaux); 1 \( \sigma \), Luluua, Kapanga, i.1933 (Overlaet); 1 \( \sigma \), Katanga, Kipopo, 29.x.1961 (Maréchal) (MRAC); 2 \( \varphi \), Elisabethville (= Lubumbashi), 25.iv.1939, 15.xi.1939 (Brédo) (IRSNB). Zambie: 1 \( \sigma \), Kamankundu River, Ikelenge, N. Mwinilunga, 5.v.1972 (Pinhey, de Moor) (NMB). Angola: 1 \( \sigma \), 12 miles (19 km) SW. of Luimbaie, ca 1680 m, 20–21.iii.1972, general sweeping (BMNH Southern African Expedition) (BMNH). Malawi: 1 \( \sigma \), SE. shore Lake Nyasa, between Fort Maguire and Fort Johnston, 6–17.iii.1910
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Myla species. 111–114, calida: (111) dorsal view of phallotheca, conjunctiva and vesica; (112) lateral view of same, dorsal to left; (113) ventral view of same; (114) apical view of same. 115, 116, spermatheca of (115) microphthalmal; (116) onceroma. 117–121, left lateral view of apex of left second valvula of ovipositor of (117) microphthalmal; (118) onceroma; (119) hoploxyys; (120) calida; (121) granula.

(Neave) (BMNH). South Africa: 1♂, Transvaal, Pretoria, 26.xi.1973 (Jacobs); 1♂, Utrecht, 4.xi.1967 (Kroon); 1♀, Camperdown, 17.iv.1908 (Leigh) (TM); 1♂, Transvaal, 10 miles (16 km) NE. of Cullinan, 27.i.1962 (Capener); 1♀, no precise data (Capener) (J. A. Slater coll.); 1♂, Umbilo (Bevis); 2♀, Transvaal, Argent, 29.iii.1942 (Capener); 1♀, Pondoland, Port St John, 15–31.v.1923 (Turner); 1♂, Natal, Tugela River nr Weenen, iii.1897; 1♂, Natal, Karkloof, 10.ii.1897 (?) for 2.x.1897; 1♂, 1♀, Natal, Howick; 1♂, Natal, Estcourt; 3♂, 2♀, Estcourt, xi.1896; 4♂, Estcourt (Marshall) (BMNH). Possibly belonging to this species: Zaire: 1♂, Mongende, 17.iv.1921 (Schouteden) (falsely labelled as a paratype of Myla gracilis Schouteden but not from a locality mentioned in the original description) (MRAC).

Myla onceroma sp. n.

(Figs 80, 116, 118)

Length: ♂♂, 8-2-9-2 mm; ♀♀, 8-6 mm.

Head (Fig. 80) not elongate or acute anteriorly. Eyes small. Length of antennal segment I divided by width of head including eyes in male 0-73-0-84, in female (one only seen) 0-78. Ratio of lengths of antennal segments in male about 1-00:0-83:1-02:1-19, in female as 1-00:0-81:1-04:1-04. Length of rostral segment I divided by width of head including eyes in male 0-70-0-75, in female 0-78. Ratio of lengths of rostral segments in male about 1-00:0-82:0-43:0-65, in female as 1-00:0-77:0-42:0-63.

Pronotum (Fig. 80) with posterolateral angles shortly produced anteriorly, bearing short spines; width across apices of spines divided by width of head including eyes in male 1-99-2-20, in female 2-03. Length of posterior tibia divided by length of posterior femur 0-94-0-97.

Abdominal sternites III to VII with posterolateral angles produced into short, acute spines. Male genitalia similar to those of M. microphthalmal. Female with bulb of spermatheca (Fig. 116) longer than that of M. microphthalmal and with apical projection of second valvula (Fig. 118) very short.

General coloration dark red-brown or brown. Midline of head and pronotum concolorous, without darker median stripe.

Remarks. This small species is probably most closely related to M. microphthalmal but may be distinguished from it by the much shorter antennae, shorter head and much less strongly produced pronotal angles, which approach the form of those of M. niokensis but bear longer apical spines. It is a montane
form, perhaps descended from the ancestral population that gave rise to *M. microphthalma* but is now greatly specialized, particularly in the form of the second valvulae of the ovipositor, after long isolation.

**Distribution.** Known only from three localities at high altitudes in Cameroun and south-eastern Nigeria.

**Material Examined**

Holotype ♂, **Cameroun**: Bamenda, 17.xii.1955 (*Bechyne, Exped. Mus. G. Frey*) (BMNH).
Paratypes. **Cameroun**: 4 ♂, as holotype but dates 7.xii.1955, 8.xii.1955, 13.xii.1955 and 17.xii.1955 (BMNH); 2 ♂, 1 ♀, Mt Bamboutos (MRAC).
Non-paratypic material (received after description was drawn up). **Nigeria**: 3 ♂, 4 ♀, SE. State, Obudu C.R., 21 and 23.iii.1971 (*Medler*) (University of Ibadan).

**Myla gracilis** Schouteden

(Figs 83, 94, 98, 108–110)

*Myla gracilis* Schouteden, 1938: 293. **LECTOTYPE** ♂, **ZAIRE** (MRAC), here designated [examined].


Length: ♂, 8-4–9-8 mm; ♀, 9-00–10-0 mm.


Pronotum (Fig. 83) with posterolateral angles strongly produced anterolaterally, terminating in slender spines, posterolateral margins with one to three prominent, piceous or black tubercles; width across apices of posterolateral spines divided by width of head including eyes in male 2-57–3-18, in female 2-74–3-09.

Abdomen with posterolateral angles of sternites III to VII produced as fine spines (Fig. 94). Connexivum rather narrow; laterotergite V twice as long as wide. Paramere (Figs 108–110) slender, with apical tooth long and both teeth on a common stem that arises terminally or subterminally from the blade. Female with second valvula tapering to narrowly rounded apex.

Pubescence of head, pronotum, scutellum, thoracic pleura, abdominal venter laterally and basally, laterotergites, clavus, corium, antennal segment I, coxae, trochanters, femora and rostrum comprising fairly short, flattened, scale-like, decumbent (except on appendages), white hairs; hairs on thoracic pleura (Fig. 98) and declivitous area of pronotum very distinctly longer than distance between adjacent hair insertions and tending to form three or four transverse bands on deolivent area of pronotum. Areas of abdominal venter and appendages that are devoid of scale-like pubescence with short, suberect, colourless hairs.

Coloration generally as in *M. hoploxys* but never heavily tinged red. Scutellum with midline and small, apical knob usually creamy white. Large tubercles of anterolateral margins of pronotum and apices of posterolateral spines piceous to black. Veins of hemelytral membrane brown, uninterrupted.

**Remarks.** This species differs from all others of the genus in the greater length of the scale-like pubescence. The posterolateral pronotal angles are more strongly produced in this species than in any of its congeners. The combination of these two features gives *M. gracilis* a superficial resemblance to *Clavigralla schnelli* (Villiers). Indeed, the type-series of *M. gracilis* contains three individuals of *C. schnelli*, one of which bears a label with the legend, 'holotypus'. This type designation has never been published and Schouteden's very detailed description of the antennifers, rostrum, antennae, femoral spines and male genital capsule leaves no doubt that he was describing a species of *Myla*. I have, therefore, ignored the unpublished 'holotype' designation and here select one of the 'paratypes' as lectotype. Linnavuori (1971: 175; 1978: 35–36) used the name *M. gracilis* for what is evidently *C. schnelli* and established the unnecessary new nominal species *Myla graciloides* for *M. gracilis* proper. In his 1971 paper, Linnavuori cites the localities Sudan, Congo and Ivory Coast but in 1978 he cites only the 'type' from Sudan; this citation is effectively a lectotype designation. There is some variation in the pronotal posterolateral spines which are usually laterally directed but sometimes anterolaterally directed.

**Distribution.** West and Central Africa.
Distribution of Pseudophloeinae

Preamble

Without a complete phylogenetic analysis of the subfamily, incorporating the Palaeartic genera, a comprehensive account of its zoogeography is not possible. In undertaking the present revision I have considered every species of the subfamily, including the Palaeartic ones, in relation to the diagnostic features of every genus, and I am reasonably certain that all of the genera currently recognized are monophyletic in origin and holophyletic in composition. However, I have not fully investigated the relationships among all the genera of the subfamily.

Two presumably holophyletic groups of genera are recognized: the tribe Clavigrallini (see Dolling, 1978; 1979a) and a large group of genera including all of those confined to the North Temperate Zone and all of the tropical genera except for Vilga, Risbecocoris, Paramyla, Hoplolomia and Indolomia. The first two of these genera are probably not descended from the most recent common ancestor of the two big groups while the last three may be related to the non-clavigralline group in some way (see Table 1). The distribution of the various genera of Pseudophloeinae in the major zoogeographical regions is summarized in Table 2. The Afro-tropical region in this table excludes the Mascarene area (Madagascar, Mauritius, Réunion and Rodriguez), which is shown separately. The Oriental region is taken to include New Guinea and the Solomon Islands but Australia is excluded and its pseudophloeine fauna is tabulated in a separate column.

Table 1 Distribution of two characters in the subfamily Pseudophloeinae.

<table>
<thead>
<tr>
<th>Character</th>
<th>Antevannal vein absent</th>
<th>Antevannal vein present</th>
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</thead>
<tbody>
<tr>
<td>Posterior femur without basal tubercle</td>
<td>Vilga, Risbecocoris</td>
<td>Clavigrallini</td>
</tr>
<tr>
<td>Posterior femur with basal tubercle</td>
<td>Hoplolomia, Indolomia, Paramyla</td>
<td>Remaining genera</td>
</tr>
</tbody>
</table>

Neotropical

The only genus of Pseudophloeinae represented in the Neotropical region is Vilga, which is endemic to the New World. The 14 species were divided among six subgenera by Dolling (1977),
who commented that the differences among these subgenera were of the same degree as those separating some Palaearctic genera. One subgenus, whose single species is facultatively brachypterus, occurs from the extreme southern U.S.A. to El Salvador; all the other subgenera are confined to the Neotropical region and are widely sympatric there, with the exception of one subgenus whose three species are confined to the temperate and largely mountainous regions of Argentina, Chile and Peru. This latter subgenus, through a general reduction of spininess of the body and legs and a flattening and broadening of the body, superficially resembles the tropical montane and temperate South African genus *Paramyla* and the Palaearctic *Arenocoris* and *Bathysolen* Fieber.

Nearctic

The presence of a single species of the otherwise Neotropical genus *Vilga* in Mexico and adjacent areas has been mentioned above. In addition, two genera of Pseudophloeini are shared between the Palaearctic and Nearctic regions.

*Coriomeris* Westwood has 16 species in the Palaearctic and another four in the Nearctic. The Nearctic species (see Dolling & Yonke, 1976) are mutually very similar and have strictly parapatric distributions, suggesting recent entry into and radiation within the region. Species of *Coriomeris* are found within the Arctic Circle in Alaska, Yakutia and Karelia, so there would seem to be no climatic barrier to migration across the Bering Straits even today.

*Ceraleptus* Costa has five Palaearctic and four Nearctic species, none of them shared between the two regions. Its nearest relatives appear to be *Microtelocerus* Reuter and *Urartucoris* Puchkov, both genera with very restricted distributions in the mountains of the central southern Palaearctic, so a Palaearctic origin for *Ceraleptus* seems probable. Its American species are rather diverse and fall geographically into two pairs, one pair sympatric along the Pacific coast of North America and the other pair sympatric in the south-eastern U.S.A. (Froeschner, 1963). Members of the genus do not occur at such high latitudes as the extremes penetrated by *Coriomeris* and this fact, coupled with the greater diversity and more complex distribution pattern shown by the species of *Ceraleptus*, suggests that the genus has been present in the Nearctic region longer than has *Coriomeris*, presumably arriving in one or more immigration episodes during an era of warmer climate than that of the present day.

Palaearctic

Twelve genera and about 39 species of Pseudophloeini occur in the Palaearctic region; only one of these species is shared with another region: *Arenocoris intermedius*, whose range includes western temperate Asia, Iberia and the northern coastal countries of Africa and extends southwards into Chad and Ethiopia. As indicated above, the Palaearctic genera *Coriomeris* and *Ceraleptus* have both entered North America and have endemic species there.

The Palaearctic intrusions of two species of the tribe Clavigrallini, *Clavigralla scutellaris* (into Afghanistan) and *Gralliclava horrens* (into Japan) are mentioned below; no other genus of the subfamily is represented in both the Palaearctic and Afrotropical or the Palaearctic and Oriental regions.

Afrotropical and Oriental Clavigrallini

The well-defined tribe Clavigrallini comprises four genera whose interrelationships are unclear. With the exception of two minor intrusions into the Palaearctic region, mentioned below, the tribe is confined to the tropical regions of the Old World.

*Clavigralla* Spinola is the largest genus of Pseudophloeininae, with 46 described species. It has clearly undergone most of its radiation on the African mainland, where 38 of its species are found. Only one species, *C. elongata* Signoret, which is widespread on the African mainland, is present on the smaller offshore Afrotropical islands. It has reached São Tomé and the Cape Verde Islands in the Atlantic (Dolling, 1979a: 28 erroneously reported it from the Canary Islands on the basis of a mislabelled specimen from the Wollaston collection; the card bears a
Table 2  Number of species of each genus of Pseudophloeinae in the regions indicated. Species occurring in more than one region are scored in parentheses in regions other than those of their putative origin as are genera with no endemic species.

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<th></th>
<th>Neotropical</th>
<th>Nearctic</th>
<th>Palaeartic</th>
<th>Afrotropical</th>
<th>Macarene</th>
<th>Oriental</th>
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<td>32+(1)</td>
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</table>

1  _Anoploceris_, Bathysolen, Bothrostethus, Loxocenemis, Microtelocerus, Nemocoris, Stroblotoma, Ulmicola, Urartucoris.

colour-coded mark that indicates its true provenance as the Cape Verde Islands), and Madagascar, Mauritius, Réunion, Rodriguez and the Seychelles in the Indian Ocean. It has also been reported from Arabia. In 1979 I had seen no specimens of the species from the mainland of West Africa, where it seems to be largely replaced by _C. shadabi_ Dolling and _C. breviceps_ Dolling. I have now seen specimens of it from two localities in Senegal. _C. elongata_ is the only representative of the subfamily in these Atlantic and Indian Ocean islands with the exception of six endemic species in Madagascar. One of these, _C. tuberculicollis_ (Reuter), is a taxonomically isolated species with several plesiomorphic features; it has probably been present in Madagascar much longer than any other species of the tribe. Three Malagasy species are closely similar to _C. elongata_ and may be either local derivatives of it or descendants of a single, _elongata_-like immigrant. The other two endemics are members of the _C. tomentosicollis_ Stål group but belong to different subgroups and clearly derive from two separate immigrations. Thus, Madagascar seems to have been colonized on at least four and possibly five separate occasions by Clavigrallini, but there is evidence for local radiation stemming from only one of these invasions. _Clavigralla_ is evidently a recent arrival in the Oriental region. Its three Oriental species all belong to the same subgroup of the _tomentosicollis_-group. One of them, _C. scutellaris_ (Westwood), which is probably the sister-species of _C. tomentosicollis_, is also found in north-eastern Africa and Arabia; in Asia it extends as far northwards as Afghanistan. The other two are vicariant sister-species, one confined to Sri Lanka and southern India and the other distributed from northern India to southern China and Vietnam; the Indian population of this second species is recognizably distinct from the populations further east.
Oncaspidia Stål has a single, widespread species endemic to Africa.

Clavigralloides Dolling has the most easterly centre of distribution of any genus of Pseudophloeinæ. Three of its five species occur in New Guinea; one of these three is, as far as is known, endemic while the other two extend southwards into northern Australia and one of these also spreads northwards to southern China. Closely related to these two is a species restricted to the Lesser Sunda Islands. The fifth member of the genus is rather isolated taxonomically and is divided into northern Indian and a southern Chinese subspecies.

Gralliclava Dolling species are distributed from India to Australia. They fall into two groups, one with a plesiomorphic condition of the male genital capsule and a variety of unusual paramere shapes, and the other with an apomorphic condition of the capsule and rather uniform parameres. The first group comprises six known species with restricted distributions; three of these are Indian; one is found in the Himalayas and at high altitudes in southern China and Laos, one is known only from its high altitude type-locality in Java, and one, surprisingly, is known from a single specimen taken on a small Australian island in the Torres Strait. The four species of the second group between them occupy an almost continuous range from Sri Lanka and India to Japan, the Solomon Islands and tropical Australia. One is known from two specimens, one from Timor and the other from Flores. The most widespread species, G. horrens Dohrn, is also known from Timor, from Wetter and the Sulawesi group, and thence northwards to Japan (Japanese records, all from Kyushu, are summarized by Kawazawa, 1978) and westwards to India and Sri Lanka. A third species is common in New Guinea and is also recorded from Ambon and the Admiralty, Bismarck and Solomon groups. The fourth species has been collected from many localities in Queensland and the Northern Territory of Australia but it has never been found elsewhere, nor has any other species of the genus been taken in Australia. The almost complete allopatry of these four species and the fact that the Torres Strait separates two of them suggests a very recent radiation of this group.

Afrotropical and Oriental Pseudophloeinæ

Apart from the intrusive Arenocoris intermedius, the present revision recognizes seven genera with 25 species in the Afrotropical region and six genera with 17 species in the Oriental. Two of these genera and none of the species are shared between the two regions. The largest genera are the wholly Afrotropical Myla, with 11 species, and the shared Psilolomia, with 13.

Risbecocoris, with five described species, occupies a probably almost continuous belt of grassland and semi-desert from Senegal via Arabia to Delhi, taking in the Air mountains and northern Kenya as well. This type of habitat has probably been available in the area for a very long time and dispersal across it between Africa and Asia would present no problems for an organism as well adapted to it as is Risbecocoris. It makes little sense to attribute part of this arid zone to the Afrotropical region and part to the Oriental in the context of the biogeography of such organisms.

Psilolomia displays its greatest diversity in the Oriental region. A group of dark-coloured species, whose characteristic habitat is probably forest clearings, extends no further westwards than eastern India while a group of yellowish species, probably characteristic of dry, open woodland, is distributed from West Africa to South East Asia. Only four species of this group occur in Africa; they have had little or no success south of the Equator. One of them, Psilolomia nigeriensis, shows a tendency to split into northern and southern races in Nigeria, perhaps in response to differing climatic conditions. A single migration in the fairly recent past from India into Africa via a more humid Arabia seems the most probable explanation for its occurrence in both continents. Large areas of apparently suitable terrain remain unoccupied by this genus in eastern and southern Africa.

