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# Systematics of Indo-Pacific fireflies with a redefinition of Australasian *Atyphella* Olliff, Madagascan *Photuroluciola* Pic, and description of seven new genera from the Luciolinae (Coleoptera: Lampyridae)

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## Abstract

This major systematic revision of fireflies (Coleoptera: Lampyridae) concentrates on the genera related to *Atyphella* Olliff in the Luciolinae. Seven new genera and 19 new species are described, which with two exceptions occur in the area encompassed by Australia, the Republic of Palau, Federated States of Micronesia, Papua New Guinea, Indonesia (West Irian), Solomon Islands, New Caledonia, Vanuatu and Fiji. Keys to the genera and subgenera of the Luciolinae are included. The revision is based upon a phylogenetic analysis of 343 morphological characters of males, females and larvae of 112 Luciolinae species, including the type species of the six genera and four subgenera of the Luciolinae *sensu* McDermott (1966). The genus *Atyphella* Olliff is redefined and redescribed from 23 species including 14 endemic Australian species, and nine species from the wider study area. *A. leucura* Olivier, *A. scabra* Olivier and *A. testaceolineata* Pic are redescribed. *A. palauensis* Wittmer is elevated to species level from *A. carolinae palauensis* Wittmer and redescribed. *Aquilonia* **gen. n.** is described for *Aq. costata* (Lea), transferred from *Atyphella* Olliff. *Convexa* **gen. n.** is described for *C. wolfi* (Olivier), transferred from *Atyphella*. *Gilvainsula* **gen. n.** includes the new species, *G. similismessoria* **sp. n.**, and *G. messoria* (Olivier), transferred from *Atyphella* Olliff. *Lloydiella* **gen. n.** includes four species; *Ll. majuscula* (Lea) transferred from *Atyphella*, and three new species, *Ll. japenensis* **sp. n.**, *Ll. uberia* **sp. n.**, and *Ll. wareo* **sp. n.** *Pygatyphella* (Ballantyne) is elevated to generic status from *Luciola* (*Pygatyphella*) Ballantyne and redescribed from 22 species including ten new species *Pygat. japenensis* **sp. n.**, *Pygat. karimui* **sp. n.**, *Pygat. kiunga* **sp. n.**, *Pygat. limbatifusca* **sp. n.**, *Pygat. nabiria* **sp. n.**, *Pygat. okapa* **sp. n.**, *Pygat. russellia* **sp. n.**, *Pygat. tomba* **sp. n.**, *Pygat. uberia* **sp. n.**, and *Pygat. wisselmerenia* **sp. n.**, with *uberia* representing specimens known in previous analyses as ‘Sisiak’. *Pygat. eliptaminensis* (Ballantyne), *Pygat. marginata* (Ballantyne), *Pygat. peculiaris* (Olivier) and *Pygat. pulcherrima* (Ballantyne) are transferred from *Luciola* (*Pygatyphella*) Ballantyne. *Pygat. tagensis* (Ballantyne), *Pygat. hounensis* (Ballantyne), *Pygat. obsoleta* (Olivier), and *Pygat. undulata* (Pic) are transferred from *Atyphella* Olliff; *Pygat. obsoleta* is reassessed, geographic varieties are suggested, and the species redescribed from a greatly expanded number of specimens. *Pygat. ignota* (Olivier), *Pygat. plagiata* (Blanchard) and *Pygat. salomonis* (Olivier) are transferred from *Luciola* Laporte and redescribed. *Pygat. limbatipennis* (Pic) is transferred from *Atyphella salomonis* var *limbatipennis* Pic, and redescribed. *Magnalata* **gen. n.** is described for three species, *M. rennellia* **sp. n.**, *M. limbata* (Blanchard) transferred from *Luciola*, and *M. carolinae* (Olivier) transferred from *Atyphella*. *Missimia* **gen. n.** is erected for a single species *M. flavida* **sp. n.** based on four specimens dealt with in previous phylogenetic analyses as ‘Mt Missim’. *Photuroluciola* Pic is elevated to generic status from *Luciola* (*Photuroluciola*) Pic and redescribed from its single species *Photuro. deplanata* Pic. *Asymmetricata* **gen. n.** is erected for two SE Asian species *As. ovalis* (Hope) and *As. circumdata* (Motsch.), both transferred from *Luciola* and redescribed. Where available, females are associated and are characterised briefly. *A. testaceolineata*, *M. limbata*, *Pygat. huonensis*, *Pygat. limbatipennis*, *Pygat. peculiaris*, and *Pygat. uberia* **sp. n.** are identified by light patterns. Discussion addresses: the interpretation of female aptery, the extent of the labrum, numbering of abdominal segments using actual segment number, and use of the term ventrite to reflect visible abdominal sternites. Functional morphology of many terminal abdomen modifications is addressed as is the range and nature of colour patterns. Determination of polarity in various states of bipartite light organs is overviewed, as are problems with the homology of characters, and difficulties in interpretation of characters in soft bodied insects especially those preserved in ethanol.

**Key words:** *Aquilonia* **gen. n.**, *Asymmetricata* **gen. n.**, *Convexa* **gen. n.**, *Gilvainsula* **gen. n.**, *Lloydiella* **gen. n.**, *Magnalata* **gen. n.**, *Missimia* **gen. n.**, *Pygatyphella* (Ballantyne), Australia, Republic of Palau, Federated States of Micronesia, Papua New Guinea, Indonesia, Solomon Islands, New Caledonia, Fiji, Vanuatu, taxonomy, new species, identification keys, morphological phylogenetic analysis

## Introduction

During the 1969–70 voyage to Papua New Guinea of the scientific vessel *Alpha Helix*, many Luciolinae fireflies were collected as part of behavioural studies and sent to Ballantyne for identification. The lack of an appropriate taxonomic framework (apart from Ballantyne & McLean, 1970 for *Pteroptyx* Olivier), led Ballantyne to refer to possible new species by code names in correspondence with the participants of the expedition. Lloyd (1973b) used some of those code names and indicated that the definitive taxonomy would follow. Some taxa were fully described including *Luciola aphrogeneia* (Ballantyne & Buck, 1979) and several *Pteroptyx* species (Ballantyne, 1987 a, b) (see Table 3). Six species of fireflies from the *Alpha Helix* identified by Ballantyne, including one new species, were placed within the *Atyphella* Olliff complex (Ballantyne & Lambkin 2000, 2001, 2006). While this study initially addressed the remaining taxa within the *Atyphella* complex from the *Alpha Helix*, other taxonomic issues that relate to *Atyphella* Olliff were found to require investigation, resulting in this major revision of the group.

*Atyphella*, erected by Olliff (1890) for several Australian species, was distinguished mainly by the largely concealed male head, a character, which apparently caused Olliff confusion, as he erroneously placed the genus in the Lampyrinae [See Ballantyne (2008) for a discussion of the nature of head coverage and its inappropriate use within the Luciolinae]. McDermott (1966) submerged *Atyphella* into *Luciola*, and Ballantyne's reassignment of *Atyphella* to generic status (in Calder, 1998), was based on eight Australian species without phylogenetic analysis. Ballantyne and Lambkin (2000, 2001) confirmed the status of *Atyphella* with phylogenetic analyses of the Luciolinae using 23 species of *Atyphella* (16 Australian and 7 New Guinean). Ballantyne and Lambkin (2006), using the same species but an extended range of characters, indicated a polyphyletic nature for *Atyphella*, and the need for further investigation. The analyses presented here address the status of *Atyphella*, including all species originally described as, or subsequently assigned to, *Atyphella*.

The status of *Luciola* (*Pygatyphella*) Ballantyne has been previously incompletely addressed. Ballantyne (1968) erected *Luciola* (*Pygatyphella*) for eight species of New Guinean fireflies, distinguished by a striking dorsal colour pattern, and unusual terminal abdominal structure. The name of this subgenus reflected both the perceived similarity to *Pygoluciola* Wittmer, and to *Atyphella* Olliff. Ballantyne and Lambkin (2000, 2001, 2006) assigned *L. (Pygat.) huonensis* Ballantyne, *L. (Pygat.) obsoleta* Olivier and *L. (Pygat.) undulata* Pic to *Atyphella*, but no formal actions were taken concerning the status of the subgenus *Pygatyphella* and the remaining five species therein. This study addresses the status of all the species originally assigned by Ballantyne (1968) to *Luciola* (*Pygatyphella*), and their placement is resolved.

Additionally, Ballantyne and Lambkin (2000, 2001, 2006) addressed two populations of New Guinean fireflies by code name only (viz. ‘Mt Missim’ and ‘Sisiak’), and their taxonomic placement is resolved herein.

*Atyphella obsoleta* (Olivier) may comprise a series of cryptic species that are capable of synchronous flashing. Lloyd (1972:163) described the mating behaviour of *Luciola obsoleta* as 'the most complex reported for any lampyrid'. He considered such complexity suggested the possibility of a complex of cryptic species. Ballantyne (1968) had described a range of colour variations within *obsoleta* and highlighted the distinctiveness of specimens from Wisselmeren, in the Kamo valley of Irian Jaya. This paper addresses the possible existence of cryptic species in *Atyphella obsoleta*. It thus includes certain species characterised first by their light patterns as well as more conventional means.

## Material and methods

The phylogenetic analysis of the Luciolinae is considerably expanded both in number of species addressed and breadth of characters scored (Tables 4, 5, Appendix 1). The analysis addresses 112 species and includes the type species of the six genera and four subgenera of the Luciolinae *sensu* McDermott (1966). Taxon sampling includes all the species scored in Ballantyne and Lambkin (2006), with many groups represented by considerably more species. We included representatives of all species groups Ballantyne recognised within *Luciola*, except for a *L. chinensis* L. and *L. cerata* Olivier group (Table 6).

*Atyphella* Olliff and *Pygoluciola* Wittmer are scored from all known species. All species assigned to *Luciola* (*Pygatyphella*) by Ballantyne (1968) are re-examined from a wide representation. An extensive character matrix (Table 1) includes 343 characters: 279 male, 33 female and 31 larval, fully described in Appendix 1. Types were examined where possible, and dissected where their condition was appropriate. This is clearly indicated in the text. Specimens for phylogenetic analysis additional to those used in Ballantyne and Lambkin (2000) are listed in Table 6.

With the increased number and breadth of the taxon sample the morphological terminology used in Ballantyne and Lambkin (2000) and phylogenetic characters in Ballantyne and Lambkin (2006) were considerably expanded to accommodate the variability encountered in this study. Most are explained beneath their listing (Appendix 1). Other important issues are more fully elaborated at the beginning of Appendix 1.

Specimens of genera and species other than those genera addressed here, or which have not been treated previously (Ballantyne & Lambkin 2000, 2001, 2006), are either scored from published work and/or individual specimens (specimens will be deposited as taxonomic vouchers in ANIC, or their museum of origin). Table 6 lists these with authority for identification. Some constitute new species in genera other than those under investigation here.

Females are now associated for several species. Ballantyne and Lambkin (2006) made tentative associations based on label data if only one species was known from a given area. Presently, however, association of sexes may be based on label data, morphology including colour patterns, or the most reliable method, mating pairs. The method of association is made clear in the text. If more than one morphologically distinct female occurred with a collection of males and could not be reliably associated, the specimens are listed but not described. Females are characterised at the generic level and briefly at the specific level. Many females are part of an investigation into the nature of bursa plates and it is anticipated certain features will be more accurately characterised there (Ballantyne work in progress).

Ballantyne (1987a) discussed the use of code names and Behaviour Vouchered specimens. Because the behavioural work of Lloyd (1972, 1973a, b) preceded the taxonomy many species for which a taxonomic framework did not exist were identified by code names and Table 3 summarises their use. All specimens of James Lloyd's collection from the 1969/70 expedition to Papua New Guinea are prefaced by "G". In this study G numbers have been retained on specimens, are quoted in the specimen examined listings, and many constitute Behaviour Vouchers. Orange labels in the Lloyd collection indicate the signals of the individual were electronically recorded in flight before actual capture, and such measurements were given in Lloyd (1973b).

Flashing data were extracted from Lloyd (1973b), his field records (deposited with his collection), or from correspondence on such records between Lloyd and Ballantyne (copy held by Ballantyne).

Dates are expressed as day of month (Arabic)/month (roman)/ year in full. Latitudes and longitudes are abbreviated e.g. 17.15S=17 degrees 15 minutes south. Localities in Papua New Guinea and the Solomon Islands are attributed to the appropriate Province.

Species are fully redescribed where no subsequent treatment other than the original description is available. Species redescribed more recently have an abbreviated treatment.

Most whole body pictures (dorsal and ventral) were taken with a Canon 30D 100 mm camera mounted on a tripod in natural light by Jenny Horsnell of CSU. Ballantyne used an Altra 20 camera mounted on an Olympus SZX12 stereomicroscope. Appendix 2 attributes pictures. Ballantyne drew all line figures.

Ballantyne is the sole author of all new taxa and provided all descriptions, photographs and diagrams in the taxonomic section. Lambkin undertook the phylogenetic analysis based on information provided by Ballantyne, wrote the phylogenetic methods, and interpreted phylogenetic relationships in the Luciolinae.

Abbreviations, taxonomic characters

| | |
|---|---|
| ASD | smallest distance between inner margins of antennal sockets |
| ASW | antennal socket width measured along the same horizontal line as for ASD |
| BP | basal piece aedeagus |
| FS | antennal flagellar segments |
| GHW | greatest head width (across eyes, measured parallel to ASD) |
| LL | lateral lobes, aedeagus |
| LO | light organ |
| MFC | metafemoral comb |
| ML | median lobe aedeagus |
| MN | mesonotal plates |
| MPP | median posterior projection ventrite 7 |
| MS | mesoscutellum |
| PLP | posterolateral projections posterior margin ventrite 7 |
| SIW | smallest interocular width (measured horizontally, may be on the same level as ASD, above it if the eyes are closer there) |
| T7, 8 etc | abdominal tergites |
| V6, 7 etc | abdominal ventrites, referred to by actual, not visible number |

Depositories

Holotypes are deposited in their museum of origin. Some paratypes are in Dr. Lloyd's collection (Lloyd) for ultimate distribution at his discretion. Material from the following collections was examined (curators in parentheses):

| | |
|---|---|
| AMS | Australian Museum, Sydney (M Moulds) |
| ANIC | Australian National Insect Collection, CSIRO Entomology, Canberra (T Weir) |
| BPBM | Bernice P Bishop Museum, Honolulu (A Ramsdale) |
| DAPM | Department of Agriculture, Port Moresby (in ANIC). |
| JS | J. Sedlacek collection, Brisbane, Australia (in Queensland Museum collection) |
| Lloyd | J E Lloyd collection, Gainesville Florida (J E Lloyd) |
| MCSN | Civic Museum Genoa (R. Poggi) |
| MNHN | Natural History Museum, Paris (J Menier) |
| MV | Museum of Victoria |
| NHML | Natural History Museum, London (M Barclay) |
| QM | Queensland Museum (G Monteith) |
| SAM | South Australian Museum, Adelaide |
| UQIC | University of Queensland, Brisbane |
| USNM | United States National Museum, Washington |

Specimen contributor abbreviations

WB=W Brandt; EF=E Ford; NK=N Krauss; COB=C W O'Brien; JS=Joe Sedlacek (JH, MS members of Sedlacek family); RS=R Straatman; PS=P Shanahan; JLG=J L Gressitt.

**Phylogenetic analysis**

Our earlier phylogenetic analyses of the Lampyridae (Ballantyne & Lambkin, 2000, 2001, 2006) are, in the present work, massively expanded to include 112 Luciolinae species, including the type species of the six genera and four subgenera of the Luciolinae *sensu* McDermott (1966). A full list of taxa is given in Table 1,

TABLE 1. Data matrix: 112 taxa, 343 characters; Polymorphisms shown below.

```
                           111111111122222222223333333333444444444455555555556666666666777
Taxon/Character   123456789012345678901234567890123456789012345678901234567890123456789012
------------------------------------------------------------------------------------------
Ph trivittata     000200000b0-0a0000ca011000001000000--00----4a000010a0001000000111100----
                      1
Phot deplanata    01020110210-1b0000-b000111001000000a-110-0010221001110010000000a001100-
L italica         000201100a0-0c0000d-01010110-200000-a110-004c111001110110000000-1011112
B hypocrita       0002111000a-0d0000-d00010110-000000--110-004-2110111211100000000-1010---
                                       1
L H parvula       000211100c030-0000b-000101001200000b-110-004-1110011101100000000-1011112
                                       1
Lamp syriaca      00020111--b10-0000-e00010110-100000-b110-004-1110011101110000000b1010---
L dejeani         000211100d0-0-0000-f01010110-300000--110-004d2210011101100000000-1011112
New Caledonia 1   000201100-040e0000a-000101001300000--110-004e11100102020-0000000-1110---
New Caledonia 2   0002111030-10-001a100101010013000000c-110-004-1110000212100000000c1110---
B antipoda        0003111030c10-001b1001010100130000000-d110-004-11100002121000000000-1010---
L leii            00010110105-b-001c0000010110-100000--110-004v121001110110000000v1011112
L ficta           00030110106va-0000e-00010110-100000e-110-004-12100111011000000000-1011112
L cruciata        00020110307105 0001-g02110110-200000--110-002000100011011000000000-1011112
L owadai          0002011030810-0001f-01110110-100000-e110-0010001000110111000000000-1011112
L substriata J    000201101---000000g-01110110-100100--110-004w2210001101100000000w1011112
L substriata F    000201101---000000-h01110110-100100f-110-004-22100011011000000000-1011112
L aquatilis       000201101---000000h-01110110-100100--110-004-22100011011000000000-1011112
L cowleyi         00000111-ed500001d0001110001130000-f111010102210010212 0-0000000d1010---
                     3
Pygo guigliae     1002112030-00-0001k-011101001100000--110-004-2210011100110010100e1011112
Pygo hamulata     1002112030g10h0001-k021101001100000-g110-004-2210011100110010100-1011112
Pygo kinabalua    1002112030f10-0001--021101001100000g-110-004-2210011100130010100-1011112
Pygo stylifer     1002112030-10g0001j-021101001100000--110-004f2210011100110010100-?011112
Pygo sartoi       1002112030h10-001f110111010011000 00--110-004g2210011100100010200-1011112
Pygo quingyu      0002112030-10-0001-j021101001100000--110-004-2210011101110000000-0011012
                                                                                     1
Pygo wittmeri     1002112030-10-0001m-021101001100000--110-004-2210011100120010100-1011112
Aquil costata     00001111--j-000000--011101000100000--110-00202210011101100000000k1011111
                     3                        1                           1
As circumdata     000221100-0-0j0000-n011101001000000-h110-00202210011101100000000-1011112
As ovalis         000221100-060-0000n-021101001000000j-110-00202210011101100000000-1011112
M limbata         000211100-0-0-00008s020101000000000m-110-00202210011101100000000f1011110
                      2
G messoria        000211100-070-00007-021101000000000--110-002022101111011100000000 91011110
G similismessoria 000211100-0-0t0000-u021101000000000-n110-0020221011110110000000 0-1011110
                      2
Missimia flavida  0002011030e10f001e121111010012000 00--110-004b011001100014 0021ab10100----
Ll majuscula      000211100-0-0-001-100111010010000 00-m110-0010221011110110000000 0-1011111
Ll uberia         000211100-080-0000-v021101001000000n-110-00202210111101100000000g1011111
Ll japenensis     0002111030-10m001h1102110100100000 0--110-00202210111101100000000-1011111
                                                                                       2
Ll wareo          000211100j0-0n001j110211010010000 00--110-00202210111101100000000-1011111
                          3
C wolfi           001221100-0-0k0000-t021101001000000--110-00202210111101100000000-1011111
                                                             4
A aphrogeneia     0002111000-10p00009c000101000001000--11111110221101110110 0000000-1010---
                          2                 1 11
A atra            000221100-0d0-0000--021100011000000-p1110102022100111020-1000000m1110---
A brevis          000221100k0-0u0000t-021100011000000--111010102210111102101000000-1?10---
M carolinae       000221100g0-0r0000--021101001000000-j110-00002210111102100000000-1011010
                                                                                       1
A conspicua       000221100-0e0-0000-x011100011000000q-11101020221001110111110000 0-1010---
                                                                        2
A dalmatia        0002211020-10-0001--021101001000000h-111010102210011101100000000-1010---
                          3
A ellioti         000221100-0-0-0000u-011100011000000--111010202210011102100000000-1?10---
A flammans        000221100m0-0-0000-902110001100000 0--1110102022101111020-00000008 1?11112
A flammulans      000221100-0-0-0000v-021100011000000-q1110102022101111020-1000000-1?11112
A guerini         000211100-0-0-0000s-021101001000000--110-00202210111101100000000-1011110
                      2
A immaculata      0002211010m10-001810011100011100000--111010102210011102100000000-1010---
                     3   13
A inconspicua     00001111---100001-000111000113000 00--1110102022100111021010 00000-1010---
                     3                                                    1
A kirakira        000221100-090-0000q-021101001000000--110-00202210111101100000000-1011011
A lamingtonia     000221100-0-0-0000-q021101001000000k-110-00002210111101100000000-1011112
A leucura         00022110090a0-0000p-021101001000000--110-004h2210111101100000000-1011112
A lewisi          000211100-0-0-0000-w011100011000000p-111010202210111102100000000-1110---
M rennellia       000221100h0-0q0000-r021100011000000-k110-000022100111011000000000h1011010
                                                             1
A lychnus         000221100-0f0v00006-011100011000003-1110100022101121021000000000n1110---
A monteithi       000221100n0-0-0000-y011100011000000r-1110101022101121021000000000-1010---
A olivieri        000221100-0-0-0000--021100011000000-311101010221011110110000000 0-1?11012
A palauensis      000221100-0-0-0000r-021101001000000--110-00202210111101100000000j1011110
                                                                                       1
A scabra          00022110080g0-0000--021100011000000--111000212210111102100000000071010---
A scintillans     000221100-0-0-0000w-011100011000000-411101000221001210210000000 0-1010---
A similis         0002111030k10-001910011100011000000--111010102210011102101000000-1010---
A testaceolineat  000221100-0b0-0000-p021101001000000--110-00102210111101100000000-1011112
Pyg plagiata      000221100-0-0-0100450211010010000 00-z110-004-2210111101100000000-1011112
Pyg.eliptaminensis000221100-1h0-101-100211010010000 00--110-00202210012101100000000-1011112
Pyg uberia 1      0002211030n10-001r11011101001000000--110-002022100111010-0000000-1011112
Pyg  huonensis    000221100-1-0-101m100211010010000 00-r110-00202210012101100000000-1011112
Pyg  ignota       00022110061-0-101610021101001000000t-110-00202210012101100000000p1011112
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TABLE 1 CONTINUED           111111111122222222223333333333444444444455555555556666666666777
Taxon/Character   123456789012345678901234567890123456789012345678901234567890123456789012
------------------------------------------------------------------------------------------
Pyg  japenensis   000221100-0k0-101-10021101001000000--110-0020221001110110000000q1011112
                           1
Pyg  karimui      000221100-0-0z101-10021101001000000u-110-00202210011101100000000-1011112
                           1        1
Pyg  kiunga       000221100-1-0y001n10021101001000000-s110-00202210012101100000000-1011112
                               1
Pyg limbatipennis 000221100-0-080100570111010010000009-110-004-2210111101100000000-1011112
Pyg  limbatifusca 000221100w0z090100-8011101001000000--110-004z22101111011000000000y1011112
Pyg  marginata    000221100-1j0-101-100211010010000004-110-00202210012101100000000-1011112
Pyg  nabiria      000221100q0-0-00151001110100100000-5110-00202210011101100000000-1011112
                           1   1
Pyg  obsoleta     000221100r0-0-00141102110100100000-u110-00202210011101100000000-1011112
                           1   1
Pyg  okapa        00022110050m0-101q11021101001000000--110-00202210011101100000000-1011112
                           1
Pyg  peculiaris   000221100-1-0x10171002110100100000s-110-00202210012101100000000-1011112
Pyg  pulcherrima  000221100-1-0-101p1002110100100000-t110-00202210012101100000000-1011112
Pyg  russellia    000221100v0x070100--021101001000000--110-004x22100111011000000000x1011112
Pyga salomonis    000221100x0y0-0100-6021101001000000--110-004y2210111101100000000-1011112
Pyg  tagensis     00022110071-0-101-10021101001000000--110-00202210012101100000000061011112
Pyg  tomba        000221100f0-0s001g10021101001000000--110-004p2210011101100000000-1011112
                           1
Pyg uberia 2     0002111030-10-001-11011101001000000v-110-002022100111010-0000000r1011112
Pyg  undulata     000221100p1-0w101-10021101001000000--110-00202210012101100000000-1011112
Pyg  wisselmeren  000221100-0-0-101-100211010010000005-110-002022100111011000000000051011112
L australis       00000111--p-w00000xz01110110-300000--110-004q22100111011100000000-001100-
                     3        1
L flavicollis     0000011104-nv0001-0001010110-300000--110-004r22100111011200000000-001100-
                     4   21
L nigra           000001110-q-u0001s0000010110-300000-v110-004-21100111011100000004001100-
                     4   21
L anthracina      00000111-----0001-0000010110-300000-6110-004-21100111011100000000-001100-
                     3
L pupilla         00010111as---1001-0000010110-300000w-110-004-21100111011100000000-001100-
L. foveicollis    00000111-----0001t0000010110-3000006-110-004-22100111011100000000-001100-
L orapallida      00000111--r-t0001-0000010110-300000-w110-004-21100111011000000000-001100-
                     4   2
Pt platygaster    00010111--z-f000100000010110-3000011111---04-221001110112000000002001100-
                     2        1
Pt cribellata     00000111b32-e000000000010110-3000010-11---04-21100111011300000000-001100-
                            1 1
Pt corusca        00000111--3-d1001-0000010110-300001071 1---04-21100111011300000000-001100-
Pt effulgens      00000111--4-c100130000010110-3000012-11---04-22100111011300000000-001100-
Pyro beccarii     00000111--s-s1001-0000010110-300000x-110-004-22100110011000000000-001110-
                     2
Pyro.appendiculata00000111c-t-r10000-200010110-300000--110-004s22100111011000000000-001110-
Pyro similis      00000111-2-pq10000y-00010110-3000007-110-004-221001110110000000000s001110-
Pyr.quadrimaculata00000111--u-p10000-400010110-300000-x110-004-22100111011000000000-001110-
Pt macdermotti    00100111d-v-n10000z-00010110-3000010-11---04-22100011011000000000-001100-
                     2
Pt gelasina       00000111-z-qm1001y0000010110-3000110-11---04-221001110111000000003001100-
Pt malaccae       00010111e-w-k1001-0000010110-3000010y11---04-22100110011000000000-001100-
Pt tener          00000111---rj0001z0000010110-3000011011---04-22100111011000000000-001100-
Pt truncata       00000111--x-h1001-0000010110-3000011111---04t22100011011000000000-001100-
Pt sp ML          000201100t01020012000001 0110-3000010-11---04-221001110110000000000t001??0-
Pt sp MFC         00000111f-y-g000002-00010110-3000008-110-004-22100101011000000000-001100-
Colo praeusta     000201100y0s03001-00000101101100000y-110-004-221001110112000000000z001100-
                                                                       3
Colo concolor     000201100-0-0-001u000001010011 00000-8110-004-22100111011300000000-001100-
Colo plagiata     000201100u0-0-001v000001010011 00000--110-004u22100111011200000000-001100-
C okinawanus      000011100-0t0000003-001101001310000z-1110103022100111011100000000u001100-
                     2   11
C costipennis     000311100-0u04001w000011011013 10000-9111010302210011101100000000-001100-
```