Mevanidea is the only genus of Pseudophloeinæ, apart from Clavigralla, to have been found in Madagascar. The two species of the genus show classic allopatry, one in mainland Africa and the other endemic to Madagascar.
Discussion

The faunistic picture that emerges is one of greatest diversity in the tropics of the Old World with rather less diverse but long established faunas in the Palaeartic and Neotropical regions. The Neotropical and Palaeartic faunas seem to have developed in almost complete isolation from each other and from the Palaeotropical faunas. The Nearctic region, Australia and Madagascar have no endemic genera and have played only a peripheral part in the evolutionary history of the subfamily. Apart from Risbecocoris, whose range is in a transitional zone, only one genus, Psilolomia, is shared between the Oriental and Afrotropical regions. It is the only genus that can be shown to have successfully invaded and begun to diversify in a region where a diverse pseudophloeine fauna was already present.

The genus Vilga has evidently been present in the Neotropics for a very long time, perhaps since before the opening of the Atlantic Ocean; this would place the early radiation of the subfamily before the end of the Cretaceous period. Among tropical Coreoidea it is frequently the case that the distribution of the subfamilies is pantropical while the tribes are restricted to either the Old World or the New.

Dense forest and water seem to have been very effective barriers to dispersal of Pseudophloeini but less effective in the case of Clavigrallini. The more elongate condition of the hemelytra of the latter, with a tendency for the corium to extend apically along the costal margin of the hemelytron, and the deeper thorax, presumably housing larger flight-muscles, are suggestive of a more sustained power of flight which would enable its possessor to overcome the obstacles that inhibit the dispersal of Pseudophloeini. The distribution patterns of two groups of recently differentiated species illustrate this difference in dispersal ability, and hence in rates of genetic interchange. The genus Coriomeris in North America has split into four recognizable distinct closely related species without any intervening barriers of forest or water, whereas the species of the horrens-group of the clavigralline genus Graliclava are, with one very minor exception, separated by sea barriers. Parapatric speciation may also be in progress in the case of the northern and southern forms of Psilolomia nigeriensis.

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I am sincerely grateful to Dr Roberto Poggi, Museo Civico di Storia Naturale, Genoa, for sending me a drawing of the holotype of Pseudophloeus gestroi; to Prof. Dott. Carlo Vidano, Turin, for searching Spinola’s collection for the type-material of Merocoris spinicollis; to Dr H. Brailovsky, UNAM, Mexico, for donating the unique type-specimen of Indolomia concalata; and to the following colleagues for their kindness in arranging loans of material in the depositories mentioned: Dr A. E. Akingbohungbe, Ife University, Ile-Ife, Nigeria; Dr P. H. Arnaud, CAS, San Francisco; Mr J. C. Deeming, formerly IAR, Samaru; Dr U. Göllner-Scheiding, MNHU, Berlin; Mrs C. N. Higa and the late Dr J. L. Gressitt, BPBM, Honolulu; Dr A. Kaltenbach, NMV, Vienna; Prof. R. Kumar, UG, Legon; Drs I. Lansbury and M. W. R. de V. Graham, UM, Oxford; Dr R. Linnavuori, Raisio, Finland (private collection to be deposited in ZMU, Helsinki); Dr J. G. H. Londt, NMP, Pietermaritzburg; Dr J. T. Medler, University of Ibadan, Nigeria; Drs M. Meinander and A. Jansson, ZMU, Helsinki; Dr J. Nast, IZPAN, Warsaw; Dr T. Nyholm, NR, Stockholm; Dr G. Peterson, IP, Eberswalde; Dr E. C. G. Pinhey, NMB, Bulawayo; Mr P. Reavell, Empangeni, Zululand (private collection, type-material to be deposited in NMP, Pietermaritzburg); Dr G. Schmitz, MRAC, Tervuren and IRSNB, Brussels; Drs M. U. Shadab and P. Wygodzinsky, AMNH, New York; Prof. J. A. Slater, University of Connecticut, U.S.A. (private collection); Dr M. Taou and the late Dr A. Villiers, MNHN, Paris; Mr J. A. van Reenen, TM, Pretoria.

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By D. R. Ragge
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The songs of the western European grasshoppers of the genus *Omocestus* in relation to their taxonomy (Orthoptera: Acrididae)

D. R. Ragge
Department of Entomology, British Museum (Natural History), Cromwell Road, London SW7 5BD

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Synopsis

The male calling songs of 11 western European and one Canary Island species of the Gomphocerine genus *Omocestus* are described and fully illustrated with oscillograms at three or four different speeds. The courtship song is also described for the six species in which such a song is known. The songs of six species (*panteli, bolivari, uhagonii, minutissimus, llorenteae* and *simonyi*) are described for the first time. For each species a full list is provided of references to any past published work on the songs, classified according to the kind of information given. Notes on recognition, using both morphology and song, are given for each species, and two identification keys are provided, one based mainly on morphology and the other on song. The value of the song as a taxonomic character is discussed.

Introduction

The Gomphocerinae, of which *Omocestus* is one of the better known Old World genera, include most of the common European grasshoppers of open grassland and moorland. They produce the most highly developed communicative sounds of all grasshoppers and are widely used in bio-acoustic, ecological and cytogenetic research. The subfamily includes about 150 European species, of which over 20 are pests in parts of their range, seven of them being regarded as major ones (Tsyplenkov, 1970).

*Omocestus* is a widespread Palaearctic genus, including some 40 species living in habitats ranging from lush lowland meadow to steppe, open woodland and high mountains. Twenty species have been recorded from western Europe, of which three, *rufipes, petraeus* and particularly *haemorrhoidalis*, become pests when they occur in sufficient numbers, causing damage to cereal grasses, hayfields, alfalfa and other cultivated plants in western and, especially, eastern Europe (Bei-Bienko & Mishchenko, 1951; Tsyplenkov, 1970).

The conspicuous songs of Gomphocerine grasshoppers have attracted attention for centuries,


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but it is only since the pioneering work of Faber (1928) that they have been considered seriously as an aid to identification, and only during the past 30 years that their importance in taxonomic research, and particularly in resolving complexes of sibling species, has been fully recognized. This importance stems from the current belief that they provide the main mate recognition system in these insects and are thus able to maintain reproductive isolation in groups of sympatric species that would otherwise be able to interbreed freely. Perdeck (1957) established experimentally that this is true of the well-known sibling pair Chorthippus brunneus (Thunberg) and C. biguttulus (Linnaeus), and, although comparable studies on other groups of Gomphocerinae are still greatly needed, it seems likely that such studies would confirm that this function of the song is widespread in the subfamily.

Grasshopper songs can be quite easily recorded on tape and their rhythmic patterns, which provide the most useful taxonomic information, lend themselves well to oscillographic analysis. It is thus rather surprising that there has so far been no comprehensive account of these songs, presented group by group and illustrated with oscillograms. The main aim of the present paper, and of similar papers in preparation on other groups of Orthoptera, is to provide such an account, arranged systematically by group and fully illustrated with oscillograms at several different speeds. It is hoped that this form of presentation will make the information most useful in identification and taxonomy, as well as providing a basic reference work on the songs of these insects.

No information has previously been published on the songs of six of the 12 species included in this study (panteli, bolivari, uhagonii, minutissimus, llorenteae and simonyi) and no oscillograms have previously been published for a further two (petraeus and raymondi). For the species in which published information on the song is already available, references to the sources are given, classified according to the kind of information published. O. simonyi, known only from the Canary Islands, is not strictly within the scope of this paper but is included for convenience.

The song is still unknown in the following nine species of Omocestus recorded from western Europe: antigai, burri, corsicus, femoralis, kaestneri, knipperi, lopadusae, navasi and uvarovi. These species, which are all very local and often of doubtful status, are therefore excluded from this study.

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I am particularly grateful to my colleague Mr W. J. Reynolds, who made the studio recordings used in this study, helped me in reviewing the past literature on the songs, tested the identification key based on morphological characters and provided valuable comments at various stages in the preparation of the paper.

Finally I wish to thank my wife, who has given me invaluable help in all my field-work.

Abbreviations of depositories

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SONGS OF THE WESTERN EUROPEAN *OMOCESTUS*

Methods

Recording and analysing the songs

All the field recordings of the songs used in this study were made while the insects were in full sunshine using a Uher 4000, 4200 or 4200IC tape recorder and AKG D202 or (recording 222/3 only) Shibaden microphone; the tape speed was always 19 cm/s. The subjects were approached stealthily so that the microphone could be held (or rested on the ground) about 10 cm from them without causing any disturbance.

The studio recordings were made in the BMNH Acoustic Laboratory using a Kudelski Nagra IV tape recorder and Sennheiser MKH405 microphone; the tape speed was 19 or 38 cm/s. In every case a bench lamp was used to provide light and radiant heat.

Further data are given in Tables 1 and 2 for the recordings used for the oscillograms reproduced in Figs 12–128. However, the song descriptions given for each species are in most cases based on many more recordings of numerous songs, all of which were analysed oscillographically. The oscillograms reproduced in the figures were chosen as being typical of the species concerned and, in some cases, showing the extent of intraspecific variation. Although I have given in Tables 1 and 2 the ambient air temperature at the time of recording, it is really the body temperature of the singing insect that is important, and this is more dependent on radiant heat than on the air temperature; as the insects were always receiving radiant heat from the sun or a bench lamp, the conditions under which the recordings were made were more uniform than the different air temperatures might suggest.

All the oscillograms were made from recorded songs with a Mingograf 34T ink-jet recorder.

Song terminology

The bio-acoustic terms used are defined as follows.

*Calling song.* The song produced by an isolated male.

*Courtship song.* The special song produced by a male when close to a female.

*Syllable.* The sound produced by one complete up and down movement of the hind legs (Fig. 1).

*Echeme.* A first-order assemblage of syllables (Fig. 1).

*Echeme-sequence.* A first-order assemblage of echemes (Fig. 1).

Momentary breaks in the sound (of at least 1·25 ms) during the course of a syllable are referred to as ‘gaps’.

Presentation

As the main purpose of this paper is to give information on songs, I have not included either a full synonymy or a formal morphological diagnosis in the account of each species. I have, however, listed references to all past descriptive accounts of the songs (of any significance), classified according to whether they include oscillograms (including sound-level tracings), diagrams (i.e. hand-drawn representations of the songs), frequency information, musical notation, or verbal description without any of these additions; any commercially available disc or cassette recordings of the songs are also listed. These references are not intended to be exhaustive – there are many brief statements about the songs, especially in the earlier literature, that do not warrant inclusion; my aim has been to list all sources that the reader might find useful to refer to for additional or confirmatory information on the songs. The only reference I have included to a work published before the present century is to Yersin’s (1854) short but admirable account of the songs of 38 European species of Orthoptera (including two of *Omocestus*), in which he attempted, with some success, to represent them in terms of musical notation; in this largely forgotten work he demonstrated clearly for the first time the striking differences between the songs of the three closely similar species *Chorthippus brunneus* (Thunberg), *C. biguttulus* (Linnaeus) and *C. mollis* (Charpentier).

Notes are given for each species on recognition by both morphology and song, and these are
Table 1  Data for the field recordings of male songs of *Omocestus* used for oscillograms reproduced in this study. All these recordings were made from different males. Recordists’ names are abbreviated as follows: NDJ = N. D. Jago; DRR = D. R. Ragge; WJR = W. J. Reynolds.

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<td>531/3</td>
</tr>
<tr>
<td></td>
<td>SPAIN: Granada, Sierra Nevada, near Capileira, 1500 m</td>
<td>22.vi.1984</td>
<td>DRR</td>
<td>24°C</td>
<td>532/4</td>
</tr>
<tr>
<td><em>raymondi</em></td>
<td>SPAIN: Madrid, near Navacerrada, Valle de Barranca</td>
<td>27.vii.1983</td>
<td>DRR</td>
<td>22°C</td>
<td>503/5</td>
</tr>
<tr>
<td></td>
<td>SPAIN: Granada, Sierra Nevada, Puerto de la Ragua, 2000 m</td>
<td>1.viii.1983</td>
<td>DRR</td>
<td>25°C</td>
<td>506/3</td>
</tr>
<tr>
<td><em>broelemanni</em></td>
<td>FRANCE: Pyrénées-Orientales, near Saillagouse, Val d’Eyne</td>
<td>15.ix.1978</td>
<td>WJR</td>
<td>23°C</td>
<td>276/3</td>
</tr>
<tr>
<td><em>bolivari</em></td>
<td>SPAIN: Granada, Sierra Nevada, Campos de Otero, 2300 m</td>
<td>31.vii.1983</td>
<td>DRR</td>
<td>21°C</td>
<td>505/4</td>
</tr>
<tr>
<td></td>
<td>SPAIN: Granada, Sierra Nevada, Puerto de la Ragua, 2000 m</td>
<td>1.viii.1983</td>
<td>DRR</td>
<td>25°C</td>
<td>506/5</td>
</tr>
<tr>
<td></td>
<td>Same locality</td>
<td>1.viii.1983</td>
<td>DRR</td>
<td>25°C</td>
<td>507/2</td>
</tr>
<tr>
<td>Species</td>
<td>Locality</td>
<td>Date recorded and collected</td>
<td>Recordist</td>
<td>Shade air temperature</td>
<td>Recording No.</td>
</tr>
<tr>
<td>------------------</td>
<td>---------------------------------------------------------------------------</td>
<td>----------------------------</td>
<td>-----------</td>
<td>-----------------------</td>
<td>---------------</td>
</tr>
<tr>
<td><em>uhagonii</em></td>
<td>SPAIN: Madrid, Sierra de Guadarrama, La Bola del Mundo, 2200 m</td>
<td>6.viii.1983</td>
<td>DRR</td>
<td>21°C</td>
<td>508/6</td>
</tr>
<tr>
<td></td>
<td>Same locality</td>
<td>6.viii.1983</td>
<td>DRR</td>
<td>21°C</td>
<td>509/1</td>
</tr>
<tr>
<td></td>
<td>Same locality</td>
<td>6.viii.1983</td>
<td>DRR</td>
<td>24°C</td>
<td>509/5</td>
</tr>
<tr>
<td><em>minutissimus</em></td>
<td>SPAIN: Madrid, Sierra de Guadarrama, Puerto de los Leones, 1500 m</td>
<td>5.viii.1983</td>
<td>DRR</td>
<td>23°C</td>
<td>508/3</td>
</tr>
<tr>
<td><em>llorenteae</em></td>
<td>SPAIN: Granada, Sierra Nevada, near Dornajo, 1900 m</td>
<td>30.vii.1983</td>
<td>DRR</td>
<td>27°C</td>
<td>504/6</td>
</tr>
<tr>
<td></td>
<td>Same locality</td>
<td>30.vii.1983</td>
<td>DRR</td>
<td>27°C</td>
<td>505/1</td>
</tr>
</tbody>
</table>

Table 1 – cont.

Table 2  Data for the studio recordings of male songs of *Omocestus* used for oscillograms reproduced in this study. All these recordings were made from different males except for 310 and 312, which were made on different days from the same male of *panteli*. The recordist was W. J. Reynolds in every case.

<table>
<thead>
<tr>
<th>Species</th>
<th>Locality</th>
<th>Date collected</th>
<th>Date recorded</th>
<th>Air temperature</th>
<th>Recording No.</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>panteli</em></td>
<td>SPAIN: Valencia, near Requena, 700 m</td>
<td>27.vii.1979</td>
<td>30.vii.1979</td>
<td>33°C</td>
<td>310</td>
</tr>
<tr>
<td></td>
<td>Same locality</td>
<td>27.vii.1979</td>
<td>31.vii.1979</td>
<td>30°C</td>
<td>312</td>
</tr>
<tr>
<td></td>
<td>Same locality</td>
<td>27.vii.1979</td>
<td>1.viii.1979</td>
<td>29°C</td>
<td>315</td>
</tr>
</tbody>
</table>
Omocesfus raymondi

Omocestus petraeus

Fig. 1 Oscillograms of the male calling songs of two species of *Omocestus*, showing the terminology used in this paper.
followed by a more detailed descriptive account of the calling song and, when known, courtship song. I have not attempted to describe any further kinds of sound produced by the males (e.g. 'rivalry song', 'copulation song') as these are not stereotypically patterned and seldom of diagnostic value. Neither have I considered it appropriate to describe the songs produced by females when in a sexually receptive state; these songs are seldom heard in the field and are in any case broadly similar in pattern to the calling songs of conspecific males.

The songs of each species are illustrated by oscillograms at three, or sometimes four, different speeds. As the scale lines indicate, the three speeds given for all species are (after reduction for printing) 10 mm/s, 80 mm/s and 320 mm/s, and the fourth speed included for the songs of three species (see below) is 1280 mm/s. In addition, oscillograms at 10 mm/s of typical male calling songs of all 12 species are shown together in Figs 12–23 so that the more obvious differences between them can be seen at a glance.

Grasshopper songs are normally produced by both hind legs being rubbed simultaneously against the fore wings, and oscillograms of such 'two-legged' songs show the sounds produced by the movement of one hind leg superimposed on those produced by the other. The two hind legs are not always well synchronized and in some species follow different patterns of movement, so that there is sometimes a degree of 'blurring' of the oscillogram. Moreover, in 'two-legged' oscillograms that are fast enough to show the impacts of individual stridulatory pegs, it is impossible to determine which peg-impacts are produced by one leg since these are mixed with those produced by the other. Although these points are not particularly relevant to the diagnostic value of the songs, I have thought it worth including for three species (viridulus, rufipes and panteli) oscillograms taken from the calling songs of males with only one hind leg. The difference between the 'one-legged' and 'two-legged' oscillograms is hardly apparent at the slower speeds, but becomes more obvious at 320 mm/s and clearer still at 1280 mm/s. The highest speed 'one-legged' oscillogram of panteli (Fig. 89) shows the individual peg-impacts with particular clarity.

The song as a taxonomic character

Recognition of the diagnostic value of the songs of Orthoptera may be said to have begun in the mid-nineteenth century, when Fischer (1849, 1850, 1853) published a number of song descriptions in primarily faunal or systematic works, and Yersin (1852, 1853 and especially 1854) produced a series of papers specifically on the songs and their value in identification. Yersin's work of 1854, in which he described the songs of 38 European species of Orthoptera, was particularly noteworthy in that it included the first attempt to illustrate the songs graphically, in the form of musical notation.

Little further progress was made in exploiting the songs in taxonomy until Faber's work of 1928, in which he gave, for the first time, an identification key to the German Orthoptera based on their songs. Many German studies on the songs of the European Orthoptera followed, notably by Faber (especially 1929, 1932 and 1936) and Jacobs (especially 1950), culminating in two major works published almost simultaneously (Faber, 1953; Jacobs, 1953). Most of this work was concerned with the detailed description of the songs and associated behaviour, and there was still no serious attempt to use the songs in taxonomic research.

Jacobs (1950, 1953) used simple diagrams against a time scale to illustrate the rhythmic patterns of the songs. Ragge (1965) introduced a more sophisticated kind of diagram, amounting to a simplified oscillogram, and diagrams of this kind have since been used by Holst (1970), Luquet (1978), Wallin (1979) and, in a slightly different form, by Duijm & Kruseman (1983) and Bellmann (1985). Identification keys based on the songs were provided, for restricted parts of Europe, by Luquet (the Mont Ventoux area of the French Alps, Acrididae only), Wallin (Sweden), Duijm & Kruseman (Benelux) and Bellmann (West Germany). All these studies are concerned with regional faunas and contain no taxonomic research, although Luquet gives much emphasis to the importance of the songs in taxonomy.

The first serious application of the songs of Orthoptera to their taxonomy was in work on the North American crickets (Gryllidae). Following the pioneering work of Fulton (1931, 1952),
Alexander (1957) and Alexander & Thomas (1959) reviewed the taxonomy of North American species of Acheta and Nemobius, and Walker (1962, 1963) carried out similar studies on Oecanthinae; in all these studies the songs played a crucial part in resolving the taxonomy of morphologically similar species. Similar work on other groups followed, some of it reviewed by Alexander (1962) and Walker (1964). In 1972 Alexander, Pace & Otte produced an account of the ‘singing insects’ of Michigan in which they gave keys based mainly on the songs for all the Ensilera.


As can be seen at a glance from Figs 12–23, the male calling songs of the western European species of Omocestus provide most useful taxonomic characters. Recorded songs, with appropriate oscillographic analyses, can be used to identify the species even if no specimens are available for morphological study (see the key on p. 224).

The calling songs of the 12 species embraced by the present study fall into two clearly different kinds: the rapid sequence of echemes produced by petraeus, minutissimus and llorenteae, and the single or widely separated echemes produced by the remaining species. As would be expected, the rapidly repeated echemes of petraeus, minutissimus and llorenteae are composed of very rapidly repeated syllables, almost always more than 80/s, whereas the syllable repetition rate of the remaining species is almost always less than 40/s. Within this trio of species petraeus stands a little apart from the other two in having even shorter and more rapidly repeated echemes, but the songs of minutissimus and llorenteae are broadly similar to each other in pattern, differing mainly in the duration of the echeme-sequence and the number of echemes of which it is composed.

Among the remaining species, viridulus and rufipes have much longer echemes than all the others; they are very similar to each other in both calling and courtship songs, differing mainly in the duration of the calling song echeme. The songs of all the other species consist of relatively short echemes distinguished from one another by duration, syllable repetition rate, and number and distribution of gaps. The song differences shown by the four brachypterous species bolivari, uhagonii, minutissimus and llorenteae are particularly useful for field identification; two or three of these species sometimes occur together in the same locality and are sufficiently similar in appearance to be quite easily confused with one another.

Extreme caution has to be used in drawing phylogenetic conclusions from resemblances or differences in grasshopper songs, since it is well known from studies on the Chorthippus biguttulus group that apparently closely related species, capable of producing vigorous and fertile hybrids, can have strikingly different songs. From the known songs of Omocestus I am inclined to make such inferences in only two cases of song resemblance. The first is the well-known pair viridulus and rufipes, in which the strong resemblance in both calling and courtship songs suggests that they are sister species. The second is the pair of brachypterous, montane species minutissimus and llorenteae, in which the close resemblance in calling song (as well as morphology) also suggests a comparatively recent common ancestry.

**New lectotype designations**

In the course of examining type-material I have taken the opportunity of designating lectotypes for the following species included in this study.

_Gryllus rufipes_ Zetterstedt, 1821: 90.
Following Ander (1943: 10) I am regarding only two adult males from Zetterstedt’s original material (in the Zi, Lund) as being eligible as syntypes, and I have selected and labelled one of these, bearing Zetterstedt’s
ochre-yellow label (indicating Östergötland), as lectotype. I have labelled the other eligible adult male, which bears no colour-coded label, as a paralectotype.

**Acridium petraeum** Brisout, 1855: cxiv.
There is in the IRSNB, Brussels a long series of both sexes of this species, all labelled ‘Lardy’, the type-locality. These specimens are also labelled as being from the collection of de Selys Longchamps, who had earlier acquired Brisout’s collection, and it seems almost certain that they include at least part of Brisout’s type-series. I have selected and labelled a male bearing the handwritten label ‘Lardy près de Paris’ as lectotype. As there are many other specimens of this and various other species of *Omocestus* (and other genera) in the de Selys Longchamps Collection labelled ‘Lardy’, I have not attempted to determine which of these are also likely to belong to Brisout’s type-series and so have labelled no specimens as paralectotypes.

**Stenobothrus Brölemanni** Azam, 1906: 128.
Dr M. Donskoff of the MNHN, Paris has kindly sent me the male from Azam’s type-series that seems most eligible as a lectotype and I have so-labelled it.

**Omocestus Bolivari** Chopard, 1939: 172.
The type-series of this species (in the MNHN, Paris) consists of one male and one female, and I have selected and labelled the male as lectotype. The altitude given in the original description, ‘2000 m. environ’, clashes with the ‘3000 m’ given on the locality label, which I think is more likely to be accurate. I have labelled the female as a paralectotype.

**Gomphocerus (Stenobothrus) Uhagonii** Bolivar, 1876: 324.
Dr J. J. Presa of the Universidad de Murcia very kindly delivered to me by hand a male syntype of this species (from the MNCN, Madrid) labelled as being from Navarredonda, one of the type-localities, and I have labelled it as lectotype.

**OMOCESTUS** Bolívar

**Omocestus** Bolívar, 1878: 427 [as subgenus of *Gomphocerus* Thunberg]; Burr, 1904: 320 [raised to genus].
Type-species: *Gryllus Locusta viridulus* Linnaeus, by subsequent designation (Kirby, 1910: 172).

**Dirshius** Harz, 1975: 710 [as subgenus of *Omocestus* Bolívar]. Type-species: *Gryllus haemorrhoidalis* Charpentier, by original designation. **Syn. n.**

**DIAGNOSIS.** ♀♂. Head of typical Gomphocerine shape, foveolae well developed. Antennae not clubbed. Pronotal lateral carinae varying from sharply incurved to almost straight. Brachypterous to macropterous. Fore wings without bulge on anterior margin of precostal area; medial area not conspicuously widened (except in *O. uvarovi* Zanon, whose generic assignment is uncertain). Hind wings varying from transparent to strongly smoky. Ovipositor varying in length, normally without lateral teeth but sometimes showing tendency towards their development (e.g. *O. broelemanni*). Tympanal aperture slit-like.

**DISCUSSION.** Omocestus can be defined only on negative characters: it lacks the precostal bulge of *Chorthippus* Fieber, the toothed ovipositor of *Stenobothrus* Fischer, and the clubbed antennae of *Gomphocerus* Thunberg, *Gomphocerippus* Roberts and *Myrmeleotettix* Bolívar. Like several other genera in the large and rather intractable subfamily Gomphocerinae, it is no more than a group of convenience and is very unlikely to be holophyletic. Harz (1975) attempted to split it into two subgenera on the basis of the degree of curvature of the pronotal lateral carinae, but the species show every gradation between sharply incurved and almost straight carinae, and it is thus impossible to draw a clear dividing line between two subgroups.

Jago (1971) treated *Omocestus* as a subgenus of *Stenobothrus*, thus reverting to the status accorded to it by Bolívar (1897) and Yakobson & Bianki (1902). Jago’s study was based entirely on males, however, and so did not take into account the toothed ovipositor as the main diagnostic character of *Stenobothrus s. str*. I prefer to follow Harz (1975) and other recent workers on the European fauna in regarding this character as sufficient for a generic distinction. Jago also regarded Kirby’s designation of *viridulus* as the type-species of *Omocestus* as invalid on the grounds that, at the time of the original description of the genus, this species was listed by Bolívar (1878: 460) under *Chorthippus* rather than *Omocestus*. However, on p. 427 of Bolívar’s work, where *Omocestus* is first established and diagnosed, *viridulus* is clearly included in it; the heading ‘*Chorthippus*’ in the list on p. 460 has clearly been inadvertently misplaced, appearing above *rufipes* instead of in its correct position above *pullus*. I am therefore accepting Kirby’s type-species designation as valid.

The male callings songs show a wide range of patterns in *Omocestus*, varying from the prolonged single
echemes of viridulus and rufipes to the rapid sequence of short echemes of petraeus. This is not in itself an indication of polyphyly, however, as some complexes of sibling grasshopper species that are capable of interbreeding (e.g. the Chorthippus biguttulus group) show equally striking differences in male calling song.

**Distribution.** All Europe, the larger Mediterranean islands, North Africa and temperate Asia as far as China.

**Included species.** O. alluaudi Uvarov, O. antigai (Bolivar), O. aymonissabaudiae Salfi, O. bolivari Chopard, O. broelemanni (Azam), O. burri Uvarov, O. caucasicus Tarbinskii, O. corsicus Chopard, O. cuonaensis Yin, O. demokidovi Ramme, O. enitor Uvarov, O. femoralis Bolivar, O. haemorrhoidalis (Charpentier), O. heymonsi (Ramme), O. hingstoni Uvarov, O. kaestneri (Harz), O. knipperi Harz, O. lecercfi Chopard, O. lepineyi Chopard, O. llorentae Pascual, O. lopadusae La Greca, O. lucasii (Brisout), O. minutissimus (Bolivar), O. minutus (Brullé), O. megacoccus Yin, O. motuoensis Yin, O. nanus Uvarov, O. navasi Bolivar, O. nyalamus Xia, O. panteli (Bolivar), O. petraeus (Brisout), O. raymondi (Yersin), O. rufipes (Zetterstedt), O. simonyi (Krauss), O. tibetanus Uvarov, O. tzendsurenii Günther, O. uhagonii (Bolivar), O. uvarovi Zanon, O. viridulus (Linnaeus), O. znojkoii Mishchenko.

**Keys to the principal western European species of Omocestus**

The only western European species not included in these keys are very local forms, usually of doubtful status, in which the song is so far unknown.

Two keys are provided here, one based on morphological characters but with notes on song differences added where appropriate, and one based entirely on the male calling songs. Some of the species are very difficult to separate morphologically and, in the absence of song information, some specimens may not be correctly identified using the morphological key. Reference should in any case always be made to the notes given on recognition in the accounts of each species.

**Key based primarily on morphological characters**

This key is for sexually mature adults, either freshly collected or showing good colour preservation. O. simonyi, which is known only from the Canary Islands, is not included.

1. Rather brachypterous, fore wings less than 3 times length of pronotum ........................................ 2
   - Fully winged, fore wings more than 3 times length of pronotum ........................................ 10
2. Larger: length of hind femur more than 9.2 mm in $\sigma$, more than 11.0 mm in $\varphi$. (Eastern Pyrenees and Catalonia) ................................................. broelemanni (p. 236)
   - Smaller: length of hind femur less than 9.2 mm in $\sigma$, less than 11.0 mm in $\varphi$. (Not known from Pyrenees) ................................................................. 3
3. Fore wings not or hardly projecting beyond hind wings (when flexed); medial area with large dark spots .............................................................................. 4
   - Fore wings projecting well beyond hind wings (when flexed); medial area without spots .......... 5
4. Fore wings more than 2.5 times length of pronotum in $\sigma$, more than 2.1 times in $\varphi$ ........ llorentae (p. 243)
   - Fore wings less than 2.5 times length of pronotum in $\sigma$, less than 2.1 times in $\varphi$ ........ minutissimus (p. 243)

5. Male ................................................................................................................................. 6
   - Female .......................................................................................................................... 8
6. Cerci laterally compressed towards tip. ............................................................... uhagonii (p. 237)
   - Cerci simply conical, not laterally compressed towards tip ................................................ 7
7. Hind wings reaching less than halfway along fore wings (when flexed). Length of pronotum usually more than 2.5 mm. (Song a single echeme, as in Fig. 19) ............ bolivari (p. 237)
   - Hind wings reaching more than halfway along fore wings (when flexed). Length of pronotum usually less than 2.5 mm. (Song a sequence of echemes, as in Fig. 21) ........ minutissimus (p. 243)
8. Fore wings less than 1.3 times length of pronotum ................................................... bolivari (p. 237)
   - Fore wings more than 1.4 times length of pronotum ......................................................... 9

9  Ovipositor shaped as in Fig. 5, lower valves with strongly sigmoid ventral profile

- Ovipositor shaped as in Fig. 4, lower valves with weakly sigmoid ventral profile

10  Pronotal lateral carinae straight or almost so in prozona (Fig. 11). (Iberian Peninsula)

- Pronotal lateral carinae distinctly incurved or angled in prozona (not as in Fig. 11)

11  Fore wings falling well short of hind knees, their length less than 7·4 mm in ♂, less than 8·0 mm in ♀. (Mountains in S. Spain)

- Fore wings usually reaching at least to hind knees, their length more than 7·4 mm in ♂, more than 8·0 mm in ♀

12  Hind wings completely transparent (except sometimes for part of the subcostal area). Pronotal lateral carinae as in Fig. 9. (Song a rapid sequence of echemes, as in Fig. 15)
- Hind wings at least slightly smoky towards tip. Pronotal lateral carinae as in Figs 6, 7, 8 or 10. (Song a single echeme, repeated after an interval of at least several seconds) .......................................................... 13

13 Male .................................................................................................................. 14
- Female ................................................................................................................. 17
14 Abdomen with no orange or red colouring. (Song echeme lasting more than 12 s) ... viridulus (p. 226)
- Abdomen with at least some orange or red colouring. (Song echeme lasting less than 12 s) ........ 15
15 Abdomen with at least the distal 5 sternites coloured red or orange-red. Pronotal lateral carinae gently incurved in prozona, as in Fig. 7. (Song echeme lasting more than 4 s)

- Abdomen without reddish colouring on sternites or with such colouring restricted to the distal 3 or 4 sternites. Pronotal lateral carinae more strongly incurved in prozona, as in Figs 8 or 10. (Song echeme lasting less than 4 s) .......................................................... 16
16 Fore wings reaching well beyond hind knees, more than 4 times length of pronotum. (Song echeme lasting less than 2 s) .......................................................... raymondi (p. 233)
- Fore wings not or hardly reaching hind knees, less than 4 times length of pronotum. (Song echeme lasting more than 2 s) .......................................................... haemorrhoidalis (p. 227)
17 Ovipositor long, as in Fig. 2. Sides of body often green (but sometimes brown or reddish) viridulus (p. 226)
- Ovipositor shorter, similar in length to Fig. 3. Sides of body never green ........................................ 18
18 Abdomen with at least the more distal sternites coloured red or orange-red. Pronotal lateral carinae gently incurved in prozona, as in Fig. 7 .......................................................... rufipes (p. 227)
- Abdominal sternites with no reddish colouring. Pronotal lateral carinae more strongly incurved in prozona, as in Figs 8 or 10 .......................................................... haemorrhoidalis (p. 227)
19 Fore wings reaching beyond hind knees, more than 4 times length of pronotum ... raymondi (p. 233)
- Fore wings not or hardly reaching beyond hind knees, less than 4 times length of pronotum haemorrhoidalis (p. 227)

Key based on song characters (see especially Figs 12–23)

This key is based on the calling songs produced by isolated males in warm, sunny conditions. As far as couplet 5 the song differences can be easily detected by the human ear assisted by the second hand (or digital count) of a watch. From couplet 6 onwards some of the differences require oscillographic analysis, or at least the ability to play back the recorded song at a slower tape speed.

See p. 00 for definitions of the terms ‘echeme’, ‘syllable’ and ‘gap’.

1 Song a series of echemes in rapid succession (at least 1/s) .......................................................... 2
- Song a single echeme or a series of echemes separated by intervals of at least 3 s .......................... 4
2 Echemes repeated at the rate of at least 3/s (Figs 55–63) .......................................................... petraeus (p. 233)
- Echemes repeated at the rate of about 2/s .......................................................... 3
3 Song consisting of about 11–15 echemes and lasting about 6–8 s (Figs 123–128) ... llorenteae (p. 243)
- Song consisting of about 6–10 echemes and lasting about 3–5 s (Figs 117–119) minutissimus (p. 243)
4 Song consisting of a single echeme lasting more than 4 s .......................................................... 5
- Song consisting of one or more echemes, each lasting less than 4 s ........................................ 6
5 Echeme lasting more than 12 s (Figs 24–33) .......................................................... viridulus (p. 226)
- Echeme lasting less than 12 s (Figs 34–45) .......................................................... rufipes (p. 227)
6 Syllable repetition rate less than 10/s .......................................................... 7
- Syllable repetition rate more than 10/s .......................................................... 8
7 Each syllable with more than 7 gaps (Figs 108–116). (Iberian Peninsula) ..................... uhagonii (p. 237)
- Each syllable with fewer than 6 gaps (Figs 120–122). (Canary Islands) ...................... simonyi (p. 246)
8 Syllable repetition rate less than 20/s .......................................................... 9
- Syllable repetition rate more than 20/s .......................................................... 11
9 Echeme lasting more than 2 s (Figs 90–98) .......................................................... broelemanni (p. 236)
- Echeme lasting less than 2 s (Figs 64–72 or 99–107) .............................................. 10
SONGS OF THE WESTERN EUROPEAN OMOCESTUS

Figs 12-23 Oscillograms of typical male calling songs of species of Omocestus. The small numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).
The songs of the western European Omocestus

Omocestus viridulus (Linnaeus)

(Figs 2, 6, 24–33)


RECOGNITION. Males of this common species may be easily distinguished from the rather similar species rufipes and haemorrhoidalis by the lack of any red colouring on the abdomen, and females by the conspicuously longer ovipositor (Fig. 2). Both sexes also lack the dark markings in the medial area of the fore wings that are normally present in the other two species, and the pronotal lateral carinae are usually much less incurved in the prozona (Fig. 6).

In the field the conspicuously loud calling song of the male provides an easy means of identifying this species. Although similar in the quality of sound to the songs of rufipes and haemorrhoidalis, the song of viridulus is more prolonged, usually lasting for more than 12 s.

SONG (Figs 24–33). The calling song is an echeme usually lasting about 12–25 s and consisting of syllables repeated at the rate of about 15–20/s. The echeme beings quietly (the first few leg movements producing no audible sound) and gradually increases in loudness until the maximum intensity is reached after a few seconds; the echeme then continues at a constant intensity until reaching an abrupt end. The syllable repetition rate is highest at the beginning of the echeme (usually 18–20/s), gradually lessening towards the end (when it is usually 15–18/s). The song is a conspicuous summer sound in much of the European countryside, louder than the songs of most other common grasshoppers.