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                                             111111111111111111111111111111111111111111111
                  777777788888888889999999999000000000011111111112222222222333333333344444
Taxon/Character   345678901234567890123456789012345678901234567890123456789012345678901234
------------------------------------------------------------------------------------------
Ph trivittata     ---10000000001000000000000000000--a-000300ba4a234-a5-6zbcde23a09300a00
Phot deplanata    --2110000000000000000000010000000002-ca0005010060102a-000y000045b07900000
L italica         ---1100000000000000000000001000000000--d-0006010070000-b000200005630640000 0
B hypocrita       01-0100000000000000000000010000013a0-2-b501-2100-0000b-000-0000---0--0a000
L H parvula       ---0100000000000000000000010000000003-e-100-0100-0000--000-0000---0--00000
                                                              2  1
Lamp syriaca      01-1100000010000000000000001000000000---c200-0100-0001-c000-0000---0-600000
L dejeani         ---1100000000000000000000001000000000-3-d2007010080000c-000-0000--40--00000
New Caledonia 1   01-0100000000000000000000010000000004-f-100801009b000-d000200006--05-00000
New Caledonia 2   01-0100010000000000000000010000014b0---e61a-3100-c000--000-0000-7-0--0z000
B antipoda        01-0100000000000000000000010000000000-4--20091100-0000d-000-0000--50--00000
L leii            ---0100000000000000000000010000000000--x-100w1100w0000--000-0000x-w0--00000
L ficta           ---0100000000000000000000010000000000-x--100-1100-0000-e000p0000---0--00000
L cruciata        ---0100000000000000000000010000000000w--f100-0100-0000e-000-0000-v-0--00000
L owadai          ---0100000000000000000000010000000000xy--100-0100-0001--000-0000---0--00000
L substriata J    ---0100000000000000000000011100000010--y-000x0100x0000-9010q0000z--0-y00000
L substriata F    ---0100000000000000000000011100000010yz-g000-0100-0000f-010-0000-x-0--00000
L aquatilis       ---0100000000000000000000011100000010--z-000-0100-0000--010t0000--y0--00000
L cowleyi         01-0100000000000000000000010000000005---200q0000-0000-f000g0000--r0--00000
                                                          1 1
```

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TABLE 1 CONTINUED                            111111111111111111111111111111111111111111111
                  777777788888888889999999999000000000011111111112222222222333333333344444
Taxon/Character   345678901234567890123456789012345678901234567890123456789012345678901234
--------------------------------------------------------------------------------------------
Pygo guigliae     ---2100000000000000000111100000000--g-200-1100-0002--101-1000--60--00000
Pygo hamulata     ---11000000000000000000010000000007--k200-1100-0002-g101-1000-9-0-700000
Pygo kinabalua    ---2100000000000000000000100000000-6-j200-11010d002g-101-1000-8-0-500000
Pygo stylifer     ---1100000000000000000111100000000-5--200a1100a2002--101410007--04-00000
Pygo sartoi       ---1100000000000000000000100000000--h-200b1100b0002h-101-100100103-00100
Pygo quingyu      --11100000000000000000000100000000---h000-0100-00009-000-0000---0--00010
Pygo wittmeri     ---1100000000000000000000100000000-7--200-11011e002--101-10008-70--00000
Aquil costata     ---1100000000000000000000100000000--j-100c0100c0001-p000-0000a-802-00000
As circumdata     ---110000000000000000000010000000108--p100-0100-0000j---01-000-w-0--01000
As ovalis         ---0100000000000000000000100000002x0-8--1000y1110-001----01-000y-x0--1y000
M limbata         ---0100000000000000000000100000000-9-q100-0100-0000-m000-0000-d-0--00000
G messoria        ---1100000000000000000000100000000--n-100-0100g0000p-00050000g--0--00000
G similismessoria ---1100000000000000000000100000000-g-t100-0100-0000--000-0000j--0-k00000
Missimia flavida  ---21000001000000000000001000000006-b-20041100500022000-00003420820000
Ll majuscula      ---0100000000000000000000100000000--p-100-0100h0000n-000-0000h--0--00000
Ll uberia         ---01000000000000000000001000000009--r100-0100-0001-n000x0000--k0--00000
Ll japenensis     ---0100000000000000000000100000000-a--100-0100-0000--000-0000-h-0--00000
Ll wareo          ---0100000000000000000000100000000-b-s100-0100-0000-7000-0000-j-0--00000
C wolfi           ---0100000000000000000000100000000--m-100e0100-00008-000-0000--f0--00000
                                                            1
A aphrogeneia     00-0100000000000000000000100000000a--m100-0100-0000--00060000---0--00000
A atra            01-0100000000000000000000100000000h--y100-0100-0000--000-0000---0--00000
A brevis          01-0100000000000000000000100000000-j-z100-0100d0000--000-0000b--0--00000
M carolinae       --10100000000000000000000100000000-d-u100-0100-0000k-000w0000---0-e00000
A conspicua       01-0100000000000000000000100000000j--2100-0100-00006-000-0000--c0--00000
A dalmatia        01-0100000000000000000000100000000--q-100-0100j0000-h000-0000--m0--00000
                     1
A ellioti         01-0100010000000000000000100000000--k-100-0100-0000r-000-0000-b-0--00000
A flammans        ---0100000000000000000000100000000-k--100-0100-0000--00090000---0-b00000
A flammulans      ---0100000000000000000000100000000---3100d0100-0000-5000-0000--d0--00000
A guerini         ---0100000000000000000000100000000f--n100-0100-00007-000-0000-g-0--00000
A immaculata      01-0100000000000000000000100000000k---100-0100-0000-r000-0000---0-c00000
A inconspicua     00-0100000000000000000000100000000-h--100-0100-0000-6000-0000---0-a00000
A kirakira        --101000000000000000000001000002e0b--w1001d100-0000--000-0000-k-0--0d000
A lamingtonia     ---0100000000000000000000100000000e-r-100-0100-0000-k000-0000-m-0-n00000
A leucura         ---0100000000000000000000100000000c---100-0100-0000-j000-0000d--0--00000
A lewisi          01-0100000000000000000000100000??0g---200??100-0000--00080000-a-0-80b000
M rennellia       ---0100000000000000000000100000000-c--100j0100-0000m-000-0000k--0-m00000
A lychnus         01-0100000000000000000000100000000-m--100-0100-0000--000-0000c--0--00000
A monteithi       01-0100000000000000000000100000000m---100-0100e00005-000-0000---0-d00000
A olivieri        --10100000000000000000000100000000-f--000-0100-0000-q000-0000-c-0--00000
A palauensis      ---0100000000000000000000100000000-e--100g0100-0000-8000-0000--j0--00000
A scabra          01-01000000000000000000001000002d0n---2011c100-00004-000a0000---0-j0c000
                                                                 1
A scintillans     01-0100010000000000000000100000000---4100-0100-0000s-000-0000--e0--00000
A similis         01-0100000000000000000000100000000---x100-0100-0000q-000-0000--90--00000
A testaceolineat  ---0100000000000000000000100000000---v000-0100k0000--00070000m--0--00000
Pyg plagiata      ---0100000000000000000000100000001010-100-1100-0001--000r00011100--00001
Pyg.eliptaminensis---0100000000000000000000100000101010-200-1100-0001--000-0000-e-0--00001
Pyg uberia 1      ---01000000000000000000001000002f101071000e100-0002-v000f0100---0--0e001
Pyg  huonensis    ---0100000000000000000000100000001021-11100-1100-0001-s000b0000---0-f00001
Pyg  ignota       ---0100000000000000000000100000001010-100f1100-2001-t000-0000--g0--00001
Pyg  japenensis   ---0100000000000000000000100000001010-100-1100-0001--000-0000--p0--00001
Pyg  karimui      ---010000000000000000000010000000010106100-1100m2001-u000-00010100--00001
Pyg  kiunga       ---0100000000000000000000100000001021q10100h1100-0001t-000-0000---0--00001
Pyg limbatipennis ---0100000000000000000000100000001010-200z1100z2001-z000s00011100--00001
                                                              1  3
Pyg  limbatifusca ---010000000000000000000010000000010108200-1100-2001--000-00011100--00001
                                                              1  3
Pyg  marginata    ---010000000000000000000010000000010105100-0100-00013-000-0000-f-0--00001
Pyg  nabiria      ---0100000000000000000000100000001000-100-1100-2001-3000d0000---0-p00001
Pyg  obsoleta     ---0100000000000000000000100000001010-100n1100-0001--000e0000---0-q00001
                                                        2        1
Pyg  okapa        ---0100000000000000000000100000001010-100m1100-101122000-0000-n-0--00001
Pyg  peculiaris   ---0100000000000000000000100000001021p10100-1100-0001-4000v0000f--0-g00001
Pyg  pulcherrima  ---1100000000000000000000100000001010-100-1100-1000u-000c0000---0-h00001
Pyg  russellia    ---0100000000000000000000100000001010-200y1100y0001z-000-00011100-z00001
Pyga salomonis    ---0100000000000000000000100000001010-100-1100-2001--000-00011000--00001
                                                        2     1  3              1
Pyg  tagensis     ---0100000000000000000000100000001021-11100-1100f0000--000-0000--h0--00001
Pyg  tomba        ---0100000000000000000000100000001000-200k1100-0001--000-0000--n0--00001
                                                                 1
Pyg uberia 2     ---01000000000000000000001000002g1010-1000f100n0002--000-0100np-0--0f001
Pyg  undulata     ---0100000000000000000000100000001021n11100-1100-0001--100-1000e--0--00001
Pyg  wisselmeren  ---0100000000000000000000100000000-rs-100-0100-0000v-000-0000--q0--00000
L australis       --11100000000000000000000100000000--t-100p0100s0000w-000-0000p--0-r00000
L flavicollis     --11100000000000000000000100000000p---200r11000g000--000-0000---0--00000
                                                               1    1
L nigra           --11100000000000000000000100000000-s--200s110102000-w000-0000---0-s00000
                                                                    1
L anthracina      --11100000000000000000000100000000----100-0100-000111000-0000---0--00000
L pupilla         --11100000000000000000000100000000----100-0100-000112000-0000---0--00000
L. foveicollis    --11100000000000000000000100000000---9100-0100-000111000-0000---0--00000
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TABLE 1 CONTINUED

| Taxon/Character | 111111111111111111111111111111111111111111111<br>777777788888888889999999999900000000001111111111222222222233333333334444<br>345678901234567890123456789012345678901234567890123456789012345678901234 |
|---|---|
| L orapallida | --1110000000000000000000001000000000----200t0100t2000x-000-0000--s0--00000 |
| Pt platygaster | --1110000000000000000000001000110000--v-100u01010u00011000-0000--u0--00000 |
| Pt cribellata | --1110000000000000000000001001110000t---100-0100-v00011000k0000---0-v00000 |
| Pt corusca | --1110000000000000000000001001010000-w--100-11010w00011000-0000t--0--00000 |
| Pt effulgens | --1110000000000000000000001001010000----100-11010x00012000-0000-t-0-w00000 |
| | 1 |
| Pyro beccarii | ---11100000000111100110010000002h0----1000g1010h00012000-0000q--0--1g000 |
| Pyro.appendiculata | ---11100000000111100110010000002j0q---1000h1010j00012000-0000-q-0--1h000 |
| Pyro similis | ---11110010000111100110010000002k0----1000k1010k00012000h0000---0-t1k000 |
| Pyr.quadrimaculata | ---11100000000111100110010000002m0-t--1000m1010m00012000-0000---0--1m000 |
| Pt macdermotti | --121110010010100000000010011102n0--u-2002n1011n00102000-0000r--0--0n000 |
| Pt gelasina | --111100000010100000000010011102p0r---1000p1010p00002000u0000-r-0--0p000 |
| Pt malaccae | --111100000000100000100010011102-0-u--1000q1010q00011000-0000--t0--0q000 |
| | 1 |
| Pt tener | --111000000000100010000010011102q0----1000r1010r000-x000j0000---0-u0r000 |
| Pt truncata | --101000000000100010000010011102r0-v--1001s1010s00012000-0000---0--0s000 |
| Pt sp ML | --111000000000100000000010011102s0s---1000t1010t00010000-0000s--0--0t000 |
| Pt sp MFC | --111000000000100000000010011102t0----1000u100u000110000-0000-s-0--0u000 |
| Colo praeusta | --121001000000000000000010000002u0u---2000v1011y00121001-0010u-v1010v200 |
| | 2 |
| Colo concolor | --111001000000000000000010000002v0----1000w1011z00221001m0020---1100w300 |
| Colo plagiata | --121001000000000000000010000002w0z---1000x1011400221001-0010v--1010x200 |
| C okinawanus | --1110000000000000000000001000000000--w-200v1100v0000y-000n0000w--0-x00000 |
| C costipennis | --1110000000000000000000001000000000v---200-1100-0000-y000-0000-u-0--00000 |

| Taxon/Character | 1111111111111111111111111111111111111111111111111111111122222222222222222<br>444445555555555666666666677777777778888888888999999999900000000001111111<br>567890123456789012345678901234567890123456789012345678901234567890123456 |
|---|---|
| Ph trivittata | 0532000000a--0---0a--002304-6708100a00023000000000000a---0001000000010ab |
| Phot deplanata | 0453000000-a-0---0--a0034023-50610002200001100021-4-0--v-010000001002101 |
| L italica | 034-000000--a0---0b--00450-2340510002100001100001-5-0-a--000000000100-a |
| B hypocrita | 0--4000000---0a--0-b-005606-2304100021000011000001--40v---0000000?00100b- |
| L H parvula | 0--5000000---0-a-0--b00670-6-20310002100000000011-50--a-0000000100100-c |
| Lamp syriaca | 06--000000---0--a0---00580--8-02100?????0000000116-0-v-a0000000100110-- |
| L dejeani | 0-6-000000---0-b-0c--00890--7-091000211000??????????????????????????100c- |
| New Caledonia 1 | 0--6000000---0b--0-c-0092087-90-10002100001100001-7-0b--v0000000?00100-- |
| New Caledonia 2 | 07--000000--b0---0--c00--0789-0-10002100001100001---0-b--0000000?00100-- |
| B antipoda | 0---000000-b-0---0d--00--0-9-a0a10002100001100001--60w---0000000100100-d |
| L leii | 0--p000000b--0---0---00-u0v--w0-100n1000001101111---0--b-1000000000000-- |
| | 1 |
| L ficta | 0q--000000-c-0---0--x00u-0--w-0-100p1?00001100111---0---b000000000000d- |
| L cruciata | 0-q-000000--c0---0---00-v0-w--0x100q0fhyx01100001--20c---000000000000-- |
| L owadai | 0---000000---0c--0---00v-0w---0-100r0gjzy01100001---0-c--000000000000-e |
| L substriata J | 0-rs000000---0-c-0x--00w-0-x-y0z1001311001110021-r-1001--000000000100-- |
| L substriata F | 0rst000000---0--c0---00--0x-y-0-1001311001110021-s-1010c-000000000100-- |
| L aquatilis | 0stu000000---0--d0--y00-x0-y-z0-1001311001110021-t-1010---000000000100-- |
| L cowleyi | 0--m000000---0-d-0---00-t0--n-0-100031100000000101011-c0-001001000100e- |
| Pygo guigliae | 08--0000021-d0---0e--00ba0a-b-0b21003110000000010110--w--0002001000010-- |
| Pygo hamulata | 0---0000021--0---0-e-00--0-b-c0-210?????0????????????????????????0109- |
| Pygo kinabalua | 0--70000021--0---0--d00--0-a-b0-21003110000000010110--w-0002001000010f- |
| Pygo stylifer | 0-8-0000021d-0---0-d-00a-09-a-0-210??????1??????????????????????????010-f |
| Pygo sartoi | 09-80000021--0---0f--00c-0-c-d0c21003110000000101111-d0-002001001010-- |
| Pygo quingyu | 0---00000100011100---00--0-----0-10003110000000010111000--002001000110-- |