In the presence of a female the male produces longer echemes, usually lasting more than 30 s and occasionally more than a minute; one of the hind legs is moved through a noticeably wider angle than the other and produces most of the sound. After a series of these echemes with short pauses (about 10–15 s) between them, there is a quite different and much quieter echeme lasting about 3–5 s and composed of syllables repeated at the rate of about 12–16/s (Fig. 26). This is normally followed by a series of loud syllables and an attempt to copulate with the female. If this attempt is unsuccessful the male will usually produce a series of sharp 'ticks' (Fig. 27) by kicking backwards with the hind tibiae (as in the calling song of Stethophyma grossum (Linnaeus)) before beginning another sequence of courtship echemes. Usually the two hind tibiae are kicked simultaneously, but sometimes one at a time, changing haphazardly (rarely regularly) from one side to the other. The number of ticks is very variable but is usually between 5 and 15, and the repetition rate is rather irregular, generally about 1–2/s.

DISTRIBUTION. This common species occurs in fairly moist habitats throughout Europe, except for the extreme north and the southern parts of the Iberian, Italian and Balkan peninsulas; its range extends eastwards to Siberia and Mongolia.
Omocestus rufipes (Zetterstedt)

(Gryllus rufipes) Zetterstedt, 1821: 90. LECTOTYPE ♂, SWEDEN: Östergötland, Lärketorp (ZI, Lund), here designated (see p. 220) [examined]. [Validity established by von Borck (1848: 124) under Article 24 of the International Code of Zoological Nomenclature.]

Oroctopus ventralis Zetterstedt, 1821: 89. Holotype ♀, SWEDEN: Skåne, near Tranås, Åsperöd ['Esperöd'] (ZI, Lund) [examined].


RECOGNITION. The red colouring on the underside of the abdomen and the conspicuously pale-tipped palps enable both sexes of this species to be distinguished from its relatives. The distal part of the hind wings is much more smoky than in haemorrhoidalis, in which the male abdomen is occasionally reddish on the underside.

In the field the calling song of the males enables them to be recognized easily. Although quite similar in basic pattern to those of viridulus and haemorrhoidalis, the song of rufipes differs in duration, lasting about half as long as that of viridulus and about three times as long as that of haemorrhoidalis.

SONG (Figs 34–45). The calling song is an echeme usually lasting 5–10 s and consisting of syllables repeated at the rate of about 13–23/s. The scheme begins quietly and gradually increases in loudness until reaching an abrupt end, thus resembling the first half of the calling song of viridulus. As in viridulus the syllable repetition rate is highest at the beginning of the echeme (usually 17–23/s), gradually lessening towards the end (when it is usually 13–17/s).

In the presence of a female the male produces a courtship song quite similar to that of viridulus. There is first a series of echemes similar to those of the calling song but usually rather longer; this is followed by a quite different and quieter echeme lasting about 5–10 s and composed of syllables repeated at the rate of about 10–15/s (Fig. 37). There are then several loud syllables followed by an attempt to copulate with the female. The 'ticks' produced by backward kicks of the hind tibiae during the courtship song of viridulus seem never to occur in that of rufipes.

DISTRIBUTION. This species can tolerate drier conditions than viridulus and often occurs in more shaded habitats. Its distribution is very similar, but extends further south in the Iberian, Italian and Balkan peninsulas.

Omocestus haemorrhoidalis (Charpentier)

(Gryllus haemorrhoidalis) Charpentier, 1825: 165. Syntypes of both sexes, POLAND/CZECHOSLOVAKIA: 'Silesia'. There are a male (in bad condition) and two females in the MNHU, Berlin that have been regarded as syntypes of this species, but none is labelled 'Silesia' and there is some doubt that they belong to the type-series.


RECOGNITION. For the distinction between this species and petraeus see the remarks under that species. Both sexes may be distinguished from viridulus, rufipes and raymondi by the almost transparent hind wings (strongly smoky in the distal part in those three species). In the field the males can be recognized quite easily by their calling song, in which the echemes are shorter than those of viridulus and rufipes, but much longer than those of raymondi.

SONG (Figs 46–54). The calling song is an echeme lasting about 2–4 s and consisting of syllables
Figs 24-29 Oscillograms of the songs of three males of *Omocestus viridulus*. 24, 25. Calling songs of males with (24) two hind legs and (25) one hind leg, 26, 27. Parts of the courtship song showing (26) the concluding part of a main scheme followed by the quieter scheme and loud syllables that precede an attempt to copulate, and (27) the ‘ticks’ produced before the beginning of a main scheme. 28, 29. Faster oscillograms of the indicated parts of the songs shown in Figs 24, 25. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).
Figs. 30-33. Faster oscillograms of the indicated parts of the songs of Omocestus viridulus shown in Figs 28, 29, showing the differences between the songs of males with (30, 32) two hind legs and (31, 33) one hind leg.
Figs 34–40  Oscillograms of the songs of four males of *Omocestus rufipes*. 34–36. Calling songs of males with (34, 35) two hind legs and (36) one hind leg. 37. Part of the courtship song showing the concluding part of a main scheme followed by the quieter scheme and loud syllables that precede an attempt to copulate. 38–40. Faster oscillograms of the indicated parts of the songs shown in Figs 34–36. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).
Figs 41-45  Faster oscillograms of the indicated parts of the songs of *Omocestus rufipes* shown in Figs. 38-40, showing the difference between the songs of males with (41, 42, 44) two hind legs and (43, 45) one hind leg.
Figs 46-54 Oscillograms at three different speeds of the calling songs of three males of *Omocestus haemorrhoidalis*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).
repeated at the rate of about 25–40/s (about double the rate of viridulus and rufipes). The echeme begins quietly but soon reaches maximum intensity. The syllable repetition rate gradually lessens during the course of the echeme.

DISTRIBUTION. Widely distributed in continental Europe, but not known from the Scandinavian mainland and limited to mountains in the southern peninsulas. The range extends eastwards across central Asia to Mongolia, Manchuria and Korea.

**Omocestus petraeus** (Brisout)

(Figs 9, 55–63)

*Acridium petraeum* Brisout, 1855: cxiv. LECTOTYPE ♂, FRANCE: near Paris, Lardy (Brisout) (IRSNB, Brussels), here designated (see p. 221) [examined].


RECOGNITION. This species lacks the smoky coloration of the distal part of the hind wings shown by viridulus, rufipes and raymondi, and is also noticeably smaller. Distinguishing it from haemorrhoidalis is more difficult, especially if reliably identified specimens of both species are not available for comparison. *O. petraeus* is again noticeably smaller, and the head is larger in comparison to the pronotum and more convex above with shorter foveolae. The males lack the red colouring shown by the distal part of the abdomen in haemorrhoidalis, showing a yellowish colouring in this region instead.

The highly distinctive calling song, consisting of about 10–20 rapidly repeated echemes, enables males of this species to be recognized easily in the field.

SONG (Figs 55–63). The calling song consists of a sequence of about 10–20 echemes lasting about 2–5 s. The sequence begins quietly, reaching maximum intensity after about 6 echemes; even at its maximum intensity the song is rather quiet. The echeme repetition rate is usually about 4/s, and the syllable repetition rate within each echeme about 80–110/s. Each of the louder echemes lasts for about 150 ms and contains about 10–15 syllables.

In the presence of a female the male produces echemes of a quite different kind (Figs 57, 60, 63). Each echeme begins with a relatively long syllable, lasting about 20–50 ms, and this is immediately followed by a series of very short sounds, each lasting less than 5 ms, repeated at the rate of about 50/s. These echemes are produced either singly or, more often, in groups of about 2–5.

DISTRIBUTION. Western, central and eastern Europe, Asia Minor and southern Siberia. Largely absent from the Iberian Peninsula, but quite widespread in Italy and the Balkan Peninsula.

**Omocestus raymondi** (Yersin)

(Figs 10, 64–72)

*Stenobothrus raymondi* Yersin, 1863: 289. Syntypes of both sexes, FRANCE: Var, near Hyères (Raymond) (lost); the two ‘neotypes’ designated by Harz (1975: 713) are clearly invalid.


RECOGNITION. This all-brown species is most likely to be confused with haemorrhoidalis, but can be distinguished from it in both sexes by the strongly smoky distal part of the hind wings (almost transparent in haemorrhoidalis). In the field males may be distinguished from those of haemorrhoidalis by the very short echemes (lasting about 1 s) and slower syllable repetition rate (less than 20/s) of the calling song.

SONG (Figs 64–72). The calling song is an echeme lasting about 1.0–1.5 s and consisting of about 18–25 syllables repeated at the rate of 15–20/s. Each echeme usually begins quietly, rapidly increasing in intensity. Oscillograms show the syllables to have a characteristic pattern of gaps, which often becomes obscured towards the end of the echeme (Figs 67–69). The echemes are often produced singly and repeated at irregular intervals (10–15 s is typical), but sometimes they are in groups of 2–4 with much shorter intervals between them (often 2–5 s) (Figs 65, 66).

DISTRIBUTION. Known only from southern France, the Iberian Peninsula, north-western Italy and North Africa.
Figs 55–63 Oscillograms at three different speeds of the songs of two males of *Omocestus petraeus*. 55, 56, 58, 59, 61, 62. Calling songs. 57, 60, 63. Courtship song of the same male as Figs 55, 58, 61. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 216).
Figs 64–72  Oscillograms at three different speeds of the calling songs of three males of *Omocestus raymondi*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 216).
Omocestus panteli (Bolivar)
(Figs 11, 73–89)

Stenobothrus panteli Bolivar, 1887: 95. Syntypes of both sexes, Spain: Cuenca, near Uclés (?MNCN, Madrid).

References to song. No published work known to me.

Recognition. In the Iberian Peninsula, to which it is confined, panteli is most likely to be confused with viridulus; it is, however, much smaller than that species and can be further distinguished from it by the red tip of the male abdomen and the relatively short ovipositor. There is also a superficial resemblance to Stenobothrus stigmaticus (Rambur), which is similar in size and also widespread in the Iberian Peninsula, but the pronotal lateral carinae are straighter in panteli, the male cerci are conical throughout (laterally compressed at the tip in stigmaticus) and the female lacks the teeth on the ovipositor shown by all species of Stenobothrus. There is a large form (var. meridionalis Bolivar) found in the south of the peninsula, especially in mountains; this form is even more like viridulus, but confusion is unlikely as that species does not occur in southern Spain.

In the field the song may be recognized by its short duration (less than 2 s) and high syllable repetition rate (usually more than 20/s).

Song (Figs 73–89). The calling song is an echeme lasting 1–2 s and consisting of about 30–55 syllables repeated at the rate of about 18–30/s. The echeme begins quietly (sometimes after a few louder syllables) but soon reaches maximum intensity. The syllable repetition rate gradually lessens during the course of the echeme.

In the presence of a female the male first produces a different kind of echeme lasting about 2–3 s, and this is immediately followed by an echeme similar in duration and syllable repetition rate to that of the calling song but with an increase in intensity continuing through the whole echeme (Figs 77, 82, 87).

Distribution. This species is confined to the Iberian Peninsula, where it is widespread and very common.

Omocestus broelemanni (Azam)
(Figs 90–98)


Recognition. This Pyrenean species is brachypterous, the fore wings not usually reaching the hind knees in the male and reduced to short lobes (about 1.5 times the length of the pronotum) in the female; in both sexes the hind wings fall short of the fore wings by quite a large gap. There is thus no risk of confusion with viridulus, rufipes, haemorrhoidalis and the other fully winged species of Omocestus. Confusion is also unlikely with the brachypterous species occurring further south in Spain, such as ukagonii and minutissimus, which are much smaller and not known from the vicinity of the Pyrenees. The relationship of O. broelemanni with O. antigai (Bolivar) and O. navasi Bolivar has been recently discussed by Reynolds (1986).

In the field the calling song of the male is quite distinctive, consisting of echemes lasting about as long as those of haemorrhoidalis but with about half the syllable repetition rate of that species.

Song (Figs 90–98). The calling song, recently described for the first time by Reynolds (1986), is a series of echemes, each lasting about 1.5–3.0 s and consisting of about 25–45 syllables repeated at the rate of about 15–16/s. Each echeme begins quietly, reaching maximum intensity after about 1 s. Although the echemes are sometimes produced singly, they are more often repeated fairly regularly, about every 5–10 s, in a series of indefinite duration.

During the courtship song, which has also been described by Reynolds (1986), the male often produces a series of rather longer echemes (each lasting up to 5 s) and this is followed by a variable number of short echemes of small numbers of syllables (or even single syllables).
produced by one leg only (Figs 92, 95, 98). There is then a series of single syllables produced by both legs, followed by an attempt at copulation.

**DISTRIBUTION.** Known only from the vicinity of the Pyrenees, particularly the eastern end of the range.

*Omocestus bolivari* Chopard

(Figs 99–107)

*Omocestus Bolivari* Chopard, 1939: 172. LECTOTYPE ♂, SPAIN: Granada, Sierra Nevada, slopes of Mulhacén, 3000 m ['2000 m. environ' according to Chopard, loc. cit.], 10.vii.1934 (Balachowsky) (MNHN, Paris), here designated (see p. 221) [examined].

**REFERENCES TO SONG.** No published work known to me.

**RECOGNITION.** This species, known only from the higher parts of the Sierra Nevada in southern Spain, is very similar to *uhagonii*, *llorenteae* and *minutissimus*. Males may be distinguished from all three of these species by their short hind wings, which are less than half the length of the fore wings, and the females by their short fore wings, which are usually less than 1·3 times longer than the pronotum.

In the field the isolated echemes of the calling song enable males to be easily distinguished from *llorenteae* and *minutissimus*; from *uhagonii* they may be distinguished by the much faster syllable repetition rate.

**SONG** (Figs 99–107). The calling song is an echeme lasting 0·5–2·0 s and consisting of about 10–30 syllables repeated at the rate of 14–16/s. Each echeme begins quietly, soon reaching maximum intensity. Oscillographic analysis shows that there are gaps in each syllable (mainly in the later part of the syllable) and that they occur throughout the echeme; there are, however, only 2–4 gaps per syllable (Figs 102–107), many fewer than in *uhagonii*. As in *uhagonii* the echemes are repeated at irregular intervals, varying from a few seconds to over a minute.

**DISTRIBUTION.** Known only from the higher parts of the Sierra Nevada in southern Spain, usually at altitudes above 1500 m.

*Omocestus uhagonii* (Bolivár)

(Figs 4, 108–116)

*Gomphocerus* (*Stenobothrus*) *Uhagonii* Bolivár, 1876: 324. LECTOTYPE ♂, SPAIN: Madrid, Navarredonda (Avila) (MNCN, Madrid), here designated (see p. 221) [examined].

**REFERENCES TO SONG.** No published work known to me.

**RECOGNITION.** Males of this brachypterous montane species can be distinguished from the rather similar species *bolivari*, *llorenteae* and *minutissimus* by the cersi, which are laterally compressed towards the tip (simply conical in the other three species). Females can be separated from *bolivari* and *llorenteae* by the length of the fore wings, which are 1·4–1·8 times longer than the pronotum (the corresponding ratios for *bolivari* and *llorenteae* are 0·9–1·3 and 2·1–2·5, respectively), and from *minutissimus* by the much less strongly sigmoid ventral profile of the lower valves of the ovipositor (cf. Figs 4, 5).

In the field the calling song of the males enables this species to be easily distinguished from *llorenteae* and *minutissimus*, which produce echeme-sequences of a quite different kind (cf. Figs 20–22); from *bolivari* it may be distinguished by the much slower syllable repetition rate (cf. Figs 19, 20).

**SONG** (Figs 108–116). The calling song is an echeme lasting 1–2 s and consisting of about 10–15 syllables repeated at the rate of 6–7/s. Each echeme begins quietly, rapidly increasing in intensity. Oscillographic analysis shows that each syllable has a large number of gaps (commonly as many as 8) and that this pattern of gaps is maintained until the end of the echeme (Figs 111, 112). The echemes are repeated at irregular intervals, varying from a few seconds to over a minute.

In the presence of a female the male produces a series of slightly longer echemes (lasting 2–3 s) at much more regular intervals (usually 6–8 in 40 s) (Fig. 110). The echemes consist of about 15–20 syllables and at the end of some of them (usually about half) there is a group of 3–4 syllables of a different kind (Figs 113, 116), repeated more rapidly (at the rate of about 16/s). In
Figs 73–82 Oscillograms of the songs of five males of *Omostesos panteli*. 73–76. Calling songs of males with (73–75) two hind legs and (76) one hind leg. 77. Courtship song. 78–82. Faster oscillograms of the indicated parts of the songs shown in Figs 73–77. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).
Figs 83–89. Faster oscillograms of the indicated parts of the songs of Omocestus undulatus shown in Figs 78–82. Figs 86 and 89 are from a male with only one hind leg (see p. 219).
Figs 90-98 Oscillograms at three different speeds of the songs of two males of *Omocestus broelemani*. 90, 91, 93, 94, 96, 97. Calling songs. 92, 95, 98. Courtship song of the same male as Figs 90, 93, 96. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Tables 1 and 2 (pp. 216, 217).
Fig. 99–107 Oscillograms at three different speeds of the calling songs of three males of *Omocestus bolivari*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 216).
Figs 108–116  Oscillograms at three different speeds of the songs of three males of *Omocestus uhagonii*. 108, 109, 111, 112, 114, 115. Calling songs. 110, 113, 116. Part of the courtship song. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 217).
the intervals between the echemes there are quieter ‘ticking’ sounds repeated fairly regularly at the rate of about 3–4/s. The number of echemes in the series is variable but can be more than 20. The series of echemes is followed by a variable period (often more than a minute) in which the quiet ticking continues and which ends in a number of sequences of a different kind of sound, still quiet, and then an attempt at copulation. If this is unsuccessful the cycle begins again with another series of echemes.

**DISTRIBUTION.** This species has been previously known only from the mountains of central and northern Spain, but my wife and I collected a series of adults of both sexes at El Chorillo (2700 m), south of the Mulhacén peak in the Sierra Nevada, on 31 July 1983.

*Omocestus minutissimus* (Bolivar)

(Figs 5, 117–119)

*Gomphocerus* (*Omocestus*) *minutissimus* Bolivar, 1878: 424. Syntypes of both sexes, Spain: Navarra, Cascante (*Perez Arcas*); Madrid, Escorial (MNCN, Madrid; BMNH, London; probably other repositories) [♀ syntype from Escorial in BMNH examined].

**REFERENCES TO SONG.** No published work known to me.

**RECOGNITION.** Males of this small upland species may be distinguished from *uhagonii* by the cerci, which are simply conical (laterally compressed towards the tip in *uhagonii*). They can be separated from *bolivari* and *llorenteae* by the length of the hind wings, which are more than half the length of the fore wings but do not reach the fore wing-tips. Females can be distinguished from *bolivari* and *llorenteae* by the length of the fore wings, which are usually 1.4–2.1 times the length of the pronotum; the corresponding ratios for *bolivari* and *llorenteae* are 0.9–1.3 and 2.1–2.5, respectively (these two species are in any case known only from the Sierra Nevada or Sierra Espuña, where *minutissimus* does not apparently occur). Females of *minutissimus* may be separated from those of *uhagonii* by the strongly sigmoid ventral profile of the lower valves of the ovipositor (cf. Figs 4, 5).

In the field the calling song of the males, consisting of a rapid sequence of echemes, enables this species to be easily distinguished from *uhagonii* and *bolivari*; from *llorenteae* it may be distinguished by being shorter (usually lasting less than 6 s) and having fewer echemes in each sequence (usually fewer than 10).

**SONG** (Figs 117–119). The rather quiet calling song is a sequence of about 6–10 echemes lasting about 3–5 s. The sequence begins very quietly, reaching maximum intensity after about 3–4 echemes. The echemes are separated by intervals of about 100–200 ms, often becoming more widely spaced towards the end of the sequence. Each echeme begins and ends very quietly, giving a spindle-shaped oscillogram (Fig. 118). Each of the later echemes in the sequence lasts about 300–400 ms and contains about 20–30 syllables repeated at the rate of about 80–90/s. The calling song is thus very similar to that of *llorenteae*, but is quieter and shorter, and has fewer echemes composed of fewer syllables.

**DISTRIBUTION.** North-eastern, central and south-eastern Spain.

*Omocestus llorenteae* Pascual

(Figs 123–128)

*Omocestus llorenteae* Pascual, 1978: 159. Holotype ♀, Spain: Granada, Sierra Nevada, Dornajo, 2000 m, 19.ix.1975 (Pascual) (Universidad de Granada) [examined].

**REFERENCES TO SONG.** No published work known to me.

**RECOGNITION.** This species, known only from the Sierra Nevada and Sierra Espuña in southern Spain, can be distinguished from the similar montane species *uhagonii* and *bolivari* by the dark spots in the medial area of the fore wings and by the longer hind wings, which reach the tips of the fore wings; the longer hind wings also enable this species to be distinguished from *minutissimus*, which is in any case not known to occur in the Sierra Nevada or Sierra Espuña. Females of *llorenteae* also differ from those of *uhagonii* and *bolivari* in that the fore wings are more than twice the length of the pronotum.

In the field the calling song of the males, consisting of a rapid sequence of echemes, provides an easy means of distinguishing this species from most other species of *Omocestus* occurring in southern Spain.
Figs 117-122. Oszillograms at three different speeds of the male calling song of (117-119) Omosaurus minutissimus and (120-122) O. simulans. The small numbers following the figure numbers refer to the recordings from which the oszillograms were made and can be used to obtain the full data from Tables 1 and 2 (p. 217).
Figs 123–128 Oscillograms at three different speeds of the calling songs of two males of *Omocestus llorenteae*. The small numbers following the figure numbers refer to the recordings from which the oscillograms were made and can be used to obtain the full data from Table 1 (p. 217).
From minuissimus, which has a similar song-pattern, it may be distinguished by being longer (usually lasting more than 6 s) and having more echemes in each sequence (usually more than 11).

**SONG** (Figs 123–128). The calling song is a sequence of about 11–15 echemes lasting about 6–8 s. The sequence begins quietly, reaching maximum intensity after about 5–6 echemes. The echemes are usually separated by intervals of about 100–200 ms, often becoming more widely spaced towards the end of the sequence. Each echeme begins and ends quietly, giving a spindle-shaped oscillogram (Figs 125, 126). By the middle of the sequence each echeme lasts about 350–600 ms and contains about 30–50 syllables repeated at the rate of about 85–95/s. The calling song is thus remarkably similar to that of Myrmeleotettix maculatus (Thunberg), though usually of shorter duration and composed of fewer echemes.

**DISTRIBUTION.** Known only from the Sierra Nevada and Sierra Espuña in southern Spain.

**Omocestus simonyi** (Krauss)

(Figs 120–122)

Stenobothrus simonyi Krauss, 1892: 166. Syntypes of both sexes, CANARY ISLANDS: Lanzarote (Simony) (lost).

**REFERENCES TO SONG.** No published work known to me.

**RECOGNITION.** This is the only species of Omocestus known from the Canary Islands and so in practice there is no problem in recognizing it. It is similar in appearance to raymondi but is smaller (total length less than 14 mm in the male, less than 19 mm in the female). The calling song of the male is superficially very similar to that of uhagonii, oscillographic analysis being required to show that it has far fewer gaps in each syllable; it differs from that of raymondi in having a much slower syllable repetition rate.

**SONG** (Figs 120–122). The calling song is an echeme lasting about 1·0–2·5 s and consisting of about 10–20 syllables repeated at the rate of 5–10/s. Each echeme begins quietly, reaching maximum intensity about midway through its duration. Oscillographic analysis shows that there are gaps in each syllable, similar in number to those in the calling song of raymondi (far fewer than in uhagonii) but not arranged in the same pattern and maintained until the end of the echeme (Figs 121, 122). The echemes are repeated at irregular intervals.

**DISTRIBUTION.** Known only from the Canary Islands, where it occurs on Lanzarote and Fuerteventura.

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M. J. Scoble
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The structure and affinities of the Hedyloidea: a new concept of the butterflies

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Synopsis

The affinities of the Hedylidae, a group of about 40 Central and South American Lepidoptera, are reassessed. Currently, the taxon is treated as a tribe ('Hedylicae') of the Oenochrominae (Geometridae), but evidence is presented here to show that hedylids are butterflies although they look moth-like in many respects. The five generic names in the family are synonymized in this work with the oldest, Macrosoma Hübner.

The taxonomic history of the Hedylidae is discussed, and the reasons for the proposed assignment of the family to the Rhopalocera are given. A description of the family is followed by comments on characters selected for their biological or systematic interest. In this section comparisons are made between the Hedylidae and other Lepidoptera, particularly the butterflies, and their phylogenetic relationships are discussed. Hedylidae + Hesperioidae + Papilionoidea (s.str.) probably form a monophyletic taxon, although doubts have been expressed about the relationship between skippers and true butterflies. It is tentatively suggested that within the Rhopalocera, the Hedylidae are more closely related to the Papilionoidea than are the Hesperiidae to the Papilionoidea; that is, the butterflies without the Hedylidae are paraphyletic.

The evidence of the butterfly affinities of hedylids comes from adults, larvae, and pupae; the structure of the thorax and the base of the abdomen of the adult was found to be particularly revealing.

Key words: Lepidoptera, Rhopalocera, Hedyloidea stat. n., Hedylidae, Geometridae, morphology, phylogeny.

Introduction

Guenée (1857) described the Hedylidae as one of the 26 component families of the Phalénites. The Phalénites are, with modification, the equivalent of what are now called the Geometridae. The Hedylidae were treated by Prout (1910; 1931) as a tribe ('Hedylicae') of the Oenochrominae (Geometridae), and no reassessment of the relationships of the group has been attempted subsequently. In fact the Hedylidae are misplaced in the Geometridae, the most obvious reason being the absence of tympanal organs from the base of the abdomen in the former – structures that are characteristic of the latter.

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The Hedylidae consist of some 40 species, from South or Central America. Below, I argue that not only is this group misplaced in the Geometridae but also that its phylogenetic affinities are with the butterflies (Rhopalocera: Hesperioidea or skippers, and Papilionoidea or true butterflies) despite the moth-like external appearance of the adult insects.

Both Guenée (1857) and Prout (1910; 1931) noted certain similarities between hedylids and butterflies. Guenée even went so far as to name one species _napiaria_ because it resembled the pierid butterfly _Pieris napi_ (L.). He named another species _heliconiaria_ since it reminded him of certain species of the papilionoid genus _Heliconius_ Kluk. Prout (1910; 1931) noted the butterfly-like shape of the adults, and the remarkable girdled pupa in the two species for which he had information. However, neither of these workers suggested that these features meant that hedylids and butterflies were related, and they presumably regarded the similarities as independent derivations. Prout (1931) was clearly uncomfortable about the geometrid affinities of the group since he suggested that the 'Hedylicae' might deserve even a separate family status. However, neither he nor Guenée apparently considered that the butterfly-like features they observed might actually be homologous in the taxa concerned and thus indicative of true affinity. Why?

There are two reasons, one philosophical and one practical. We tend to develop a conception of a given taxon. We think of butterflies as a package, and develop what might be termed a butterfly _Gestalt_ - colourful, diurnal lepidopterans with clubbed antennae and ampelisiform rather than frenate wing-coupling. This is not to say that we do not recognize exceptions. Males of the skipper _Euschemon_ Doubleday have a frenulum and retinaculum; satyrides generally are not brightly coloured, many butterflies do not have strongly clubbed antennae, and a few are nocturnal. By definition, exceptions do not destroy a _Gestalt_. But hedylids do not conform to the traditional butterfly package. They do not have clubbed antennae; in some species these structures are even bipectinate. In males of most species the frenulum and retinaculum are very well developed, and the wing pattern in most species bears little resemblance to that of butterflies (Figs 1–18). Most species seem to be nocturnal.

Most taxa are diagnosed by a _set_ of attributes rather than by a single character or very few characters. Even so, such diagnoses often need qualification to incorporate those taxa that do not fit - for example, primitive species that have not yet acquired all the attributes of the majority, or those specialized species that have lost them secondarily. Crowson (1970), noting the essentialist nature of such diagnoses, called the groups Aristotelian to distinguish them from taxa delimited phylogenetically. Crowson also coined the phrase 'the non-congruence principle' to suggest that it is most unlikely that a taxon can be defined on more than one or two characters, since when a taxon originates many of the characters found in later members of the group have not yet evolved. Characters we regard as typical of a given taxon do not evolve at once. Therefore, in the present case, we should not expect the ground plan of the butterflies as a whole or even the true butterflies to exhibit the characteristics of the more advanced members of the group. It should not, then, be unexpected to find a group strongly affiliated to the butterflies that does not fit our conception of them. However, if it is our stated aim to produce, as far as possible, a phylogenetic classification, then merely one derived character shared between two taxa provides evidence of monophyly. In fact, the Hedylidae possess several such characters.

Having rejected the idea that hedylids might be related to butterflies, neither Guenée nor Prout looked further. This may largely have been because morphological studies were less extensive in Guenée's time than they are today. Much the same can be said of Prout, who had a remarkable ability to observe structures and their significance on dried specimens, but did little dissection. (Only late in his career did he study genitalia.) In fact many of the characters that support the suggestion that hedylids are butterflies are to be observed only after detailed examination of the sclerites of the thorax and the base of the abdomen.

The present study evolved from a project to re-diagnose the Oenochrominae (Geometridae), and to exclude those groups that currently make the subfamily unnatural (non-monophyletic). The extraordinary combination of attributes of the Hedylidae demonstrates that their affinities lie neither with _Oenochroma_ Guenée (the type genus of the Oenochrominae) and its relatives, nor with the Geometridae as a whole. In particular, abdominal tympanal organs, which are
typical of geometrids, are absent from hedylids. Also, prolegs are present on abdominal segments 3 to 6 and 10 of the larva, unlike most geometrids where their number is reduced. The first tergum of the abdomen is strongly ‘pouched’ (a condition described for papilionoids by Ehrlich, 1958b), and pre- and postspiracular bars are present. The abdomen is curved and flattened laterally, particularly in the male. The remarkable pupa is attached to a leaf by a silken girdle: there is no cocoon. The apical tibial spurs of the hindleg are absent in all species except the male of one. The precoxal (or paracoxal) sulcus of the mesothorax joins the ‘marginopleural’ sulcus. In the metathorax the furcal apophysis is weakly sagittate in dorsal view. The pretarsus is lost from the forelegs of the male although minute claws are present, and the tarsomeres are reduced to two by fusion. The head of the larva is extended into a pair of extremely long horns, and there is an anal comb on abdominal segment 10. These characters are all represented in various butterflies. In contrast, the moth-like features include the absence of clubs on the antennae, and a well-developed frenulum and retinaculum in the males of most species, although they are reduced and functionless in a few. The wing venation is peculiar: $R_3$ and $R_4$ share a common stem, but $R_2$ is separate from the cell and is not stalked with $R_3$. $R_1$ and $R_2$ are distinctly sinuate. Special modifications of the wings, including a complex of small chambers at the base of the forewing and a prominent flap extending from $S_c$, are described below.

The body of this work aims to provide the evidence that suggests that hedylids are butterflies. Are the apparent butterfly attributes genuinely shared-derived characters of hedylids and butterflies or are they convergent or parallel developments? In short, are the Hedylidae more closely related to the butterflies than to any other lepidopterans?

A further question is: are the Hedylidae more closely related to the true butterflies (Papilionoidea) than to the skippers (Hesperioidea), or does the family represent the sister group of the Rhopalocera as a whole?

A general description of the characters found in this family is provided, together with a summary of its biology and distribution. This is followed by observations on selected structures with comments on their systematic importance. Finally, the evidence for the affinity of the Hedylidae with the Hesperioidea and the Papilionoidea is assessed.

Material

The observations were based on specimens housed in the British Museum (Natural History). Juvenile stages of one species were lent by Mr R. O. Kendall, San Antonio, Texas.

Examination of the structure of the thorax was necessarily limited to avoid breaking up numerous specimens. From the study of more easily observed characters the family Hedylidae appears to be a homogeneous group, and thoracic structures probably do not differ significantly between species. Thoracic structure was examined in species that showed most structural variation in the genitalia.

HEDYLIDAE Guenée


Guenée (1857) described the family for three genera, Hedyle Guenée, Venodes Guenée, and Phellinodes Guenée. With the exception of Prout (1910; 1931), most authors have been content to describe new species or genera without discussing the taxonomic relationships of the group as a whole. Prout, in both these works, dealt with all the genera and species. He treated the taxon as a tribe – the ‘Hedylicae’ – of the subfamily Oenochrominae (Geometridae). Authors who preceded Prout assigned the genera to various infrafamilial categories of the Geometridae, some of which are not currently in use, with no justification for their action. Kendall (1976), in his notes on the life-history of one species, used the name Hedylidae, therefore effectively reviving Guenée’s original status.

The use of the name Hedylidae is fully justified by Guenée’s priority, Kendall’s subsequent usage, and the absence of any competing name.
Generic synonymy

The species of the family show no fundamental structural difference from each other, and form a highly compact group, particularly in the male genitalia, wing venation, wing shape, legs and antennae. Below, I synonymize the five genera that are currently accepted. Three of these are monotypic.

*Macrosoma tipulata* Hübner and *Lasiopates hyacinthina* Warren are species that exhibit the greatest differences from the majority of the family. The valvae of the male genitalia of *hyacinthina* (Fig. 79) are of a more complex shape, the two components of the gnathos are not fused medially, and the juxta is characteristic.

One reason for the proliferation of genera in the Lepidoptera is that since the study of the male genitalia became universal, there has been a strong tendency to treat as genera those groups where there is a morphological 'gap' in these structures. The consequence has been that although a family may contain a few large genera there are usually several anomalous species. If these are then excluded from one of the main genera each has to be assigned to a new genus. In a family with several large genera it may be impossible to decide to which genus such 'outlier' species should be assigned. The description of a new genus therefore becomes inevitable. In a family with one large genus there is often a good case to be made for including all species within that genus and using lower categorical rank, e.g. subgenus, or simply species-group, to distinguish outliers. In the present case, despite the synonymy, I have not so divided *Macrosoma* in this way. This is best left until such time as a revision of all the species is undertaken. The synonymized names can then be used as subgenera, if required.

**MACROSUMA** Hübner

*Epirrita* Hübner, 1808. [Name unavailable, see Fletcher, 1979.]


*Macrophila* Walker, 1862: 1463, 1465. Type species: *Macrosoma tipulata* Hübner, 1818 (by monotypy). [Junior objective synonym of *Macrosoma*, see Fletcher, 1979.]


Hedylidae remains the valid name of the taxon since family names are not rejected when, after 1960, their type genera are found to be junior synonyms.

General appearance

Hedylids are fairly delicate insects with curved abdomens, particularly in the male (Fig. 63). Figs 1–18 show the main variation in wing patterns: many of the species bear semi-transparent patches on the wings. The fore wings are weakly or strongly emarginate at the apex. The larva (Figs 19, 100, 101) bears a pair of very long 'horns' on the head capsule, prolegs on abdominal segments 3 to 6 and 10, a pair of furcae on the anal segment, and an anal comb. The pupa (Figs 20, 21) lacks a cocoon, and is attached to its substrate by a silken girdle.

Description

Adult

Head (Figs 22–29). Fronds narrow and protuberant (Figs 22, 23). Compound eyes large. Ocelli absent. Chaetosemata present, one chaetosema behind each eye (Fig. 22). Antenna (Figs 25–28): bases close
Figs 1-6 Adults of Hedylidae. 1, *Macrosoma heliconia* (Guenée), × 1·5; 2, *M. hyacinthina* (Warren), × 1·1; 3, *M. tipulata* Hübner, × 1·1; 4, *M. rubedinaria* (Walker), × 1·5; 5, *M. ustrinaria* (Herrich-Schäffer), × 1·5; 6, *M. leucophasiata* (Thierry Mieg), × 1·5.

Together; filiform (Figs 26, 27) or bipectinate (Fig. 25); scaled dorsally. Pilifers present. Maxillae: palpi minute, one-segmented; galeae form a well-developed proboscis, not scaled at base. Labial palpi ascending (Fig. 24), three-segmented with a deep sensory invagination on distal segment (Fig. 29). Tentorium: medial swelling on each tentorial arm (Fig. 23), but dorsal arms not developed.

Thorax (Figs 30, 31). Prothorax with membranous patagia and parapatagia; patagia protuberant. Mesothorax: anepisternum well developed, not reduced (Fig. 30); precoxal sulcus (paracoxal sulcus of Scott, 1985) joins 'marginopleural' suture (Fig. 31). Metathorax: furcal apophyses weakly sagittate in dorsal view; dorsal lamellae of secondary furcal arms fused mesally in their extension anteriorly from the arms to the furcal apophyses.

Wing venation (Fig. 32). (Following the recommendations of Wootton (1979), in this work I label the
Figs 7–12 Adults of Hedylidae. 7, Macrosoma subornata (Warren), × 1·5; 8, M. paularia (Schaus), × 1·5; 9, M. coscoja (Dognin), × 1·5; 10, M. satellitata satellitata (Guenée), × 1·1, hyaline patch arrowed; 11, M. albifascia albifascia (Warren) × 1·1; 12, M. hedyalaria (Warren), × 1·1.

branches of the radial sector as Rs₁, Rs₂, etc., to distinguish them from the radius (R₁).) Fore wing: accessory cells absent. Rs₁ and Rs₂ sinuous after branching from cell; Rs₄ stalked with Rs₃, Rs₂ not stalked with Rs₃ (although it shares a common stem with Rs₃ and Rs₄ before the three branches arise); Rs₄ remote from M₁; CuP often weakly indicated; M₂ about equal distance from M₁ as from M₂; anals forked at base. Hind wing: Rs separate from Sc+R₁ from near base of wing; M₂ about equidistant from M₁ and M₃.