| Pygo wittmeri | 0---0000021--0d--0--e00-a0b-c-0-21003110010000010110d--w0002001000010-g |
| Aquil costata | 0---000000--e0---0-f-00d-0c-d-0-1000100000110000 1-8-0--d-0000000000000-- |
| | 11 |
| As circumdata | 0--q00001a---0--e0-x-00--0---x0y2a0031100000000311--11--1-000000000000-- |
| As ovalis | 0r--00001b---0-f-0---00-w0--x-0-2b0031100000000311--11--1-0000000000008- |
| M limbata | 0---000000---0f--0-n-00nh0-g--0j10002100001100001-f-0-d--000000000010-- |
| G messoria | 0---000000---0g--0---00--0-----0-10002200001100001-k-0f---000000000010k- |
| G similismessoria | 0---000000---0-g-0-r-00--0-5--0-10002200001100001--d0x---000000000010-- |
| Missimia flavida | 1000000000---0--g0-a-011003456071000420100110000 1-3-0--f-000000000000-- |
| Ll majuscula | 0--g000000-f-0---0---02100--j-0-10003110001100001-m-0e---000000000000-- |
| Ll uberia | 0--h000000f--0---0r--00--0j---0q10003110001100001---0-e--000000000000-- |
| Ll japenensis | 0g--000000-g-0---0--q00q-0-j--0-10003110001100001--c0--e-000000000000-j |
| Ll wareo | 0-h-000000--g0---0--r00-r0----0-10003110001100001f--0---e000000000000-- |
| C wolfi | 0--d000000--f0---0--n00-j0g---0-10003110001100001e-b0--x-000000000100j- |
| A aphrogeneia | 0a--000000e--0---0g-f00-c0-d--0-10002100001100001g--0-x--000000000110-- |
| A atra | 0--9000000---0-j-0-h-00f-0e---0e100??????01100001-9-0---f000000000110-m |
| A brevis | 0b--000000-k-0---0--h00g-0---f0-100??????01100001--g0-f--000000000110-- |
| M carolinae | 0--d000000---0h--0--m00-g0---g0-10002100001100001-e-0g---000000000010h- |
| A conspicua | 0-b-000000---0m--0j--00-e0--f-0-100??????01100001h--0---x000000000110-- |
| A dalmatia | 0h--000000-e-0---0---00--0---k0-10002100001100001---0-g--000000000110g- |
| A ellioti | 0--b000000k--0---0-j-00h-0-f--0f100??????01100001-a-0y---000000000010n- |
| A flammans | 0---000000-m-0---0--j00j-0f---0-100f1000001100001--h0--g-000000000010-- |
| A flammulans | 0---000000--m0---0k--0-f0----0-100g1000001100001-b-0---y000000000010-n |
| A guerini | 0---000000--0e--0---00-q0----0-10001000001100001---0---g000000000010-k |
| A immaculata | 0---000000---0--m0-k-00--0-----0g100h1000001100001---0h---000000000110-- |
| A inconspicua | 0---000000---0j--0h--00-d0-e--0-100e1000001100001j--0--y-000000000110-- |
| A kirakira | 0---000000-j-0---0---00--0-k--0-100-1000001100001---0-h--000000000110-- |
| A lamingtonia | 0--k000000---0-k-0-s-00s-0----0s10002100001100001-n-0----000000000110-- |
| A leucura | 0-d-000000h--0---0n--00--0--g-0-10001000001100001---0--h-000000000110-- |

| TABLE 1 CONTINUED | 1111111111111111111111111111111111111111111111111111111222222222222222222 |
|---|---|
| | 444445555555555666666666677777777778888888888999999999900000000001111111 |
| Taxon/Character | 567890123456789012345678901234567890123456789012345678901234567890123456 |
| A lewisi | 0-9-000000--k0---0-g-00--0d--e0d100??????01100001--f0-y--0000000000?10m- |
| M rennellia | 0---000000---0-h-0--s00r-0--k-0r10001000001100001k--0---h0000000000010-- |
| A lychnus | 0c--000000---0-m-0---00k-0--4-0-100j1000001100001-c-0j---000000000110-- |
| A monteithi | 0-c-000000---0-n-0--k00m-0----0-100??????01100001m--0-j--0000000000110-p |
| A olivieri | 0--c000000---0--j0m--00--0----0-100-1000001100001-d-0--j-0000000000010-- |
| A palauensis | 0f--000000---0-e-0q--00--0----0-10001000001100001---0---j0000000000010-- |
| A scabra | 0---000000--h0---0---00--0----0p100m00cbd01100001--e0z---1000000000110-q |
| A scintillans | 0---000000---0n--0-m-00--0----0h100k1000001100001--j0k---000000000110p- |
| A similis | 0---000000--j0---0--g00e-0--e-0-100d1000001100001---0-k--0000000000110-- |
| A testaceolineat | 0---000000---0k--0---00-s05---0-10002100001100001n--0--k-0000000000110-h |
| Pyg plagiata | 0uvw000000---0-r-0-y-00-y0-z--101000311010110001 1-v-0---k000000000010045 |
| Pyg.eliptaminensis | 0---000000---0p--0---02100--h-0-20003110001100001-h-0-z--0000000000110-- |
| Pyg uberia 1 | 0m--000000-r-0---0---00--112110-10003110001100021---0m---00100000001110 |
| Pyg huonensis | 0-e-000000--n0---0---03100-h--0-10003110001100001-g-0--z-0000000000010-- |
| Pyg ignota | 0--e000000---0-p-0p--00pn0----0-10003110001100001--m0-m--0000000000010-- |
| Pyg japenensis | 0---000000-q-0---0---02000----0-10003110001100001p--0---z000000000001110 |
| Pyg karimui | 0-m-000000---0q--0---01100--m-0-10003110001100001--n0--m-0000000000010s- |
| Pyg kiunga | 0g--000000--p0---0-q-01100---j0-10003110001100001---0----0000000000010-- |
| Pyg limbatipennis | 0wxy000000r--0---0z--00-z0----11100031101011000 11-x-0---m000000000010063 |
| Pyg limbatifusca | 0xyz000000-s-0---0-z-00z-0----11100031101011000 11-y-0----000000000010072 |
| Pyg marginata | 0--f000000---0--p0-p-00p-0----0-20003110001100001q--0n---0000000000000-r |
| Pyg nabiria | 0k--000000--q0---0t--02100---m0-20003110001100001---0----000000000001110 |
| Pyg obsoleta | 0---000000q--0---0-t-04100----0-20003110001100001-p-0-n--0000000000010-t |
| Pyg okapa | 1000000000---0-q-0--t01110-m--0-10003110001100001r--0----0000000000010-s |
| | 2 |
| Pyg peculiaris | 0e--000100n--0---0---01100---h0m20003110001100001--k0--n-000000000110-- |
| Pyg pulcherrima | 0-f-000000p--0---0--p04100h---0n1000311000?????????????????????????110r- |
| Pyg russellia | 0tuv000000---0r--0y--00x-0y-z-1110003110?0110001 1su-0---n000000000010036 |
| Pyga salomonis | 0vwz000000---0--r0--z00y-0z---11100031101011000 11-wq0----000000000010054 |
| Pyg tagensis | 0---000000-p-0---0---00-p0----0-1000311000?????????????????????????110-- |
| Pyg tomba | 0-k-000000-n-0---0s--01100k---0-10002100001100001---0p---0000000000010-8 |
| Pyg uberia 2 | 0---000000--r0---0---00--103120t10003110001100021--p0----00100000001110 |
| Pyg undulata | 0---0000020110---0---00-k0----0k10003110001100001t--0-p--0000000000010q- |
| Pyg wisselmeren | 0---000000---0--q0---00--0m---0-10003100001100001---0----0000000000010t- |
| L australis | 0---000000--s0---0-u-04100---n0u100021000100000011qr0--p-0001000000020-- |
| L flavicollis | 0n--000000---0s--0u--04100-n--0-100032000100000011a-0----0001000000020-u |
| L nigra | 0-n-000000---0-s-0--u04100n--p0-100032000100000011b-0---p0001000000020-- |
| L anthracina | 1110000000---0--s0---04100----0-100??????10000011c-0q---0001000000020u- |
| L pupilla | 1100000000s--0---0---04100----0-100022000100000011ds0----0001000000020-- |
| L. foveicollis | 1100000000-t-0---0---04100----0-100022000100000011e-0-q--0001000000020-v |
| L orapallida | 0--n000000--t0---0-v-04100--p-0-100??????10000011f-0----0001000000020-- |
| Pt platygaster | 1010001000---0t--110104100s---0-100022000100000011g-0--q-0001000000020v- |
| Pt cribellata | 1010001000---0-t-110104100---t0-100022000100000011ht0----0001000000020-w |
| Pt corusca | 1210001000---0--t110104100--t-0-100032000100000011j-0---q0001000000020w- |
| Pt effulgens | 1200001000t--0---100104100-t--0-100032000100000011k-0----0001000000020-- |
| Pyro beccarii | 1000110000-u-0---110014100-p--0-100032000100000011m-0r---0001010000002110 |
| Pyro.appendiculata | 1200110000--u0---110014100p--q0-100032000100000011n-0-r--0001010000002110 |
| Pyro similis | 1200110000---0u--110014100--q-0-100032000100000011pu0--r-0001010000002110 |
| Pyr.quadrimaculata | 1200110000---0-u-110014100-q--0-100032000100000011q-0---r0001010000002110 |
| Pt macdermotti | 1200110000---0--u0v--04100q---0-300032000100000011z-0s---0001010000020-- |
| Pt gelasina | 1200000000u--0-v-0---04100---r0-100032000100000011r-0-s--0001010000020x- |
| Pt malaccae | 1000000000---0v--0--v04100--r-0-100022000100000011yv0--s-0001010000020-x |
| Pt tener | 0000000000--v0---0---04100-r--0-101032000100000011s-0---s0001010000020y- |
| | 1 |
| Pt truncata | 1100000000-v-0---0---04100r--s0-100032000100000011--0t---0001010000020-- |
| Pt sp ML | 1001100000v--0---0---04100--s-0-100032000100000011tw0-t--0001010000020-- |
| Pt sp MFC | 1101000000---0--v0--w04100-s--0v100032000100000011--0--t-0001010000020-y |
| Colo praeusta | 1211000000---0-w-101104100t--u0-100042000100000011u-0---t0001100000020-- |
| Colo concolor | 1111000000---1101101104100--u-0-100042000100000011-x0u---0001100000020-z |
| Colo plagiata | 1211000000-w-0---101104100-u-v0-100042000100000011v-0-u--0001100000020z- |
| C okinawanus | 0p--000000w--0---0-w-00t-0u-v-0w00002100011100001uwy0--u-0000000010110-- |
| C costipennis | 0-p-000000--w0---0w--00--0-v--0-00002100011100001vxz0---u000000001011027 |

| TABLE 1 CONTINUED | 111222222222233333333334444444444555555555566666666667777777777888888888 |
|---|---|
| Taxon/Character | 789012345678901234567890123456789012345678901234567890123456789012345678 |
| Ph trivittata | -0290001010000001101000 00-1100a0--0-0-000010000031000000400001000000000??? |
| Phot deplanata | 104700091-0010a2-0001a0-10000-0a-0-0-011-0000??????????????????????????? |
| L italica | -05610210100010 0a0000010-0000-0-a0-0-0000000000220000112000000000010000??? |
| B hypocrita | -0--11210100010 0b0000000-0000-0--0-0a000000000022000012?0122000010000??? |
| L H parvula | -0--11210100010 0c0000010-0000b0--0-0-000000000122000012201220000 10000??? |
| Lamp syriaca | b0-51121010001 00d0000010-0000-0b-0-0-0000000000000000224012200001 0000??? |
| L dejeani | -0--102101000100e0000010-0000-0-b0-0-00000000??????????????????????????? |
| New Caledonia 1 | c06-112101020001f0000000-0000-0--0-0b2000110???????????????????????????? |
| New Caledonia 2 | d0-4112101020001g0000000-0000c0--0-0-2000110???????????????????????????? |
| B antipoda | -07-112101020001h0000000-0000-0c-0-0-2000110???????????????????????????? |
| L leii | -0w-101101020001 00001-00-0010-0-c0-0-0000000000200000004000000000 10000110 |
| L ficta | -0--101101020001 00001-00-0000-0--0-0c000000000020000000400000000010000??? |
| L cruciata | e0-w10110100000110000-00-0000d0--0-0-00001000002000000020001000010 0000ab |
| L owadai | -0--10110100000110000-00-0000-0d-0-0-00001000??????????????????????????? |

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L substriata J    -0xy000001000000100000000-0000-0-d0-0-0000000000200000004000000000100000ca
L substriata F    f0yz000001000000100000000-0000-0--0-0d0000000000200000004000000000100000???
L aquatilis       -0z-00000100000010000000-0000e0--0-0-00000000002000000040000000001000000bc
L cowleyi         -0--0000020200020101y-00-0000-0e-0-0-00000000???????????????????????????
                                                      1
Pygo guigliae     g0-30000020200010101cd00-0000-0-f0-0-000000001020000000400110111110011101
Pygo hamulata     -0--0000020200010101de00-0000-0--0-0f00000000???????????????????????????
Pygo kinabalua    -0--0000020200010101bc00-0000-0f-0-0-000000001020000000400110000111110???
Pygo stylifer     -08-0000020200010101ab00-0000f0--0-0-00000000???????????????????????????
Pygo sartoi       -09-0000020200010101f-00-0000-0g-0-0-000000000020000000400010000100101010
Pygo quingyu      -0--0000010210120000000-0100-0-e0-0-0000100000200000004000000000100000101
Pygo wittmeri     -0-2000002020001010ef00-0000g0--0-0-100000001020000000400110000100000101
Aquil costata     -0--00000100000200000000-0000-0--100n00000000000100000020000000001000???
As circumdata     -0-x000001020001000 1--00-0010-0-g0-0-00000000???????????????????????????
As ovalis         -0--000001020001000 1g-00-0010-0--0-0g000000000022000000200000000010000???
M limbata         -0e-0000010000001000000200-0000-0h-0-0-00000000002200000020000000001000???
G messoria        -0h-0000010000020000000200-0000-0--100j00000000???????????????????????????
G similismessoria -0k-0000010000020000000200-0000k0--100-000000000022000000200000000010000???
Missimia flavida  -03810110102000110000200-0010-0--0-0e0000000100200000000200212000100 01???
Ll majuscula      -0--00000100000200000200-0010-0--100h000000000021000000100000000010000???
Ll uberia         -0-m00000100000200000200-0010-0j-100-00000000???????????????????????????
Ll japenensis     -0--00000100000200000200-0010j0--100-00000000002100000020000000001 0000???
Ll wareo          k0--00000100000200000200-0010-0-j100-0000000000021000000200000000010000???
C wolfi           -0--00000102000100000000-0000-0-h100-000100000122000000200000000010000???
                                                                     4
A aphrogeneia     a0a-00000102000100000000-0000h0--0-0-0000000000220000000000000000010000???
A atra            -0--00000102000100000000-0000-0--0-0p0000000000220000021012200000010000???
A brevis          m0b-00000102000100000000-0000-0q-0-0-00000000???????????????????????????
M carolinae       -0--00000102000100000000-0000-0-m0-10b0000000???????????????????????????
A conspicua       n0-b00000102000100000000-0000-0-q0-0-000000000102000132201220000010000???
A dalmatia        -0--00000100000100000000-0000-0-k0-0-00000000???????????????????????????
A ellioti         -0--00000102000100000000-0000-0--0-0q00000000???????????????????????????
A flammans        -0c-00000100000100000000-0000r0--0-10c000000000220000010012200000100 00???
A flammulans      -0--00000100000100000000-0000-0r-0-10d0000000???????????????????????????
A guerini         -0--00000100000100000000-0000-0k-0-10a0000000???????????????????????????
A immaculata      -0-c00000102000100000000-0000-0-r0-0-00000000???????????????????????????
A inconspicua     -0--00000102000100000000-0000-0-p0-0-0000000000420000321012200000100 00???
A kirakira        -0m-00000102000200000100-0000-0m-0-0-00000000???????????????????????????
A lamingtonia     -0-p00000101000100000000-0000n0--0-0-00000000???????????????????????????
A leucura         h0-e00000102000200000200-0000-0--0-10-000000000220000004000000000100 00???
                                      3
A lewisi          -0--00000102000100000000-0000p0--0-0-0000000001120001420012200000100 00???
M rennellia       -0-n00000100000100000000-0000m0--110-00000000???????????????????????????
A lychnus         p0-d00000102000100000000-0000-0--0-0r000000000022000002001220000010000???
A monteithi       -0--00000102000100000000-0000s0--0-0-00000000???????????????????????????
A olivieri        -0d-00000100000100000000-0000q0--0-0-000000000022000001000000000010000???
A palauensis      j0-k00000100000100000000-0000-0n-1-10-000000000220000012011200000100 01???
A scabra          -0--00000102000200000000-0000-0-s0-0-00000000???????????????????????????
A scintillans     -0--00000102000100000000-0000-0s-0-0-000000000022000022401220000010000???
A similis         -0-a00000102000100000000-0000-0p-0-0-000000000022000032401220000010000???
A testaceolineat  -0--00000102000200000000-0000-0--0-0m00000000???????????????????????????
                                      1
Pyg plagiata      61110000010200010000000 0-0000-0-40-0-00000000???????????????????????????
Pyg.eliptaminensisr0f-00000102000110000000-000101000-0-000000000022100000200000000010001???
Pyg uberia 1      00--0000000200020000000100000-0--0-0w000000000022000000200000000010001???
Pyg  huonensis    -0-f000001020001000 1nj00-0000-0--100s000000000022000000200000000010001???
                                                                 1
Pyg  ignota       -0-g000001020001000 1--00-0000-1010-0t00000000???????????????????????????
Pyg  japenensis   00n-000001020002000 1s-00-000101010-0-0000000000221000002000000000100 00???
Pyg  karimui      -0--000001020002000 1up00-000101010-0-000000000022100000200000000010000???
Pyg  kiunga       -0j-000001020002000 1rn00-0000v0-80-0-00000000???????????????????????????
Pyg limbatipennis 21000000010200010000000 0-0000-07-0-0-00000000002201010040000000000100 00???
Pyg  limbatifusca 31000000010200010000000 0-0000-08-0-0-00000000002201010040000000000100 00???
Pyg  marginata    -0--00000102000200000000-0000-1010-0-00000000???????????????????????????
Pyg  nabiria      00--000001020002000 1t-00-000111010-0v00000000???????????????????????????
Pyg  obsoleta     -0p-000001020002000 1xq00-000101010-0-000000000022000000200000000010000???
                                                1                1
Pyg  okapa        -0-q000001020002000 1v-00-000111210-0-000000000022000000200000000010000???
Pyg  peculiaris   -0g-00000102000100000000-0000u0-90-11e000000000221000002000000000100 01???
                                    1
Pyg  pulcherrima  -0--00000102000200???00-0000-1110-1u00000000???????????????????????????
Pyg  russellia    51000000010200010000000 0-0000-06-0-0-00000000???????????????????????????
Pyga salomonis    71000000010200010000000 0-0000-0-50-090000000 0???????????????????????????
                    11
Pyg  tagensis     q0-h000001020002000 1qm00-0000-0-u100-00000000???????????????????????????
Pyg  tomba        -0--000001020001000 1k-00-0000-0-n0-0-00000000???????????????????????????
Pyg uberia 2     00--0000000200020000000100000-0-v0-0-00000000???????????????????????????
Pyg  undulata     -0--000001020002000 1pk00-0000t0--0-0-00000000000022?00000200000000 1???????
Pyg  wisselmeren  s0--000001020002000 1w-00-000101010-0-000000000022000000200000000010000???
L australis       t0q-00000a0000b2-0000r02-0000-0w-0-0-000000000000000000040000000001 0000???
L flavicollis     -0-r00000b0000c2-0000-02-0000-0--0-0x000000000040000000400000000010000???
L nigra           -0--00000c0000d2-0000s02-0000-0x-0-0-000000000000000000040000000001 0000???
L anthracina      -0--00000-0000-2j000??02-0000-0-w0-0-00000000???????????????????????????
L pupilla         u0--00000-0000-2k000??02-0000-0--0-0y00000000???????????????????????????
L. foveicollis    -0--00000-0000-2m0001-02-0000-0-70-0-00000000???????????????????????????
L orapallida      -0--00000d0000e2n0001-02-0000-0--0-0-000000000000000000040000000001 0000???
Pt platygaster    -0--00000t0000u2p0001w02-0000-0y-0-0-000000000000000000040000000001 0000???
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TABLE 1 CONTINUED

| Taxon/Character | |
|---|---|
| | 222222222222222222222222222222222222222222222222222222222222222222222222 |
| | 111222222222233333333334444444444555555555566666666667777777777888888888 |
| Taxon/Character | 789012345678901234567890123456789012345678901234567890123456789012345678 |
| Pt cribellata | -0--00000u0000v2q0001-02-0000-0--0-0-00000000000000000040000000010000??? |
| Pt corusca | -0--00000v0000w2r0001-02-0000-0-x0-0z00000000000000000040000000010000100 |
| Pt effulgens | v0-v00000w0000x2s0001x02-0000-0--0-0-00000000000000000040000000010000100 |
| Pyro beccarii | 00-s00080e0010f2t0001-0220000-0-60-0-00000000001000000040000000010000??? |
| Pyro.appendiculata | 00--00070f0010g2u0001t0220000-0z-0-0-00000000000000000040000000010000100 |
| Pyro similis | 00r-00060g0010h2v0001-0220000-0-y0-0300000000????????????????????????100 |
| Pyr.quadrimaculata | 00--00050h0010k2w0001-0220000-0--0-0-00000000??????????????????????????? |
| Pt macdermotti | w0-t00000k0010m2x0001-02-0000-03-0-0-00000000?4000000004010000001?001??? |
| Pt gelasina | -0--00000m0000n2y0001u02-0000-0--0-0400000000001000000040000000010000??? |
| Pt malaccae | -0s-00000n0010p2z0001-02-0000-0-z0-0-00000000001000000040000000010000100 |
| Pt tener | -0--00000p0010q220001z02-0000-0--0-0500000000000000000040000000010000100 |
| Pt truncata | x0-u00000q0010r230001v02-0000-0-20-0-00000000001000000040000000010000100 |
| Pt sp ML | -0t-00000r0010s240001-02-0000-04-0-0-00000000??????????????????????????? |
| Pt sp MFC | -0--00000s0010t250001-02-0000-0--0-0600000000004000000040000000010000??? |
| Colo praeusta | y0u-00000x0010y260001-02-0000-09-0-0-00000000012000000040000000010000??? |
| Colo concolor | -0--00000y0010z270001-02-0000-0-30-0-00000000??????????????????????????? |
| Colo plagiata | -0--00000z00109280001y02-0000-0--0-0700000000002000000040000000010000??? |
| C okinawanus | z0v-000001120001000000000-0000-05-0-0-0000000000210010003100000010000??? |
| C costipennis | 40--0000011200010000000000000-0000-0--0-08000000000021001000310000000100 |

| Taxon/Character | |
|---|---|
| | 2222222222233333333333333333333333333333333333333333333 |
| | 8999999999900000000001111111111222222222233333333334444 |
| Taxon/Character | 9012345678901234567890123456789012345678901234567890123 |
| Ph trivittata | ?????????????????????????????????2011-000-13-0-11110000 |
| Phot deplanata | ?????????????????????????????????1ca----a-----b11????1a |
| L italica | ?1???????????????????????????????1-x-a---a-b---01001a1b |
| B hypocrita | ??101101101-10101001010110100a0001ay--a-cb---a-01000000 |
| L H parvula | ??2021010000--0-100000-000000b0001-b---a------a11011b1c |
| Lamp syriaca | ?????????????????????????????????400b---0-0-0d-11110000 |
| L dejeani | ?????????????????????????????????-00-b--0-0a00-01????00 |
| New Caledonia 1 | ?????????????????????????????????1-z--b-dc---b-00????00 |
| New Caledonia 2 | ?????????????????????????????????1bc---b---d---01????00 |
| B antipoda | ?????????????????????????????????1-2c---bd----c01????00 |
| L leii | 020100010000--0-100000-0000022000-00-c--0-0-00-01000000 |
| L ficta | ??0100??0000--0-100000-0000022000-00--c-0-140-e01101y01 |
| L cruciata | c10100010000--0-100000-00000220001f----c-24--9-11011z15 |
| L owadai | ??0100???000--0-100000-00000220001--d---e3-5---00????1- |
| L substriata J | b00000???01-011110000110001121111-00--d-0-0-00-01100000 |
| L substriata F | ??000011101-011110000110001121111-00---d0-0-00f01100000 |
| L aquatilis | a0000011101-011110000110001121111y00e---0-110c-01100000 |
| | 1 |
| L cowleyi | ??000100101-0111011001101110?0000p00-e--0-0c00-11????00 |
| | 1 |
| Pygo guigliae | 00???????????????????????????????-00-f--0-0-00-11010000 |
| Pygo hamulata | ?????????????????????????????????-00--f-0-0-00j01????00 |
| Pygo kinabalua | ?????????????????????????????????-00f---0-0e00-11010000 |
| Pygo stylifer | ?????????????????????????????????500---e0-0-00h01????00 |
| Pygo sartoi | 00???????????????????????????????600g---0-0-00-11110000 |
| Pygo quingyu | 00000111101-0011011101001210100011g---e------0g10011-1- |
| Pygo wittmeri | 00???????????????????????????????-00---f0-0f00-11010000 |
| Aquil costata | ?????????????????????????????????700---m0-0-00-01100000 |
| As circumdata | ?????????????????????????????????-00---g0-13--k01????16 |
| As ovalis | ?????????????????????????????????x00h---0-13---0110011- |
| M limbata | ??2021000000--0-100110-010100m000-00--j-0-10-e-01101c1e |
| G messoria | ?????????????????????????????????0k-m-------0g-01????00 |
| G similismessoria | ?????????????????????????????????-00-m--0-0-00p01100100 |
| Missimia flavida | ?????????????????????????????????0ed-d------0-d01000000 |
| Ll majuscula | ??2021000001--0-100110-000100p0001-ek---fj-g--m01001e1h |
| Ll uberia | ?????????????????????????????????1-g--k--h----n01????1m |
| Ll japenensis | ?????????????????????????????????1-f-k---g---f-01001f1k |
| Ll wareo | ?????????????????????????????????1-h---k-f-h---01001g1n |
| C wolfi | ?????????????????????????????????-00---j0-11-8-01101d1f |
| A aphrogeneia | ??2020000000--0-100010-000100c0001-ja----e---h-11010000 |
| A atra | ??2010000000--0-100000-000100e0001-4--n-------u11000000 |
| | 11 |
| A brevis | ?????????????????????????????????-p11000--13---11????00 |
| | 1 |
| M carolinae | ?????????????????????????????????1-n---h-m---j-01????01 |
| | 1 1 |
| A conspicua | ?????????????????????????????????1--p--------m-11110000 |
| A dalmatia | ?????????????????????????????????b10-g--0-0-0-q11????01 |
| A ellioti | ?????????????????????????????????-910000--14--v11????01 |
| A flammans | ??2010000000--0-100010-000100f000-q12100-s13-5-11110101 |
| A flammulans | ?????????????????????????????????--10100--13-n-11????01 |
| | 1 |
| A guerini | ??2021000000--0-100000-010100n0001-q--m--pan---01????1g |
| A immaculata | ?????????????????????????????????1-s-p--------w01????1d |
| A inconspicua | ?????????????????????????????????1-3-n-----p-6-11110000 |
| A kirakira | ?????????????????????????????????1-m--h--k----r11????1q |
| A lamingtonia | ?????????????????????????????????d-12011--13--s11????01 |
| A leucura | ?????????????????????????????????-00-h--000k-0-11110101 |
| | 1 |

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TABLE 1 CONTINUED 2222222222233333333333333333333333333333333333333333333
                  8999999999900000000001111111111222222222233333333334444
Taxon/Character   9012345678901234567890123456789012345678901234567890123
-------------------------------------------------------------------------
A lewisi          ?????????????????????????????????-n10100-r13---11000001
M rennellia       ?????????????????????????????????-00-j--0-110--01????1p
                                                                 1
A lychnus         ??2011000000--0-110010-000100g0008-02100-t13-4-11110000
                                                     1
A monteithi       ?????????????????????????????????1-t--p----q---11????00
A olivieri        ??2011000100--0-110010-010100h000-m0---n-q1307-11110101
A palauensis      ?????????????????????????????????-00j---0-0-00-01110100
                                                                 1
A scabra          ?????????????????????????????????1r-q------r---11????00
A scintillans     ??2011000100--0-110110-000100k0001-5---p-----p-11010000
A similis         ??2010000000--0-100110-000100d0001-rn--------k-11010000
A testaceolineat  ?????????????????????????????????c-11100--13---11????01
Pyg plagiata      ?????????????????????????????????1----4--589---11????00
Pyg.eliptaminensis?????????????????????????????????--0--r-110--0-11110101
Pyg uberia 1      ?????????????????????????????????m00u---0-0--1311100101
                                                                    1
Pyg  huonensis    ?????????????????????????????????--0-q--110--0x11110101
Pyg  ignota       ?????????????????????????????????-s0---r110s-0y11????01
Pyg  japenensis   ?????????????????????????????????--0--s-110u-0-11110101
Pyg  karimui      ?????????????????????????????????--0t---100--0211100101
Pyg  kiunga       ?????????????????????????????????g-0-r--110--0z11????01
Pyg limbatipennis ?????????????????????????????????--05-8--7110-901101-18
Pyg  limbatifusca ?????????????????????????????????z40-6-7-8110w-11111-19
Pyg  marginata    ?????????????????????????????????--0s-5-0-11---11????01
Pyg  nabiria      ?????????????????????????????????-80---s110--0-11????01
Pyg  obsoleta     ?????????????????????????????????ku0-5-t000--0-11110101
                                                          11
Pyg  okapa        ?????????????????????????????????h-0-t-5110v-0-11110101
Pyg  peculiaris   ?????????????????????????????????f-0---q110--0-11110101
Pyg  pulcherrima  ?????????????????????????????????-t0-s--110t-0-11????01
Pyg  russellia    ?????????????????????????????????020-4---476---11????00
Pyga salomonis    ?????????????????????????????????13----4-698-v-01????17
Pyg  tagensis     ?????????????????????????????????--0r---110--0-11????01
Pyg  tomba        ?????????????????????????????????--0--g-------t11????00
Pyg uberia 2      ?????????????????????????????????n00-u--0-0--1-11????01
Pyg  undulata     ?????????????????????????????????e-0--q-110--0-11100101
Pyg  wisselmeren  ?????????????????????????????????j-0--t-110--0-11110101
L australis       ??0100000000--0-1000110000100q0001-u--u--u-w-q-01001h1r
L flavicollis     ??0100000000--0-1000110000100r000qv0---u--101-000101k1s
                                                                1
L nigra           ??0100000000--0-1000110000100s0001-vv--------2-00001m1t
L anthracina      ?????????????????????????????????17--v-------3-01????1-
L pupilla         ?????????????????????????????????1----v------r-01????1-
L. foveicollis    ?????????????????????????????????1w----v------401????1-
L orapallida      ??0100??0000--0-1000110000100t000r-0w----v120z001101n1u
                                                                1
Pt platygaster    ?????????????????????????????????16--w---x---s-00001r1y
Pt cribellata     ?????????????????????????????????1----w----z---00001s1z
Pt corusca        1????????????????????????????????1-----w--2----01001t12
Pt effulgens      11???????????????????????????????1--x----9---t-01001u13
Pyro beccarii     ?????????????????????????????????1-6-x----0x--501001p1v
                                                                   1
Pyro.appendiculata1????????????????????????????????--7--x--w110y-01101q1w
Pyro similis      11???????????????????????????????-x0---x0-t--0601????01
Pyr.quadrimaculata?????????????????????????????????s00y-----1-0x-01????1x
Pt macdermotti    ?????????????????????????????????--0-y--0-u-00-01100100
Pt gelasina       ?????????????????????????????????0----y---v---701100101
                                                                    1
Pt malaccae       11???????????????????????????????t-0---y0-w--0-01100000
Pt tener          110100000000--0-1000010000100u000--0z---0-x--0-01110101
                                                                 1
Pt truncata       11???????????????????????????????0y--z----y----01000001
Pt sp ML          ?????????????????????????????????--0--z-0-zy-0-01????00
Pt sp MFC         ?????????????????????????????????u-0---z0-1000-01101w1-
Colo praeusta     ??0100000000--0-1000010000100v000--03---0--2-0-01100101
Colo concolor     ?????????????????????????????????05--3---------00????00
Colo plagiata     ?????????????????????????????????v-0--3---1200-01101v00
C okinawanus      ??0100000000--0-100100-000000w0001z----3-y-3-u801001x14
C costipennis     ?????????????????????????????????w004---0-3-00-01100000
```