Wing coupling (Figs 33–37). Male usually with strong frenulum and a very long, well-developed retinaculum; frenulum occasionally reduced and non-functional (Fig. 35). Female: frenulum composed of a few bristles (Fig. 36); retinaculum absent.

Wings: pattern and specializations. Figs 1–18 illustrate the variety of shape and pattern. Vestiture: rather weakly scaled; prominent piliform scales present particularly near base of wings (Fig. 38), and more
numerous on hind wing than fore wing. Upperside and underside with the same pattern. Areas of semi-transparent scales often present. Fore wing long, not broad, weakly falcate often with apex weakly emarginate; posterior edge expanded into a small lobe at base of wing in males of some species (Fig. 43), sometimes merely a very weak expansion. Holding area (Haftfeld) not present on ventral surface (nor on metascutum). Two small, but prominent chambers at base of wing (Figs 37, 42); one, predominantly in the
ventral plane, is a distension of base of Sc, the other, predominantly in the dorsal plane, a distension of Cu. Prominent ventral fold expands from Sc on underside (Figs 39, 40). Scale-enclosed pocket present at very base of underside of wing (Figs 40, 41). **Hindwing** rounded: in males often with folded area (of glassy appearance) present (Figs 10, 16, 44, 47); basally usually with associated sclerotized protuberances (Figs 44–47, 50) and specialized scales (Figs 48, 49); base of costa weakly or, when frenulum is reduced, strongly expanded into a 'shoulder' (Fig. 35), composed of extended frenulum-plate and costal region.

**Base of fore wing** (Figs 37, 51). Second median plate with substantial part hidden under base of anal veins.

**Legs** (Figs 52–62). Microtrichia present on ventral surface at base of tarsi of mid leg and hind leg of male and all legs of female.

Fore leg. Epiphysis present (Figs 52–54); tibial spurs absent. Male: tarsus (Figs 52, 55, 57, 58) two-segmented, number reduced but tarsus not shortened; pretarsus reduced to pair of minute claws (Fig. 58), empodium and pulvilli absent; tarsi not spined, but hairy; occasionally with a scent brush. Female: tarsomeres not fused, tarsi five-segmented (Fig. 54); pretarsus not reduced, bears a pair of strongly curved claws (Fig. 59) that are weakly and asymmetrically forked; pulvilli present; tarsus spined ventrally, not hairy.

Mid leg: with one pair of tibial spurs; tarsomeres not fused; pretarsus not reduced, tarsal claws weakly forked; tarsus spined on ventral surface.

Hind leg: with one pair (Fig. 61) or occasionally two pairs (Fig. 62) of tibial spurs; tibia somewhat swollen; otherwise as mid leg.

**Abdomen.** Weakly to moderately curved (Fig. 63), flattened laterally not dorso-ventrally, and narrowing slightly towards base. Tympanal organs absent.

**Pregenital abdomen** (Figs 64, 65, 68). Segment I with narrow prespiracular bar and broad postspiracular bar (tergopleural). Tergum I with large membranous pouch and strong tergal braces. Sternum II with pair of mediolateral sclerotizations anteriorly; sternal apodemes reduced.

Figs 19–21  Larva and pupa of Hedylidae. 19, larva of *Macrosoma heliconiaria* (Guenée), × 3·5; 20, 21, pupal exuviae of (20) *M. lucivittata* (Walker), × 1·5; (21) *M. nigrimacula* (Warren), × 1·5.
Male postabdomen (Figs 66, 67). Tergum VIII longer than sternum VIII forming a short hood.

Female postabdomen. Segment VII in form of a short hood over the genitalia; tergum VII large; sternum VII shorter, usually bearing a series of prominent setae on fold just anterior to the ostium bursae (Fig. 90).

**Male genitalia** (Figs 69–80). Genital capsule is 'deep' dorso-ventrally owing to length of lateral arms of vinculum. Segment IX comprises a completely sclerotized ring, i.e. tergum and sternum fused. Tegumen narrow, sometimes prominently bilobed. Uncus large, usually triangular in ventral view since it narrows apically; alternatively apex is truncated or otherwise modified (Fig. 83). Vinculum: ventral plate narrow and produced into a prominent narrow saccus; rarely, saccus is rounded. Gnathos usually large and heavily sclerotized; occasionally lateral arms do not meet medially. Valvae (Figs 77–82) simple, undivided, usually approximately triangular. Diaphragm unsclerotized, or occasionally sclerotized as a juxta into a small simple plate or, rarely, a prominent U-shaped structure (Fig. 84). Aedeagus (Figs 85–89) a simple tube; vesica unmarked, or with weak sclerotizations.

**Female genitalia** (Figs 90–99). Tergum VIII a well-sclerotized band. Anal papillae usually in form of a pair of ear-like lobes. Anterior apophyses sometimes reduced (Figs 93, 96). Posterior apophyses developed normally. Bursa copulatrix: a narrow ductus leads into a globose or sub-globose corpus; signum absent or present; if present then of a characteristic shape (Figs 98, 99).

**Egg**

An egg, found while dissecting the female genitalia of a specimen, was oval.

**Larva**

Based on *M. heliconiaria* (comb. n.) (Fig. 19, and see Kendall, 1976), with further information on *M. nigrimacula* (Warren) (comb. n.) derived from larval exuviae housed in the British Museum (Natural History). When this study was at an advanced stage, Mr T. Fox (London Butterfly House) provided a colour transparency of a larva (subsequently reared through) of *M. cascaria* (Schaus) (comb. n.), which he collected in Monte Verde, Costa Rica.

**Head.** Head-capscus bears a pair of long horn-like processes, flattened and broad in *heliconiaria* (Fig. 100), not broad in *nigrimacula* (Fig. 101). (Tips of processes out of focus in transparency of *cascaria*.) Hypognathous. Mandibles toothed. Six ocelli present. Secondary setae present.

**Thorax and abdomen.** Not pigmented. Secondary setae on dorsum capitae in *heliconiaria*, shorter and trifurcate in *nigrimacula*; row of knobbed setae run along midline in *heliconiaria*, absent from *nigrimacula*. Scoli absent. Primary setae not on pinaculi. True legs well developed, each bearing a single claw. Prolegs present on abdominal segments III to VI, and on X (Fig. 19). Plantae of ventral prolegs with crochets biordinal and uniserial; arranged in two transverse bands in *heliconiaria* and in a penellipse in *nigrimacula*. Abdominal segment X: anal plate extended into a pair of furcae; anal comb present.

**Pupa** (Figs 20, 21)

Known for five species (*heliconiaria*, notes and illustrations by Kendall (1976), and personal examination; *tipulata*, exuvial remains; *M. lucivittata* (Walker) (comb. n.), *nigrimacula*, and *cascaria* (well-preserved pupal exuviae).

The pupa is rather flattened, although raised protuberances arise from the thorax of *heliconiaria*, *lucivittata*, and *nigrimacula*, and from the abdomen of *lucivittata*, *nigrimacula*, and *cascaria*.

The pupa of all five species is attached to the substrate by a fine silk girdle around the thorax, and by a well-developed cremaster. There is no cocoon. The temporal cleavage line appears to be absent, although there is a very slight indication of a line running transversely across the top of the head. In each case (except for *heliconiaria* where a specimen was stored in alcohol) the pupa was attached to a leaf. However, as far as I know, pupation occurred in captivity in all specimens available so whether or not hetylid pupae are always attached to leaves in the wild requires confirmation.

**Host-plant**

Known only for *heliconiaria*: *Buetneria aculiata* Jacq., (Sterculiaceae). Recorded by Kendall (1976).

**Habits**

The following comments, on *heliconiaria*, are based on Kendall (1976), who has provided what appears to be the only published information. The eggs are laid singly on top of leaves of *Buetneria aculiata*. The larva eats a series of small holes in the leaf. At rest it lies along the midrib. Kendall notes that the adults of *heliconiaria* are diurnal, as opposed to nocturnal, which may be exceptional for hetylids. Similar observations were made for the larva of *cascaria* collected by T. Fox from Costa Rica (pers. comm.). The specimen was found lying along the midrib on the upper surface of the leaf. The leaf of the food-plant (unidentified) to which the pupal exuviae is attached is largely consumed. From what remains it is clear that the larva had eaten several holes in the leaf.
Parasites
*Mirax* sp. and *Apanteles* sp. (Braconidae), identified by P. M. Marsh, USDA, Washington D.C., have been reared from *heliconiaria* larvae (R. O. Kendall, pers. comm.).

Distribution
Found in Central and South America: recorded from Paraguay, Brazil, Bolivia, Peru, Ecuador, Colombia, Venezuela, Guyana, Surinam, French Guiana, Panama, Costa Rica, Honduras, Guatemala, British Honduras, Mexico, Cuba, and Trinidad.

Specimens have been collected mostly from montane rain forest, occurring in many localities in the Andes. Material has been collected at localities up to 7000 ft.

Comments on selected structures

Adult
In this section further detail is provided about structures selected for their biological or systematic interest. Emphasis has been placed on comparing the Hedylidae with other macrolepidopterans, and in particular the Rhopalocera. I include as macrolepidopterans the following taxa: Castnioidae, Hesperioidea, Papi- lioidea, Geometroidea (sensu Common, 1970), Callidulioidea, Bombycoidea (including Sphingidae and Saturniidae), and Noctuoidea. (Geometroidea is used as a term of convenience in this work. Minet (1983) argued that the superfamily is not monophyletic.)

*Head.* The compound eyes are large and constitute a relatively large portion of the total area of the head (Figs 22–24). There is some variation in size between species. The inner, dorsal angle of each eye is weakly emarginate where it meets the base of the antenna (Fig. 22). Eye-size is of little value in assessing phylogenetic relationships of higher taxa since it is related to habits. Large eyes tend to be associated with high light intensity. However, the large eyes of most true butterflies, a group that is typically diurnal, ‘are specialized for high visual acuity at the expense of relatively poor absolute sensitivity’. The reverse is apparently true of moths (Bernard, quoted in Ferguson, 1985). Most hedylids are apparently nocturnal; on independent occasions, specimens have been collected at light by A. Watson, M. J. Matthews, and V. O. Becker (pers. comm.), and by the late C. L. Collenette (label data). However, *heliconiaria* is said to be diurnal by Kendall (1976).

Figs 22, 23  Head of *Macrosoma tipulata* Hübner. 22, anterior aspect; 23, lateral aspect.

The narrow frons bulges moderately (Fig. 23), but not to the degree found for example in the Heliothinae (Noctuidae). The narrowness of the frons means that the bases of the antennae are close together (Fig. 22). The antennae are usually filiform (Figs 26, 27), but in some species they are bipectinate (Fig. 25). In those with filiform antennae, the flagellar segments are rectangular, sometimes almost square, and each bears various sensilla. Usually the sensilla are long and arranged approximately in the shape of a ‘U’ on each side of the segments. They are shorter in females. In *tipulata* the segments are uniformly covered with shorter sensilla (Fig. 27). The more distal flagellar segments bear two or three longer setae, and also a sensillum basiconicum.
Bipectinate antennae are found in both sexes of *Macrosoma (= Hedyle) heliconiaria*, and its close relatives *M. semiermis* (Prout) (comb. n.), *M. inermis* (Prout) (comb. n.), and *M. albipannosa* (Prout) (comb. n.), and in males of *Macrosoma (= Venodes) napiaria* (comb. n.). In the females of *napiaria* each pectination is reduced to a small knob on each side of every flagellar segment (Fig. 28). In those species with bipectinate antennae each pectination bears sensilla. The sensilla in males are slightly longer than in females.
The antennae extend about one-half to just under two-thirds of the length of the fore wing. Whether filiform or bipectinate they bear lamellar scales dorsally.

Chaetosemata are present, one chaetosema behind each eye (Fig. 22). They are fairly small, but can be seen on dried specimens. Ocelli are absent. The presence of chaetosemata and the absence of ocelli are conditions found in Hesperioidea, Papilionoidea, and in many Geometroidea amongst macrolepidopterans. Chaetosemata are absent from the front of the head. According to Jordan (1923), most Hesperiidae have a pair of chaetosemata additional to those on the vertex, sited between the crest of scales on the frons and the antennae. This additional pair is absent from papilionoids.

Mouthparts. The maxillary palpi are minute (Figs 22, 23), a condition found generally in larger lepidopterans. The proboscis is well developed. Its base is not scaled, which contrasts with the typically scaled condition found in Pyralidae. The labial palpus (Fig. 29) is three-segmented. The palpi are generally moderately ascending (Fig. 24) as a result of curvature of the basal segment, but are not appressed to the head as they are in papilionids and pierids. The invaginated sensory pit of the terminal segment is a character of the lepidopteran ground plan (Kristensen, 1984b). In those hedylids examined for this character, the pit is deep, or moderately deep, and narrow.

Vestiture. Long narrow scales form the main covering of the frons and vertex (Fig. 24). These scales are neither closely appressed to the head, nor do they form a strongly erect tuft. The labial palpi are covered with scales; on the lower surfaces, particularly of the two proximal segments, they are long and narrow, forming a fringe (Fig. 24).

Thorax. To judge from the distribution of the sclerotized and membranous conditions of the patagia in true butterflies (Ehrlich, 1958b), the membranous condition must have arisen independently on several occasions. The sclerotized state is regarded as primitive. The development of membranous patagia has probably occurred independently in other macrolepidopterans, although the general condition (including that of hesperiids) is of sclerotized patagia. The loss of sclerotized patagia is given as a butterfly ‘trend’ by Ehrlich (1958b).

The size of the anepisternum of the mesothorax (Fig. 30) is not reduced, i.e., there is no pronounced dorsal movement of the anapleural cleft. A reduction is a prominent and specialized feature of Papilionoidea (Brock, 1971; figures of Ehrlich, 1958b). In Hesperiidae the reduction is not so pronounced. Scott (1985) states that it is very large in moths and skippers; however, it is not large in all skippers.

In the mesothorax, the precoxal sulcus of hedylids appears to be fused with the sulcus (Fig. 31) called ‘marginopleural’ by Shepard (1930) and Brock (1971). Usually these sulci are separate in the Lepidoptera. The precoxal sulcus does not curve towards the midline as it does in moths and skippers, and the basisternum is ‘open’ – not ‘closed’ by the sulcus. Brock (1971) drew attention to the divergent fused condition in papilionoids and noted that the primitive arrangement was retained in some Hesperiidae, but almost reached the specialized condition in advanced members of the group. Scott (1985) observed that in hesperiids, although the precoxal sulcus (his paracoaxal sulcus) might meet the ‘marginopleural’, it does not fuse with it as in papilionoids. These structures are difficult to interpret and need a broader survey to test their soundness.

There are two characters of particular importance in the metathoracic furca. In his study of the integumental anatomy of the Monarch butterfly, Danaus plexippus (L.), Ehrlich (1958a) noted that viewed dorsally the apophyses of the furca were shaped like an arrowhead. That this sagittate shape might be the general condition of both Hesperioidea and Papilionoidea was suggested by Brock (1971). (Brock treated the Hesperiidae as a family of the Papilionoidea.) In the Hedylidae the arrowhead is blunt, but nevertheless it is similar to that of other butterflies. The sagittate shape was not seen in the various macrolepidopterans examined by Brock. The shape is quite different in Oenoichromina (Guenée and O. polypipala Lower (Geometridae), and Josia fornas Druce (Diopitidae), which were examined during the course of this work.

The character of the metathoracic furca considered by Brock (1971) to be the most prominent and divergent for the butterflies was that which he referred to as ‘the peculiar mesal fusion of the dorsal laminae of the secondary arms from the point of their association with the apophyses to a point level with the thoraco-abdominal conjunctival insertion’. This character was also included as one of the shared derived (apomorphic) features of the Hesperioidea and Papilionoidea by Kristensen (1976). If I understand Brock’s description correctly, this mesal fusion is present in the Hedylidae. It can best be seen in dorsal view. Despite the weight given to this character by Brock (1971), the structure seems to be present in Oenoichromina (Geometridae: Oenoichrominae) and also in Archiearis Hübner, a member of the primitive geometrid subfamily Archiearinae.

Wing venation (Fig. 32a). The venation does not seem to vary between species either in the number of veins present, or their branching pattern and disposition. In the fore wing the arrangement of the veins of the radial sector (Rs) is characteristic of the family. The sinuous course run by Rs1 and Rs2 is such that they
nearly meet at one point. The only stalking that occurs is that formed by the common stem of Rs3 and Rs4. Veins R1, Rs1, and Rs2 are all separate (at least from the cell). These veins fail to coalesce at any point so, unlike many macrolepidopterans, no secondary cells are formed. This pattern is generalized, and approximates to that exhibited by the more primitive of the macrolepidopteran elements. Unlike several lineages of higher Lepidoptera, there is no inward migration ('splitting back') of veins. The arrangement of
Rs therefore provides few clues to relationships, although it further supports the exclusion of the group from advanced geometroids, calliduloids, bombycoids, and noctuoids.

Vein $M_1$ is remote from $R_s$, a condition widely encountered, unlike the arrangement found in Epiplemidae and Uraniidae where these branches are associated. The usual geometroid condition, and indeed that of most higher Ditrysia, is that $R_s$ and $R_s$ share a common stem, and $R_s$ arises from this joint stem nearer to the cell (i.e. proximally). A notable exception is the Papilionoidea where $R_s$ and $R_s$ are often associated as in hedylids. In the Hesperioidea there is no ‘stalking’ of the veins whatsoever; all run independently from the cell to the apex of the termen. Vein $M$ is very weakly, but definitely, visible in the cell.

$CuP$ is often present, but weak.

Hind wing venation (Fig. 32b). Vein $Sc+R_1$ is remote from $Rs$ from the base of the cell; the condition contrasts with that found in geometrids and drepanids, but is not dissimilar from Epiplemidae and Uraniidae. The presence of two anal veins in the hind wing is more frequently encountered in the butterflies (including Hesperiidae), bombycoids and noctuoids amongst the higher Ditrysia, than in geometroids (s.l.). The rather generalized occurrence of both these attributes therefore is of little value in assessing the relationships of *Macrosoma*. Nevertheless both features indicate yet further the remoteness of the genus from the Geometridae.

$M_2$ does not arise nearer $M_1$ than $M_3$.