the Data Matrix. 343 morphological characters of males, females and larvae were scored (Table 1, also available as Mesquite Nexus file from the authors), and fully described in Appendix 1. Most characters are binary, but 62 characters are multistate; 44 with three states, nine with four states, and nine with five states. 250 characters are parsimony informative. The 18 characters (322–339) that describe colour, and four characters

(340–343) that describe mimicry or colour patterns were included in the phylogenetic analysis unlike our last analysis (2006) that mapped these characters onto the resultant trees to examine patterns of evolution.

**Inapplicables**

States of a morphological character describe alternative homologous conditions of structures, e.g. clypeolabral suture, present/absent. Inapplicable states occur when a character describes conditions of a structure that is not present in some taxa, e.g. position of clypeolabral suture, behind anterior eye margins/in front of anterior eye margins, in those taxa that do not have the clypeolabral suture. Some taxa have the structure but lack the condition (absence), other taxa have the structure and the condition (presence), while other taxa have neither the structure and therefore neither condition of it (inapplicable). The scoring of inapplicables as '-' in cladistic analyses is interpreted by computer algorithms as missing data, creating the same problems as missing data, and yet the data is not missing.

The data disjunction (Nixon & Carpenter, 1996), which occurs when there is missing data, creates considerable problems in phylogenetic analyses by increasing the number of solutions and reducing the data decisiveness (Goloboff, 1991) of the resulting most parsimonious trees (MPTs) (Nixon & Carpenter, 1996). Large numbers of missing values may result in taxa being placed in radically different positions on MPTs, or trees unstable to the addition of new data (Nixon & Carpenter, 1996), with the resultant strict consensus tree totally unresolved (Carpenter, 1987). Large numbers of missing entries in certain taxa may force taxa into ‘branch swapping eddies’ that generate huge numbers of MPTs and decrease resolution of the consensus tree (Ballantyne & Lambkin, 2001; Novacek, 1987). Platnick *et al*. (1991) showed that missing entries (missing scored as '?', or inapplicable data scored as '-') may produce fully resolved cladograms that cannot be supported by any conceivable assignment of the possible states. Nodes are present because of mutually exclusive optimisations of the same character and optimisations at internal nodes of unobserved conditions. Wilkinson (1995) considered that some of these trees contained linked sets of interior branches that simultaneously have zero and non-zero lengths, a problem that current computer algorithms have difficulty dealing with. Investigation of the trees that cannot be supported by any conceivable assignment of the possible states indicates that taxa are separated without information. Cladistic programs account for missing data by assigning states given the most parsimonious distribution of known characters (Novacek, 1992). The meaning of '?' in binary characters is analysed as uncertainty between states 0 and 1, but in multistate characters is open to further interpretation (Vrba *et al.*, 1994).

Taxa can float; trees can be produced with nodes not supported by any arrangement of the available states; many more trees can be produced. These all result in loss of resolution in the consensus tree, and decrease the power of inferences made concerning relationships. Computer algorithms currently available for phylogenetic analysis, place one of the available states into each of those taxa coded as '-', based on the optimisation of the data and the signal from the other characters, which is incorrect as none of the available states is present.

The most commonly used method of coding inapplicables is to use two characters, one absence/presence and the other describing the separate features. The taxa for which the second character is inapplicable are coded as '-'.

The other method of dealing with inapplicables, suggested by Maddison (1993), was to fuse the two characters to produce a single multistate character, with the absent the first state, and the other features forming the other states. Fused multistate characters create problems in primary homology assessment, and cause loss of phylogenetic information as the number of states in the multistate increases. Groupings may be supported by the inapplicable, whereas the lack of the feature may result from multiple cases of secondary loss. The issue raised by Lee and Bryant (1999) concerning the loss of phylogenetic information with fused multistate coding increases significantly as the number of states in the multistate increases. This is a problem with all multistate characters, and not confined to those with inapplicables. If both a binary character describing the absence/presence, and a multistate with the inapplicable and the states of the feature, are included no loss of phylogenetic information occurs. This becomes particularly important if the structure which is absent in some taxa, is extremely complex with many different non-homologous features to be described, as often occurs in morphologically based analyses of large numbers of taxa across both closely and distantly related groups. The addition of a more inclusive character was suggested, but dismissed, by Strong and Lipscomb (1999). A more inclusive character that defines the subgroups, may weight characters that are scored more than once for some taxa (Pleijel, 1995), and may introduce dependent characters. Both a binary character describing the absence/presence, and a fused multistate with the inapplicable and the states of the feature were included in our previous analyses (Ballantyne & Lambkin, 2000, 2001, 2006) to avoid the use of 'missing' data, and decrease the loss of phylogenetic information. This was particularly important in these analyses, as some extremely complex structures involving many characters were not present in some taxa.