Wing coupling (Figs 33-37). In males, a single-spined frenulum is usually well developed on the hind
wing (Fig. 33). It engages a long retinaculum on the fore wing (Figs 34, 37, 39). The length of the retinaculum is related to the need for it to extend over the prominent subcostal fold so as to engage the frenulum (Figs 37, 39). The frenulo-retinacular system is reduced and probably non-functional in the males of three species: *M. subornata* (Warren) (comb. n.), *M. leucoplethes* (Prout) (comb. n.), and *napiaria*. In the first two species the frenulum remains as a single spine, but it is much weaker and shorter. In *napiaria* it is reduced to a few short bristles (Fig. 35). The retinaculum of *napiaria* is lost, while in *subornata* and *leucoplethes* it is reduced to a very short, and presumably functionless structure. Although the frenulum and retinaculum are reduced in *subornata* and *leucoplethes*, the system is well developed in the closely related *M. desueta* (Prout) (comb. n.).

In females there are sometimes a few weak costal bristles on the hindwing (Fig. 36). There is no sign of a retinaculum, and functionally the frenulo-retinacular system is lost in this sex.

In Hesperioidea and Papilionoidea the frenulum and retinaculum are lost but remarkably, these structures are present in males of the hesperiid *Euschemon*. Scott (1985) notes that *Euschemon* is otherwise a typical pyrgine hesperiid and suggests an independent development of the frenulum and retinaculum through perhaps a reverse mutation. The loss of the frenulum and retinaculum or even of the retinaculum alone has occurred many times within the Lepidoptera besides the butterflies, e.g. in bombycoids, uraniids and some drepanids.

Wing surface. There is no holding area (*Haftfeld*) on the underside of the base of the fore wing and the metascutum of the thorax. These patches of velcro-like microtrichia (aculei) are absent from Hesperioidea, Papilionoidea, Geometroidea, and most Bombycoidea, a feature considered to be related to the resting position of the wings (Common, 1969; Kuijten, 1974). In general, those Lepidoptera with wings folded over the body have holding areas on the fore wings and thorax, whereas those with wings held vertically at rest or at right angles to the body do not.

Vestiture. Two kinds of scales predominate on the wing-surface (Fig. 38): (a) broad, ‘typical’, overlapping scales, and (b) hair-like scales. The wings appear to be hairy in parts. The broad scales do not provide a dense cover to the wings; hedyliids are relatively weakly scaled. In several species there are small hyaline patches devoid of scales, or larger areas with semi-transparent scales. The small hyaline patches may be seen with the naked eye on some specimens (Figs 10, 16). The hair-like scales are more dense on the basal section of the upperside, and somewhat more dense on the underside.

Figs 1–18 illustrates the main kinds of wing patterns in the Hedyliidae. Of particular note is that the markings on both dorsal and ventral surfaces are, with very minor exceptions, the same, compare Fig. 12 with Fig. 18. At least one hedylid may hold its wings vertically at rest so exposing the underside (R. O. Kendall, pers. comm.) although this requires confirmation. Such a resting position may be related to the strong patterning on the underside. In *M. subornata* the posterior half of the underside is pale and contrasts

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**Fig. 37** *Macrosoma hyacinthina* (Warren), base of fore wing, ventral aspect; anterior chamber (ac), posterior chamber (pc), subcostal fold (fd).
sharply with both the rest of the underside and with that of the upper surface. The habit of holding the wings vertically is common among butterflies, and is also to be seen in several geometrids. (I am grateful to Dr K. Sattler for suggesting the resting position of heidylids.)

There are several relatively distinct wing-patterns in heidylids, as well as other patterns that are less distinct. Frequently, elements of one subgroup are found in another. For example, large areas covered by semi-transparent scales are present in many species as are small, but distinctive, white triangular marks on the costa of the fore wing near the apex. In some species the apex of the fore wing bears a large patch of either chestnut or dark brown. The illustrations show the distinctive emargination of the apex of the forewing, a condition found in many species, and the weakly falcate shape of them all. The comments that follow are an adjunct to the black and white photographs to provide a guide to colour.

*M. heliconiaria* (Gueneé) (Fig. 1). Ground colour darkish grey-brown with translucent patches on fore and hind wings. The small triangular mark on the costa of the fore wing is white.

*M. hyacinthina* (Warren) (comb. n.) (Fig. 2). Ground colour dark grey-brown with a purple iridescence. More brown than grey at apex of fore wing. The pale patches on both wings are covered with semi-transparent scales except for the subtriangular mark on the costa of the fore wing, which is white.

*M. tipulata* Hübner (Fig. 3). A pale species. The wings bear large areas of semi-transparent scales. The darker areas are pale brown, and the small irregular patches on the fore wing are white, edged with darker brown.

*M. rubedinaria* (Walker) (comb. n.) (Fig. 4). Ground colour brown. The small dark streaks are dark brown, edged with white.

*M. ustrinaria* (Herrich-Schäffer) (comb. n.) (Fig. 5). A pale species. The darker scales scattered unevenly over the wing surfaces are pale brown.

*M. leucophasiata* (Thierry-Mieg) (comb. n.) (Fig. 6). The pale areas are white and the dark parts dark to very dark grey-brown.

*M. subornata* (Warren) (Fig. 7). Ground colour brown, dark brown near apices of wings. The patch on the costa is cream, and the patch below it and the tiny spot to one side are white. On the underside the posterior half of the fore wing is pale, contrasting markedly with the equivalent section of the upper surface.

*M. paularia* (Schaus) (comb. n.) (Fig. 8). Ground colour of fore wing pale grey-brown flecked and streaked with dark brown. The large spot at the apex of the fore wing is a warm pale brown. The large pale area on the hind wing is composed of semi-transparent scales.

*M. coscoja* (Dognin) (comb. n.) (Fig. 9). Ground colour pale brown. Apex of fore wing dark brown. The small patch at the base of the strong apical patch is composed of semi-transparent scales.

*M. satelliata* (Gueneé) (comb. n.) (Fig. 10). Ground colour a darker brown than that of *coscoja*. Otherwise similar to that species. The small ‘white’ spot at the base of the hind wing represents the glassy modification in males discussed below.

*M. albifascia albifascia* (Warren) (comb. n.) (Fig. 11). Ground colour grey-brown. The pale area on the fore wing is semi-transparent. The apex of the fore wing is a warm pale brown thickly edged with dark brown. The very dark streak and patches on the fore wing are also dark brown.

*M. hedylaria* (Warren) (comb. n.) (Figs 12, 18). The colour pattern is extremely similar to *heliconiaria*, although the apex of the fore wing is more brown than grey-brown. The name *hedylaria* is obviously a composite of *Hedyle* (the genus in which *heliconiaria* was described but which is treated as a junior synonym of *Macrosoma* in the present work) and *heliconiaria*.

*M. lucivittata* (Walker) ♂ (Fig. 13). Ground colour brown. The pale areas are covered with semi-transparent scales and many brown piliform scales. ♀ (Fig. 14). Similar to the male but with a distinct semi-transparent spot near the apex of the fore wing.

*M. nigrimacula* (Warren) (Fig. 15). Ground colour brown, flecked and spotted with dark brown. The semi-transparent areas are poorly defined on the upper surface in this species. On the underside of the fore wing the posterior half bears a large pale grey area that contrasts with the rest of the wing.

*M. leptosiata* (Felder) (comb. n.) (Fig. 16). Ground colour brown. Both fore and hind wing edged with darker brown distally, particularly on the fore wing.

*M. napiaria* (Gueneé) (Fig. 17). Ground colour off-white, formed by a covering of semi-transparent scales. The veins of the fore wing are a more strongly pigmented shade of cream.

Modification of the fore wings (Figs 37, 39–43). The base of the fore wing bears some apparently unique modifications. These take the form of a ventral expansion of vein Sc into a fold, and the presence of two small, rounded chambers developed within the bases of certain veins. A pocket is also present and is enclosed by a dense fringe of scales. These modifications occur within both males and females. In addition, a distinct lobe is formed near the anal edge of the fore wing in males of some species.
Figs 38–43  Fore wing structure (ventral aspects) of Hedyliidae. 38, vestiture of fore wing of Macrosoma tipulata Hübner; 39, base of fore wing of M. hyacinthina (Warren) to show subcostal fold (fd); 40, 41, scanning electron micrographs of base of fore wing of M. tipulata Hübner; (40) × 16, large arrow indicates pocket, small arrow shows base of retinaculum, (41) detail of pocket × 40,? tympanum (tm); 42, base of fore wing of M. hyacinthina (Warren), arrow indicates position of membrane (see text); 43, lobe at base of fore wing of M. hyacinthina (Warren).
The expansion of Sc on the underside of the fore wing is prominent (Figs 37, 39, 40). There is some variation in its extent between species, but the form is basically similar. This fold is a hollow outgrowth of the vein (although both membranes are close together and not ‘ballooned’). The fold extends a short way along the wing. At the extreme base of the fore wing, Sc is expanded into a hollow chamber (Figs 37, 42) the main part of which lies ventral to the plane of the wing. This chamber is divided from the fold by a membrane that runs at right angles to the plane of the wing. The position of this membrane is arrowed in Fig. 42; it is visible as a dark line in this view. The chamber is invaginated caudally effectively providing another pocket, which is enclosed by a thick fringe of hair-scales (Figs 40, 41). The posterior wall of the chamber is invaginated. From the ventral exterior lip of this invagination arises a thick fringe of hair-scales (Fig. 40 and particularly Fig. 41). Below this fringe, and presumably protected by it, is an extremely delicate, transparent membrane. This is supported by a cuticular frame at the base of Cu, also lying in the ventral plane of the wing. Stretched over the other (posterior) side of this frame is a whitish membrane, which closely resembles the tympanum found in the auditory organs of certain Lepidoptera (Fig. 41).

Lying mainly within the dorsal plane of the fore wing is another small, closed chamber (Figs 37, 42). This chamber is an expansion of the base of the cubitus, ‘Cu₂’ in the terminology of Sharplin (1963).

Figs 44–47 Scanning electron micrographs of specialized structures on hind wing (ventral aspects) of Hedylidae. 44–46, Macrosoma tipulata Hübner: (44) general view of area × 16, (45) detail of squat protuberance, × 140, (46) detail of finger-like protuberance, × 160; 47, M. zikani conferta (Warren) (comb. n.), base of hind wing × 16.
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Although the function of these chambers is unknown, there are several similarities with the tympanal organs found at the base of the fore wing in many nymphalid butterflies. The structure of these alar tympanal organs is summarized by Bourgogne (1951). In both hedylids and those nymphalids with these organs, the tympanum is situated at the base of vein Cu. Unlike thoracic or abdominal hearing organs, there is no tympanic cavity; instead, the tympanum is superficial. In nymphalids, the membrane is protected by scales, but in hedylids it is more exposed. In most of those nymphalids with alar hearing organs, veins Sc and Cu are swollen basally, and the tracheal air sacs within the swellings communicate with the tympanic sac (Bourgogne, 1951). It is uncertain whether there is a functional relationship between the sacs, but it should be noted that not all nymphalids with hearing organs have swollen veins. In the Hedylidae the veins are not swollen.

It is well known that some butterflies respond to sound. Swihart (1967) demonstrated the sensitivity to
sound of a small chamber at the base of each hind wing of *Heliconius erato* (L.). He also found a similar, but smaller, chamber at the base of each fore wing.

No information is available on the question of whether hedylids respond to sound, but on circumstantial evidence it seems likely that the modifications at the base of the fore wing function as an auditory organ.

The possibility that the chamber enclosed by the fringe of hairs is a scent pouch cannot be discounted, but the pocket is present in both males and females. The presence of 'scent pockets' tends to be sexually dimorphic in lepidopterans, but is not always so.

A small lobe extends from the anal edge of the fore wing near its base in the males of some species. It is prominent in *hyacinthina* (Fig. 43). A very weakly developed expansion of this area is found in many species.

Modifications of the hind wing (males). These are present in many species. Viewed with the naked eye they appear as small, oval, glassy areas at the base of the wing on both the upper and the under sides (Figs 10, 16). The modifications take the form of a folding of the wing membrane, making the surface appear rather crinkled or distorted when viewed under a dissecting microscope. Their appearance under the scanning electron microscope is shown in Figs 44 and 47. From this area one or more protuberances arise on the under side of the wing (Figs 44–47, 50). The area is covered with specialized scales.

In *hyacinthina* the modified area may be roughly divided into an inner, approximately oval section, which bears short piliform scales on both surfaces, and an outer section with both piliform scales and semi-transparent laminar scales. A prominent knob-like structure is present on the underside.

The modifications of the hind wing are well developed in many other species, and less pronounced in several more. Modifications present in one species may be absent from closely related ones. In *M. bahiata* (Felder) (comb. n.) for example they are present, while in *coscoja*, a close relative, they are not. In the same group of species the structures are less strongly pronounced in *M. albistria* (Prout) (comb. n.) and *M. uniformis* (Warren). In *tipulata* two protuberances are present (Fig. 44) of which one is relatively squat (Fig. 45), and the other is a long digitate structure, which is slightly swollen apically (Fig. 46). The function of these protuberances is uncertain, but since they are confined to the males they are probably scent organs of some kind. Figs 48 and 49 illustrate the specialized scales found on the surface of the structure in *tipulata*. The longitudinal ridges are strongly serrated (Fig. 49).

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Wing base. According to Dr R. de Jong (pers. comm. and in prep.), to whom I am indebted for sketches and information, the second median plate of the fore wing is always partly hidden under the base of vein 1A in both Hesperioidea and Papilionoidea. The general ditrysian condition seems to be that the plate is not obscured by 1A. In the Hedylidae the second median plate is small and partly obscured by 1A (Fig. 51).

Legs. An epiphysis is present on the fore leg of both males and females (Figs 52–56). The presence of this structure is widespread among macrolepidopterans including the Hesperiidae (with a few exceptions) and Papilionidae, but it is lost in many Pieridae, Nymphalidae, Libytheidae, and Lycaenidae.

In males the fore tarsi are modified (Figs 55, 58). Although they are not reduced in length (in fact they are long or very long) the segments are mostly fused so that only a long proximal segment and a short distal segment are present. In *tipulata* the proximal segment is extremely long (Fig. 55).

The pretarsus of the fore leg is reduced to a pair of small claws in males (Figs 52, 58). In some species these claws are minute, and in all species they are only very weakly curved. There is no aorilium, or empodium, nor are there pulvilli on the fore tarsi of males. The fore tarsi bear a prominent fringe of piliform scales giving them a feathery appearance. There are no spines.

In females the fore tarsi are not modified (e.g. *tipulata*, Fig. 56). There are five tarsomeres and the pretarsus bears claws that are strongly curved and asymmetrically forked, pulvilli, and a large aorilium. The tarsomeres are covered with laminar, not piliform, scales, and a series of small spines is present.

The mid and hind tarsi in both males and females are five-segmented, spined, and with a normally developed pretarsus with claws, pulvilli and an aorilium. The mid leg is generally longer than the hind leg, but shorter than the fore leg.

Microtrichia or aculei (‘tiny spines’ of Scott, 1985) are not present on the dorsal aspect of the tarsi, unlike the Papilionidae, Pieridae, some Nymphalidae and some Lycaenidae. According to Scott they are absent from hesperiids and from other macrolepidopterans. Microtrichia are, however, present on the ventral aspect of the tarsi of Hedylidae although their distribution is patchy, being best developed on the pulvilli. They are absent from the fore tarsi of males. Ventral microtrichia are probably widespread in Lepidoptera.

A single pair of tibial spurs is present on the midleg of both sexes (Fig. 61). The hind leg of the male of *tipulata* bears two pairs of tibial spurs (Fig. 62), but usually hedyliids (including the female of *tipulata*) have one pair distally on the hind tibia. The proximal pair of spurs is found in many Lepidoptera, e.g. some Thyrididae, some Hesperiidae, some Drepanidae, many Bombycoidea (including Sphingidae), and many Noctuoidea (including Notodontidae). This loss is a classic example of a character that is prone to independent reduction in many groups. Therefore the loss of spurs in most hedyliids and in papilionoids does not provide strong evidence for their monophyly. In one female specimen of *hyacinthina* there is apparently no pretarsus at all on the hind leg: the tarsus ends in a flask-shaped tarsomere (Fig. 60). There is no sign of claws arising from this last tarsomere. Of the two other females in the collection of the British Museum (Natural History), one has lost both hind legs while in the other the tarsi, including the pretarsus, are normal. In many species the hind tibia is slightly swollen.

A scent pencil occurs on the fore tibia of males of five species (*hyacinthina*, *lucivittata*, *M. klagesi* (Prout) (*comb. n.*), and *nigrimacula*, and probably (only one specimen available) on *M. latiplex* (Dognin) (*comb. n.*). The pencil comprises a bunch of long hairs arising from the inner surface of the tibia. It is particularly well developed in *hedylaria*.

The modifications of the legs of the Hedylidae are all found within other butterflies. Information for Hesperioidea and Papilionoidea is summarized in a useful table by Scott (1985: table 1). Pulvilli and the aorilium are lost from the legs of Papilionidae, some Pieridae, and some Nymphalidae. In the Papilionidae and the Pieridae the tarsomeres are not fused. In Nymphalidae the male fore legs are small although the tarsomeres are not lost or fused. In Lycaenidae the male fore legs are reduced to a single tarsomere together with reduction or loss of claws. The proximal pair of tibial spurs on the hind leg is absent from all true butterflies (Ehrlich, 1958b; Scott, 1985) and hedyliids (with the exception of the male of *tipulata*), but these spurs are present in skippers. Scent brushes, when present, tend to be found on the hind legs of butterflies; they occur on the fore legs of Hedylidae.

Abdomen. The abdomen is distinctly curved, particularly in males (Fig. 63), and is laterally flattened. Not only are these features butterfly-like, but from my initial observations they resemble true butterflies (Papilionoidea) rather than skippers (Hesperioidea). This interpretation, however, remains tentative.

Tergum I is ‘pouched’ (Figs 64, 68), that is, there is a pocket-like outgrowth of tergum I posteriorly that overlaps tergum II. Ehrlich (1958b) used the word ‘pouched’ to describe the typical papilionoid condition. The pouching in hesperiids is not strong, and in some papilionids the pouch is reduced (Ehrlich, 1958b).

On segment I there are pre- and postspiracular bars. The prespiracular bar (Figs 64, 68) is a narrow sternopleural structure, which extends anteriorly from the antero-lateral margin of sternum II, and curves around the spiracle. The presence of a prespiracular bar is the general condition in macrolepidopterans, including hesperioids and papilionoids, although it is lost in pierids (Ehrlich, 1958b). The presence of this
structure in the Hedylidae is therefore of no particular phylogenetic significance. Brock (1971) considers that both pre- and postspiracular bars are secondarily developed within the Papilionoidea and Hesperioidea (his Papilionoidea) and analogous to similar structures in certain Pyraloidea, Geometroidea and Noctuoidea. It is not entirely clear why Brock does not consider them homologous.