There are situations where an inapplicable is not an issue. If the inapplicable only occurs in the outgroup, is pleisiomorphic, is autapomorphic, or is confined to a monophyletic group, the recoding as an extra state is not problematical. Unfortunately, whether the inapplicable state is confined to a monophyletic group or is pleisiomorphic is not known before the analysis of the characters. However most published examples have discussed inapplicables in basal groups, where it may not be problem to the analysis. Most systematists are confronted by several losses either apomorphically in well-separated groups, or both pleisiomorphically and apomorphically.

We have used a new option for dealing with inapplicables that includes a unique state for each taxon in each character that is inapplicable. By using Mesquite (Maddison & Maddison, 2006) we have been able to use up to 33 states (0–9, alphabet except for nonallowed i, j, and o) for each character (See Table 1). Where more than 31 taxa were inapplicable for a character, one taxon in a species group was scored with the unique state and the remainder scored '-'. This method prevents grouping based on the inapplicable state, and overcomes the problems of missing data and primary homology assessment. Lambkin is currently assessing the effect of this method of scoring inapplicables.

**Character analysis**

Phylogenetic analyses presented here do not prejudge the relative informativeness of characters (Kallersjö *et al.*, 1999; Larson & Dimmick, 1993). All character changes were weighted equally (Farris, 1990). Character polarity was determined using outgroup comparison (Maddison *et al.*, 1984; Nixon & Carpenter, 1993), with the taxon *Photuris trivittata* Lloyd *et* Ballantyne designated as the outgroup. Characters with more than one derived state were coded as multistate, not in binary form (Meier, 1994), and treated as unordered (non-additive). Cladistic analyses completed 1000 random step-wise addition heuristic searches, with each replicate restricted to 10 million rearrangements and 32,000 MPTs, TBR branch swapping, MULPARS, and branches having maximum length zero collapsed to yield polytomies using PAUP*4.0b10 (Swofford, 2002).

Strict (Schuh & Farris, 1981) and majority-rule consensus (Margush & McMorris, 1981) were computed using PAUP*. The 50% majority rule consensus shows all nodes that are found in more than 50% of the trees. Groups are preserved in the majority rule consensus tree even if there are some MPT that support conflicting groups (Margush & McMorris, 1981). Baker and DeSalle (1997) described a measure, Partitioned Bremer support (PBS), based on Bremer support (BS) (Bremer, 1988, 1994; Kallersjö *et al.*, 1992), to measure the support from each data partition for each node of the tree from a combined data matrix. Partitioned Bremer support summarises the topological support from the separate partitions present in the combined data. DeSalle and Brower (1997), Baker *et al*. (1998), Remsen and DeSalle (1998), Gatesy *et al*. (1999), Lambkin *et al.* (2002), and Lambkin (2004) all used PBS to examine the new relationships that sometimes emerge when information is combined. Partitioned Bremer support values were calculated with TreeRot v.2 (Sorenson, 1999) for seven partitions; male, male genitalia, female, larvae, male colour, female colour, and crypsis (Table 1), with 20 heuristic searches of the data with each replicate restricted to 10 million rearrangements and 32,000 MPTs. Unfortunately as TreeRot v.2 uses inefficient reverse heuristic searches, i.e. heuristic searches finding the MPTs *without* a node for calculation of BS and PBS, occasionally the shortest MPT are not found, and BS and PBS is overestimated.

## Phylogenetic results

Analysis of 343 characters of the data matrix in Table 1 produced 739 MPT of length 3387, consistency index (Kluge & Farris, 1969) 0.797, consistency index without uninformative characters (Kluge & Farris, 1969) 0.716, retention index (Farris, 1989) 0.749, and rescaled consistency index (Farris, 1989) 0.597. The strict (Fig. 1) and 50% majority rule (Figs 2, 3) consensus trees were calculated. A tree filter, created in PAUP*, found that two of the 739 MPT were compatible with the 50% majority rule consensus tree. One of these, MPT 262 (Figs 2, 3) was chosen as the preferred MPT, and the corresponding % of MPTs found with that node, BS (bold), and node numbers shown along the branches. Partitioned Bremer supports for the seven partitions (male, male genitalia, female, larvae, male colour, female colour, and crypsis), BS, and node numbers corresponding to Figures 2 and 3 are given in Table 2. Where TreeRot v.2 was unable to find the shortest MPT, as evidenced by non-0 BS for 29 nodes not found in 100% of MPT and therefore not in the strict consensus tree, the BS is not highlighted in yellow in Table 2 and not in bold in Figures 2 and 3. These are cases where BS and PBS are overestimates. Partitioned Bremer supports for the morphological partitions: male external (chars. 1–154; 154 characters), male genitalia (chars. 155–261; 107 characters), female (chars. 262–290; 29 characters), larvae (chars. 291–321; 31 characters), male colour (chars. 322–337; 16 characters), female colour (chars. 338–339; 2 characters), and crypsis (chars. 340–343; 4 characters), shown in Table 2 clearly show that the phylogeny is strongly supported by the male genitalic characters. Of the 19 nodes that receive PBS higher than 5 (Table 2, blue highlight, italicised), 18 are supported by the male genitalic character partition. Support is also received from larval, male colour, and crypsis characters, despite their low number. Overall the male external, female, and female colour characters do not support the topology presented by the 50% majority rule consensus tree. Of the 10 nodes that receive PBS lower than -5 (Table 2, red highlight, underlined), all the disagreement comes from the female genitalic characters.

## Phylogenetic Relationships
(Figs 2–3)

This paper addresses the status of *Atyphella*, including all species originally described as, or subsequently assigned to *Atyphella*, as well as those species tentatively identified as *Atyphella* by Ballantyne in Lloyd (1973b). We also examine the status of all the species originally assigned by Ballantyne (1968) to *Luciola* (*Pygatyphella*), and the possible existence of cryptic species in *Atyphella obsoleta.*

Ballantyne and Lambkin (2000, 2001) confirmed the status of *Atyphella* with phylogenetic analyses of the Luciolinae using 23 species of *Atyphella* (16 Australian and seven New Guinean). Ballantyne and Lambkin (2006), using the same species but an extended range of characters, indicated a polyphyletic nature for *Atyphella*, and the need for further investigation. This study, with an expanded taxon sample for the Luciolinae, was initially commenced to complete the taxonomy of the species identified as *Atyphella* spp. The phylogenetic analysis including 112 taxa provides strong support for a clade of 14 species of *Atyphella* (Fig. 3, node 69, BS=4, PBS♂colour=3.9). While poorly supported as found in only 69% of the MPT, the majority rule consensus tree provides evidence for the placement of a total of 23 species in the genus *Atyphella* (Fig. 3, node 78) including 14 endemic Australian, and 10 species from the wider study area. Three new species: *A. dalmatia* **sp. n.**, *A. kirakira* **sp. n.**, and *A. lamingtonia* **sp. n.** are described. *Atyphella palauensis* Wittmer is elevated to species level from *A. carolinae palauensis* Wittmer.

TABLE 2. Partitioned Bremer Supports and Bremer Supports for all nodes. Bremer supports bold, yellow highlight. Bremer Supports which should be 0; bold italics, not yellow. Significantly positive Partitioned Bremer Supports: italics, blue highlight. Significantly negative Partitioned Bremer Supports: underlined, red highlight.