The postspiracular bar is well-developed in the Hedylidae. It is a tergopleural structure (Figs 64, 68), which just fails to meet the sternum. According to Brock (1971) the postspiracular bar is derived from terga I and II. Ehrlich (1958b) considered the presence of a postspiracular bar to be specialized within the Papilionoidea, where he presumably considers it to have evolved independently within the group. Scott (1985) records the bar as absent in Papilionidae (Ehrlich said it was reduced or absent), present or absent in Nymphalidae, present and large in Libytheidae, and absent in Lycaenidae. He notes its presence in or absence from Hesperioidea and its absence from other macrolepidopterans. Both Ehrlich and Scott consider the structure as derived. The occurrence of a similar structure in some other macrolepidopterans

Figs 59–62 Legs of Hedylidae. 59, pretarsus of *Macrosoma tipulata* Hübner, ♀, showing weak fork of claw; 60, last (5th) tarsal segment of hind leg of *M. hyacinthina* (Warren), ♀; 61, 62, hind tibia of (61) *M. hedylaria* (Warren), ♂, (62) *M. tipulata* Hübner, ♂.
Figs 63–67 Abdomen of Hedylidae. 63, 64, Macrosoma bahiata (Felder), lateral aspect: (63) whole abdomen, (64) base of abdomen, small arrow – pre spiracular sclerotization, large arrow – post spiracular sclerotization; 65, sternum II (st II) of M. pualaria (Schaus); 66, segment VIII of M. semiermis (Prout), ♂, lateral aspect; 67, tergum VIII (tg VIII) of M. tipulata Hübner, ♂.

(e.g. Thyrididae) noted by Brock is probably too isolated to suggest that the structure in the butterflies is not derived.

The tergal groove is well developed and leads into a strong tergal brace – the internal ridge of the groove (Fig. 64).

There are no abdominal tympanal organs in the Hedylidae.

Male genitalia (Figs 69–89). The lateral arms of the vinculum are long, so the genital capsule appears 'deep', that is, expanded dorso-ventrally. The natural way to mount these structures for microscopic slide preparation is laterally, since if they are mounted ventrally they tend to topple over on the slide. Most
butterfly systematists mount male genitalia laterally for the same reason. The genitalia of the Hedylidae are similar to those of many butterflies in the shape of the genital capsule. They might be regarded as fairly generalized butterfly genitalia, but this does not provide strong evidence for the monophyly of hedylids and other butterflies since the arrangement might be primitive. Certainly the Castniidae also have genitalia that are 'deep'. The lateral arms are fused with the tegumen so that segment IX of the abdomen forms a closed ring (e.g. Figs 73, 74), a feature noted as a tentative ground plan character of the Amphiesmenoptera (Kristensen & Nielsen, 1979: 126; Kristensen, 1984b: 150). The condition frequently encountered in the Lepidoptera is that of a distinct separation of the tergum and sternum of segment IX.

The valva is approximately triangular, and unmodified. This condition is found in many species of macrolepidopterans including many butterflies.

There are no particularly striking modifications of the main components of the genitalia. The greatest
Modifications are the shapes of the uncus in *heliconiaria* (Fig. 83), the valva (Fig. 79) and juxta (Fig. 84) of *hyacinthina*, and the simplification of the genitalia of *tipulata* (Fig. 72).

Female postabdomen and genitalia (Figs 90–99). Tergum VII is longer than tergum VI and forms a weak hood over the genitalia, when they are not extended. Tergum VIII is well-sclerotized and narrow (Fig. 90), and gives rise to a pair of thin, anterior apophyses. In most species examined these are sclerotized, but in some they are membranous (staining in Chlorazol black E), and short (Figs 93, 96). Presumably, in those species with reduced apophyses the muscles are functionless during oviposition. In *hyacinthina* and
Figs 77–84 Male genitalia of Hedyliidae. 77–82, valvae of (77) *Macrosoma heliconiaria* (Guenée), (78) *M. semiermis* (Prout), (79) *M. hyacinthina* (Warren), (80) *M. lamellifera* (Prout) (comb. n.), (81) *M. nigrimacula* (Warren), (82) *M. napiaria* (Guenée); 83, uncus of *M. heliconiaria* (Guenée), ventral view; 84, juxta of *M. hyacinthina* (Warren), valvae at different plane of focus.
Figs 85–89 Male genitalia, aedeagus, of Hedyliidae. 85, *Macrosoma heliconiaria* (Guenée); 86, *M. hyacinthina* (Warren); 89, *M. napiaria* (Guenée).

*hedylaria* the reduced anterior apophyses are usually bent inwards (medially) at their ends at about right angles. Reduced anterior apophyses are found in many butterflies.

Terga IX and X form a sclerotized band more narrow than tergum VIII. The posterior apophyses, which are derived from this, are sclerotized rods.

Ventrally, sternum VII is folded before the ostium bursae thus forming a lip to this aperture. The lip is nearly always fringed with strong setae (Fig. 90). The sclerotizations around the ostium bursae include anterior, posterior, and lateral components. The antevaginal and postvaginal sclerites are small, while the lateral sclerites (derived from sternum VIII) are large and extend laterally to unite with the anterior apophyses in those species where they are sclerotized. The extent of these ostial sclerotizations varies between species. In *heliconiaria* the lamella postvaginalis is absent as are the setae on the fold of sternum VII. In *tipulata* the sclerotizations are virtually absent (Fig. 97).
Figs 90–91 Female postabdomen and genitalia of Hedylidae. 90, *Macrosoma hedylaria* (Warren), abdominal sternum VII, ventral aspect, antrum (an); 91, *M. lucivittata* (Walker), lateral aspect.

Figs 92–95 Female genitalia of Hedylidae. 92–94, ventral aspect of (92) *Macrosoma rubedinaria* (Walker), (93) *M. hyacinthina* (Warren), anterior apophysis arrowed, (94) *M. rubedinaria* (Walker) to show well-sclerotized anterior apophyses; 95, *M. lucivittata* (Walker), lateral aspect.
The ostium bursae leads into the ductus bursae, the first part of which is funnel-shaped with sclerotized walls, the antrum (Fig. 94). Beyond this the ductus bursae is narrow, membranous, and usually long. It expands suddenly into a globose or slightly elongate-globose membranous corpus bursae (Fig. 91). The corpus bursae may bear a single signum of a characteristic shape (Figs 98, 99), or the signum may be absent.

The weakly telescoped ovipositor ends in a pair of large, soft, setose, ear-like lobes (Figs 92, 93).

**Juvenile stages**

The shape of the egg varies within the Lepidoptera, but it is essentially flat or upright (Chapman, 1896). Many butterflies have upright eggs. In the Hesperiidae, however, they are flat. The oval egg dissected from the macerated abdomen of a female hedylid appears to be of the flat variety, but its shape did not resemble that of the hesperiid egg. Since both flat and upright eggs are found within single families, or even single genera, (Hinton, 1981), the gross shape of the egg is of limited phylogenetic significance.

The larva (Fig. 19) exhibits features of various butterfly families rather than any one of them. Its horn-like processes (Figs 19, 100, 101) strongly resemble those of many Nymphalidae. The secondary setae on the body are like those of some pierids. The crochets on the ventral prolegs of the final instar, which are arranged in a penellipse or as transverse bands, are neither like those of hesperiids (in which they form a circle) nor like papilionoids (where, in post first instars, they are usually arranged in a mesoseries). An anal comb (found in Hedylidae) is usually present in Hesperiidae and at least some Pieridae among the macrolepidopterans.

The pupa (Figs 20, 21) resembles that found in Papilionidae (see Igarashi, 1984) or Pieridae, amongst the butterflies, in that it is attached to the substrate by both a girdle and a cremaster, and that there is no cocoon. A girdle is present in some sternhine geometrids, e.g. *Anisodes* Guenée (see Common, 1986) and *Cyclophora* Hübner. However, these genera lack the other butterfly characters discussed in the present
work. Furthermore, whereas the girdles of butterflies (including hedylids) are thoracic, those of sterrhine geometrids are spun around the abdomen (Holloway, pers. comm. – information derived from unpublished manuscripts housed in the British Museum (Natural History); and see Fig. 3 of Common, 1986 for an Anisodes girdle). The presence of a thoracic girdle is probably a ground plan character of the Rhopalocera, although weak cocoons are usually present in hesperiids. Loss of the cocoon is a typically papilionoid character, although it is present in Parnassius Latreille (Papilionidae) and weak and web-like in some satyrines. The girdle is present in Pieridae and Papilionidae, but is lost in Nymphalidae and many Lycaenidae.

A temporal cleavage line is said by Scott (1985) to be present in Hesperiidae, but absent from Papilionoidea. Mosher (1916) referred to the line as the epicranial suture. The apparent absence of the line in the Hedylidae is therefore like that of true butterflies rather than that of skippers. A temporal cleavage line is found in many moths. Mosher notes its presence in Lycaenidae, although Scott (1985: table 1) records it as absent from that family.

**Discussion**

The Hedylidae exhibit a high degree of structural uniformity. Several characters seem to be unique to the family, which provides evidence for its suspected monophyly. The most striking are the small chambers at the base of the fore wing, the protuberances on the underside of the hind wing, the sinuous course of veins $R_5$ and $R_6$ of the radial sector in the fore wing, and the long fore tarsi of the male composed of only two tarsomeres.

Two important questions about the phylogeny of the Hedylidae need to be discussed. First, are hedylids members of a taxon composed of Hesperioidea plus Papilionoidea plus themselves, i.e., are they butterflies in the broadest sense? Second, if so, what are the relationships of hedylids, hesperiids, and papilionoids to each other: do hedylids represent the sister group of the taxon Hesperioidea plus Papilionoidea (i.e. the Rhopalocera), or are they more closely related to the Hesperioidea or to the Papilionoidea than are either of these two related to each other? I shall argue that the Hedylidae are indeed ‘butterflies’ in the broadest sense. That they may represent the sister group of the Papilionoidea remains an intriguing possibility. This possibility is not a conclusion of this work: it would be premature and requires further comparison of the three taxa involved.
A separate, but related, problem is how to treat the nomenclature. Papilionoidea and Hesperioidea are widely used names, although Hesperioidea, consisting as it does of a single family, is redundant (Farris, 1976; Wiley, 1979), assuming that the Megathyminae are not viewed as an independent family. How should the Hedylidae be treated?

Although the butterflies are one of the best studied groups of organisms, the published evidence for their monophyly is certainly not overwhelming. Ehrlich (1958b) regarded hesperiids as papilionoids that retain a great many primitive characters. Both Ehrlich and Kristensen (1976) retained the two superfamilies and did not synonymize them, Ehrlich because he considered the phenetic distance between them sufficiently great, and Kristensen because he considered the sister-group relationship a reasonable working hypothesis but one that required confirmation. Although the consensus is that hesperiids and papilionoids do form a monophyletic group, the characters on which this argument is based are not entirely convincing.

Kristensen (1976) records six possible specialized characters (apomorphies) shared by the two taxa, two of which he considers doubtful. However, none of them have been examined in a great number of species of butterflies and moths. Until they are examined they must remain somewhat in doubt. A particular problem with these characters is that they are not observable on dried specimens. Some of the characters can only be seen on alcohol-preserved, or fixed material (e.g. the twist in the oblique lateral dorsal muscle of the mesothorax, and the structure of the aorta in the mesothorax). Those that can be observed on dried specimens require maceration of the head or thorax, and have been examined, inevitably, in a limited number of Lepidoptera. A detailed study of the relationships of the Hesperioidea and the Papilionoidea is being undertaken by Dr R. de Jong, who has found several specialized characters considered to support the sister-group relationship of the two taxa. If hedylids are the sister group of papilionoids then several of de Jong’s characters will have to be treated as homoplasious. It would be premature to treat the Hedylidae as the sister group of the Papilionoidea while de Jong’s detailed work is in progress. For this reason it has not been possible to make unequivocal statements about precisely which taxa some of the characters ‘define’.

Recently Scott (1985) has discussed the phylogeny of the butterflies. From his table 1, the characters that appear to support the monophyly of the papilionoids and hesperioids are: the presence of a postspiracular bar, found in skippers but not in Papilionidae, some Nymphalidae, and Lycaenidae, and the presence of a secondary sternopleural sulcus, variable in size, but present in all butterflies.

No other specialized features are tabulated by Scott as unique to the adults of all butterflies, with the possible exception of the absence of spurs on the tibia of the mid leg. However, although the spurs are absent from skippers, they are lost only in Papilionidae within the true butterflies so the condition is likely to be a parallel development.

Of the attributes of the Hedylidae described and discussed above, 13 are of particular significance in the discussion of the question of the relationship of the Hedylidae to the skippers and true butterflies. Of these several resemble the condition in true butterflies rather than skippers.

(1). Apophyses of metathoracic furca sagittate. The sagittate condition appears to be a specialized character of the three taxa. It certainly deserves examination in many more species to establish that it is definitely absent from moths and therefore diagnostic of butterflies.

(2). Pupa girdled. Ehrlich (1958b) and Scott (1985) regard a girdled pupa in butterflies as primitive and its absence as specialized. Scott considers this condition to have been present in the ancestor of hesperioids and papilionoids. There is no general survey of the occurrence of girdled pupae in the Lepidoptera, so to suggest that the condition is diagnostic of hedylids, hesperioids, and papilionoids needs to be treated with caution. This attribute derives its taxonomic strength in conjunction with others.

(3). Second median plate of fore wing lies partly under the base of vein 1A. Although this character requires examination in a wide range of Lepidoptera, it appears to support the view of the monophyly of the Hesperioidea plus the Papilionoidea (de Jong, pers. comm.) plus the Hedylidae.

(4). Presence of an anal comb in the larva. This structure, which is present in Hesperioidea


and Hedyliidae, seems to be confined to the Pieridae in the Papilionoidea. It may reasonably be assumed to be a ground plan character of the Papilionoidea. The presence of an anal comb in the Tortricidae is probably an independent development. However, if the Macrolepidoptera are not monophyletic then the closest relatives of the Rhopalocera may be found among the microlepidopterans. The tortricoid/cossoid assemblage might be a serious contender.

(5). Presence of a postspiracular bar on the first abdominal segment. Postspiracular sclerotizations are present on the first abdominal segment of non-ditrysin moths (see for example Kyrki, 1983; Kristensen, 1984a – lateral lobe of tergal I’ lo in his figure 2). That the presence of a secondary sclerotization (postspiracular bar) is a character of the ground plan of hedyliids, hesperioids, and papilionoids is a reasonable supposition. The presence of a postspiracular bar in certain Pyraloidea (those without tympanal organs), certain Geometroidea (Drepanidae, Thyatiridae, and most Uranidae), and Noctuoidea (many families) (Brock, 1971) must cast some doubt on the value of the structure as an indicator of the monophyly of hedyliids, hesperioids, and papilionoids. The postspiracular bar is recorded as absent from macrolepidopterans by Scott (1985: table 1), although he made no comment on the postspiracular sclerotizations in the macrolepidopteran families discussed by Brock (1971).

(6). Reduction of anterior apophyses in female genitalia. The weak, reduced anterior apophyses in some Hedyliidae is a condition found also in many butterflies (de Jong, pers. comm.). Whether this is a ground plan character of hedyliids, hesperioids, and papilionoids, or whether it is one that is subject to extensive parallelism is unknown.

(7). Abdomen curved, particularly in males. As noted above, the shape of the abdomen resembles that of the true butterflies rather than that found in skippers. This character is only doubtfully a unique derivation of Hedyliidae + Papilionoidea. A detailed study, preferably measuring the degree of curvature, is needed to ascertain whether the condition in Hedyliidae and Papilionoidea is greater than that found in Hesperiidae.

(8). Abdominal tergum I strongly ‘pouched’.

(9). Precoxal (paracoxal) sulcus joins ‘marginopleural’ sulcus. This character appears to be a specialization of the Hedylidae and the Papilionoidea. The main objections to this view are that the sulci are difficult to observe, and that they have been examined in relatively few species.

(10). Pupal cocoon lost. Unlike the condition in hesperioids, the cocoon of hedyliids and most papilionoids is lost. Loss of a cocoon occurs elsewhere in the Lepidoptera, so this character is of doubtful value and derives its strength in consideration with others.

(11). Loss of temporal cleavage line in pupa. The loss of this cleavage line in both hedyliids and papilionoids is further, although rather weak, evidence for their close relationship.

(12). Crochets of ventral prolegs of larva not forming a complete circle. This character is based on an examination of only two species. The penellipse of nigrimacula, and the transverse bands of heliconiaria are neither the typical circle of hesperiids nor the usual mesoseries of papilionoids. It is possible, considering other characters of the family, that the hedylid condition is part of a transformation series circle → penellipse → mesoseries, but this remains a tentative suggestion.

(13). Loss of pretarsus in the fore leg of males. Reduction or loss of the pretarsus is widespread in butterflies. A reduction of the pulvilli and arolium is the condition found in all legs of the most primitive papilionoids. The initial reduction, confined as it is to the fore legs of the male, appears to be the first stage of a reduction fully established in the papilionoids. Therefore either the character is a shared specialization of the Hedyliidae plus Papilionoidea or it has developed in parallel in the two groups. The possibility remains that the pretarsus is redeveloped (a reversal) in hesperiids.

Nomenclature
The Papilionoidea are generally regarded as a separate superfamly from the Hesperioidae, although Brock (1971) combined the two in Papilionoidea. In the present study I follow convention and retain both taxa as superfamilies since the relationships between the Hesperioidae and the Papilionoidea is being studied in detail by R. de Jong. Also, Kristensen (1976) noted some uncertainties about the sister group
relationship of the two groups, and recently Stallings et al. (1985, quoting C. L. Remington) made a similar point.

It would be premature to formally assign the Hedyliidae to the Papilionoidea at this stage, so to retain equivalence of rank they are treated as a superfamily (Hedylidea stat. n.). Consequently, the Rhopalocera now include three superfamilies Hesperioidea, Hedylidea, and Papilionoidea, all of interchangeable position (sedis mutabilis, Wiley, 1979).

Epilogue: a suggested phylogeny

Although this work concluded with the conservative suggestion that hedylids are rhopalocerans of which the precise relationships remain uncertain, the following dendrogram (Fig. 102) is a fully resolved three taxon statement presented to stimulate critical assessment.

![Dendrogram to suggest possible phylogenetic relationships of Hesperioidea, Hedylidea and Papilionoidea. Numbers represent the characters in the Discussion. Relative strengths and weaknesses of the characters are not indicated, but are considered in the text.](image)

Fig. 102  Dendrogram to suggest possible phylogenetic relationships of Hesperioidea, Hedylidea and Papilionoidea. Numbers represent the characters in the Discussion. Relative strengths and weaknesses of the characters are not indicated, but are considered in the text.

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British Museum (Natural History)

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