| *node* | *1* | *2* | *3* | *4* | *5* | *6* | *7* | *8* | *9* | *10* | *11* | *12* | *13* | *14* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| male | -1.87 | 2.93 | -2.76 | 6.19 | -0.07 | -4.57 | -6.42 | -1.90 | 9.94 | -1.16 | 1.22 | 0.20 | -0.70 | -3.71 |
| male gen | -0.02 | 4.11 | 0.90 | *8.37* | 0.01 | *7.80* | 4.96 | 0.04 | *7.25* | 0.30 | 3.77 | 1.99 | 2.72 | 2.70 |
| female | 0.00 | 0.11 | 0.00 | -2.00 | 0.00 | -1.00 | 0.00 | 0.00 | -2.92 | 0.00 | -3.95 | 0.88 | -1.00 | -0.22 |
| larvae | 0.96 | 1.03 | 0.97 | 0.51 | 0.54 | -0.03 | 0.83 | 0.96 | -0.46 | 0.97 | 2.97 | 0.97 | 0.92 | 0.87 |
| male colour | 0.83 | 0.93 | 2.85 | -0.01 | 0.47 | 0.90 | 1.82 | 0.82 | 0.46 | 0.89 | 1.01 | 0.03 | 0.93 | 2.70 |
| female colour | -0.96 | -1.06 | 1.03 | -1.51 | -0.54 | 0.05 | 0.01 | -0.96 | -0.94 | -0.97 | -1.97 | 0.03 | -0.92 | 0.08 |
| crypsis | 2.05 | -0.05 | 0.01 | 2.45 | 1.59 | -0.15 | 0.80 | 1.05 | 1.67 | 0.97 | 0.94 | 0.91 | -0.96 | 0.58 |
| **BS** | **1.00** | **8.00** | **3.00** | **14.00** | **2.00** | **3.00** | ***2.00*** | **0.00** | **15.00** | **1.00** | **4.00** | **5.00** | **1.00** | ***3.00*** |
| *node* | *15* | *16* | *17* | *18* | *19* | *20* | *21* | *22* | *23* | *24* | *25* | *26* | *27* | *28* |
| male | -1.85 | -1.88 | -3.98 | -0.63 | -3.64 | -4.72 | 0.80 | -0.76 | -0.92 | 9.13 | -0.79 | -4.26 | -3.38 | -0.81 |
| male gen | *6.77* | 3.11 | 1.37 | 1.84 | 2.80 | 2.84 | *5.89* | 3.90 | -0.42 | 3.05 | *6.73* | 1.41 | 4.21 | 2.08 |
| female | -0.05 | 0.00 | 0.00 | -0.96 | -0.92 | 0.00 | -1.20 | -1.89 | 0.65 | -3.01 | -2.84 | -0.02 | -0.69 | -0.99 |
| larvae | -0.03 | 0.97 | 0.89 | 0.03 | 0.78 | 0.09 | 0.72 | 0.14 | 0.96 | 2.97 | -0.03 | 0.48 | -0.03 | -0.03 |
| male colour | -0.95 | 0.91 | 2.79 | 0.93 | 1.83 | 3.83 | 2.42 | -0.10 | 0.91 | -0.02 | 0.86 | 2.39 | 2.88 | 0.81 |
| female colour | 0.03 | -0.97 | -0.89 | -0.03 | 0.18 | 0.03 | -0.73 | 0.83 | -0.07 | -1.94 | -0.97 | -0.01 | 0.03 | -0.90 |
| crypsis | -0.93 | 1.86 | 1.82 | 1.82 | -0.03 | 1.92 | 3.11 | 0.89 | 0.89 | 1.81 | 0.04 | 1.01 | -0.01 | 2.84 |
| **BS** | **3.00** | **4.00** | ***2.00*** | **3.00** | ***1.00*** | **4.00** | **11.00** | **3.00** | ***2.00*** | **12.00** | **3.00** | **1.00** | **3.00** | **3.00** |
| *node* | *29* | *30* | *31* | *32* | *33* | *34* | *35* | *36* | *37* | *38* | *39* | *40* | *41* | *42* |
| male | -0.14 | -2.08 | -6.57 | -3.11 | -1.09 | -1.73 | -5.19 | -1.18 | -0.06 | -5.11 | 2.28 | -0.56 | 3.49 | -3.60 |
| male gen | 2.62 | 1.06 | 4.03 | 3.11 | 1.44 | 0.84 | *7.57* | 3.99 | 2.58 | *5.17* | -0.87 | 2.87 | *6.87* | 2.80 |
| female | -0.78 | 0.00 | 0.00 | -0.58 | -0.33 | 0.00 | 0.00 | 0.00 | *5.00* | -0.24 | -2.00 | -1.00 | 0.14 | 0.05 |
| larvae | 1.49 | 0.94 | 0.90 | 0.39 | 0.97 | 0.88 | -0.03 | -0.03 | 1.84 | 0.22 | 3.97 | 0.69 | 0.87 | -0.03 |
| male colour | 1.61 | 1.08 | 2.80 | 1.12 | 2.94 | 0.84 | 0.85 | 1.11 | 2.87 | 1.50 | -0.20 | 0.89 | -0.02 | 0.89 |
| female colour | -1.17 | -0.94 | 0.00 | 0.40 | -1.90 | -0.81 | 0.04 | 0.03 | 0.03 | -0.22 | -0.97 | -0.26 | -0.87 | 1.02 |
| crypsis | 0.37 | 1.93 | 0.84 | 0.69 | 0.97 | 0.97 | -1.24 | 1.08 | -2.26 | 0.68 | 1.79 | 0.36 | -0.48 | 2.87 |
| **BS** | **4.00** | **2.00** | **2.00** | ***2.00*** | **3.00** | ***1.00*** | **2.00** | **5.00** | **10.00** | ***2.00*** | **4.00** | **3.00** | **10.00** | **4.00** |
| *node* | *43* | *44* | *45* | *46* | *47* | *48* | *49* | *50* | *51* | *52* | *53* | *54* | *55* | *56* |
| male | -2.14 | 0.08 | -0.54 | 0.73 | -1.67 | -4.86 | 0.35 | 0.07 | -1.61 | -2.13 | -1.14 | -0.78 | -0.91 | -5.43 |
| male gen | 0.41 | 1.55 | 3.57 | 3.42 | 3.86 | 4.97 | 0.35 | 0.97 | 4.47 | *10.15* | 1.09 | -1.06 | 0.86 | 2.47 |
| female | 0.00 | -1.01 | 0.00 | -2.00 | 0.00 | 0.00 | 0.03 | 0.00 | -1.00 | 0.96 | 0.00 | 0.00 | 0.00 | -0.09 |
| larvae | 1.97 | 3.97 | -0.02 | 2.83 | 0.47 | -0.03 | 0.84 | 0.97 | 0.02 | 0.00 | 0.81 | 0.97 | 0.04 | 1.38 |
| male colour | 1.90 | -0.84 | -0.06 | 0.92 | -0.04 | 1.92 | 0.93 | 1.99 | 0.03 | 0.99 | 0.78 | 0.90 | 0.04 | 3.66 |
| female colour | 0.03 | 0.01 | 0.03 | -0.97 | -0.47 | 0.03 | 0.13 | -0.97 | 0.09 | 0.03 | -0.82 | -0.97 | 0.03 | -0.47 |
| crypsis | 0.83 | 0.24 | 1.02 | 0.07 | 0.85 | -0.03 | -0.63 | 0.97 | 0.00 | 0.01 | -0.72 | 1.94 | -0.07 | 1.48 |
| **BS** | **3.00** | **4.00** | **4.00** | **5.00** | **3.00** | **2.00** | **2.00** | **4.00** | ***2.00*** | **10.00** | **0.00** | ***1.00*** | **0.00** | ***3.00*** |
| *node* | *57* | *58* | *59* | *60* | *61* | *62* | *63* | *64* | *65* | *66* | *67* | *68* | *69* | *70* |
| male | -0.92 | -1.78 | -3.69 | -0.78 | -2.62 | 1.07 | -3.99 | -4.42 | -2.81 | -2.14 | -1.92 | -5.82 | -1.91 | -4.40 |
| male gen | 1.29 | -1.04 | *5.93* | 1.87 | 1.90 | 2.95 | 4.77 | *5.43* | 2.09 | 2.11 | 3.68 | 3.88 | 0.04 | 4.67 |
| female | 0.00 | 0.00 | -1.00 | -1.00 | 0.00 | -0.97 | 0.00 | 0.00 | -0.03 | 0.09 | -0.39 | -1.00 | 1.00 | 0.00 |
| larvae | 0.81 | 0.97 | -0.03 | 0.96 | 0.28 | 0.53 | -0.03 | -0.03 | 0.77 | 0.46 | 0.44 | 0.97 | 0.97 | -0.03 |
| male colour | 0.02 | 0.86 | 0.00 | 0.01 | 0.83 | -0.47 | 1.05 | 0.93 | 0.90 | 0.54 | 1.30 | 2.92 | 3.90 | 1.85 |
| female colour | -0.84 | -0.97 | 0.03 | 0.04 | -0.21 | -1.20 | 0.03 | 0.03 | -0.87 | 0.12 | 0.05 | -0.97 | -0.97 | 0.03 |
| crypsis | -0.37 | 2.96 | -0.24 | 0.90 | -0.18 | 1.09 | 0.18 | -1.94 | 0.95 | 1.82 | 1.86 | 2.02 | 0.97 | -0.12 |
| **BS** | **0.00** | **1.00** | **1.00** | **2.00** | **0.00** | ***3.00*** | **2.00** | **0.00** | **1.00** | **3.00** | **5.00** | **2.00** | **4.00** | ***2.00*** |
| *node* | *71* | *72* | *73* | *74* | *75* | *76* | *77* | *78* | *79* | *80* | *81* | *82* | *83* | *84* |
| male | -0.09 | -7.30 | -7.02 | -2.28 | -1.96 | -3.27 | -1.67 | -8.41 | -1.66 | -2.64 | -2.07 | -2.02 | -1.28 | -4.57 |
| male gen | 0.77 | 1.75 | *5.22* | 1.97 | -0.01 | 2.32 | 3.69 | *7.63* | 2.89 | 3.31 | 4.97 | 1.19 | -0.21 | 4.83 |
| female | -0.11 | 0.00 | -1.00 | -1.07 | 0.00 | -0.74 | 0.00 | 0.01 | -1.99 | -0.40 | 0.00 | 0.00 | 0.62 | 0.77 |
| larvae | 0.97 | 1.93 | 0.51 | 2.56 | 0.97 | 0.82 | -0.01 | -0.03 | -0.03 | 0.83 | -0.03 | -0.03 | 0.84 | -0.03 |
| male colour | 2.42 | 2.94 | 2.86 | 0.84 | 1.00 | 1.01 | -0.02 | 1.83 | 0.80 | 1.03 | 0.06 | -0.13 | 1.57 | -0.20 |
| female colour | -0.95 | 0.03 | -0.51 | -0.96 | -0.97 | -0.23 | 0.01 | 0.03 | 1.03 | -0.03 | 0.03 | 0.03 | -0.21 | 0.04 |
| crypsis | 0.00 | 2.66 | 2.94 | 0.93 | 1.97 | 2.09 | 0.99 | -0.05 | 0.97 | -0.10 | -1.97 | 0.97 | 0.67 | 1.16 |
| **BS** | ***3.00*** | ***2.00*** | ***3.00*** | ***2.00*** | ***1.00*** | ***2.00*** | **3.00** | ***1.00*** | **2.00** | ***2.00*** | **1.00** | **0.00** | ***2.00*** | **2.00** |
| *node* | *85* | *86* | *87* | *88* | *89* | *90* | *91* | *92* | *93* | *94* | *95* | *96* | *97* | *98* |
| male | -0.96 | -1.68 | -1.67 | -3.06 | -7.00 | -6.07 | -1.82 | 2.93 | -2.70 | -3.73 | -2.62 | 0.06 | -2.02 | -2.22 |
| male gen | -0.78 | 0.98 | 3.76 | 3.24 | *7.14* | *7.38* | 1.04 | *9.58* | 1.90 | 0.73 | 2.80 | -0.02 | *10.77* | 0.45 |
| female | 1.82 | 0.00 | -0.03 | -0.33 | 0.00 | -0.58 | 0.00 | 0.00 | -1.97 | 0.00 | 0.00 | 0.00 | -0.09 | -0.03 |
| larvae | 0.97 | 0.65 | 0.08 | 0.61 | -0.03 | -0.03 | 0.13 | 0.71 | 1.93 | 0.97 | 0.15 | 0.97 | 0.13 | 0.83 |
| male colour | 0.92 | 0.90 | 1.31 | 0.91 | 1.89 | 1.30 | -0.01 | 2.11 | 0.90 | 1.93 | 0.87 | -0.04 | 0.84 | 1.08 |
| female colour | -0.97 | -0.67 | -0.07 | -0.61 | 0.03 | 0.03 | -0.13 | -0.79 | -0.97 | -0.97 | -1.14 | -0.97 | 0.03 | 0.15 |
| crypsis | 1.00 | 0.82 | 0.63 | 0.24 | -1.03 | -0.03 | 0.78 | 0.47 | 2.90 | 2.08 | 2.95 | 1.00 | -0.67 | 0.75 |
| **BS** | ***2.00*** | ***1.00*** | **4.00** | ***1.00*** | ***1.00*** | ***2.00*** | **0.00** | **15.00** | ***2.00*** | ***1.00*** | **3.00** | ***1.00*** | **9.00** | ***1.00*** |
| *node* | *99* | *100* | *101* | *102* | *103* | *104* | *105* | *106* | *107* | *108* | *109* | | | *ALL* |
| male | -2.20 | 1.21 | -3.32 | -3.03 | -0.41 | 0.75 | 4.33 | 1.04 | 2.59 | -0.76 | -1.33 | TOT MALE | | -179.20 |
| male gen | 2.92 | 2.74 | 2.30 | 4.90 | 0.93 | 1.32 | 0.96 | 3.74 | 0.58 | 2.86 | 3.66 | TOT MALE GEN | | 327.40 |
| female | 0.01 | -0.42 | -0.10 | 0.00 | 0.08 | -1.07 | -2.85 | -1.40 | -2.00 | 0.00 | -1.86 | TOT FEMALE | | -42.92 |
| larvae | 0.36 | 0.86 | 0.60 | 0.97 | 0.97 | 2.16 | 0.86 | 1.75 | 3.97 | 0.97 | 2.21 | TOT LARVAE | | 86.18 |
| male colour | 1.56 | 0.46 | 1.07 | 0.05 | -0.04 | 0.39 | -0.23 | -0.72 | -1.00 | -0.05 | 0.23 | TOT MALE COLOUR | | 111.98 |
| female colour | 0.06 | -0.83 | 0.17 | -0.97 | -0.97 | -1.41 | -1.97 | -1.02 | -0.97 | -0.97 | -1.35 | TOT FEMALE COLOUR | | -48.48 |
| crypsis | -0.70 | -1.02 | 0.27 | 0.08 | 2.44 | 2.86 | 2.90 | 0.61 | 0.83 | 0.95 | 1.44 | TOT CRYPSIS | | 87.04 |
| **BS** | ***2.00*** | **3.00** | ***1.00*** | **2.00** | **3.00** | **5.00** | **4.00** | **4.00** | **4.00** | **3.00** | **3.00** | TOT | | **342.00** |

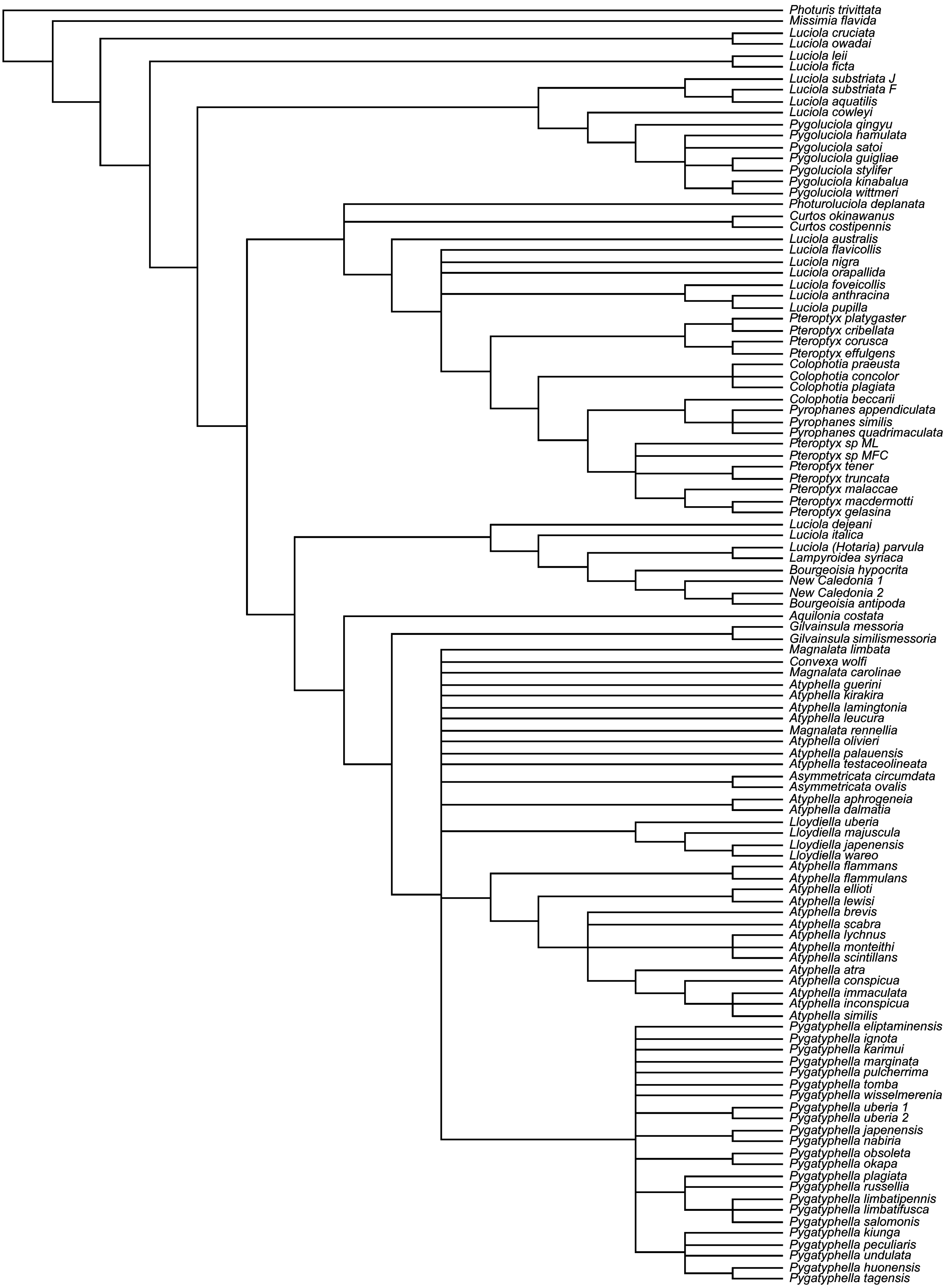


**FIGURE 1.** Strict consensus of 739 most parsimonious trees of length 3387 from phylogenetic analysis of 112 taxa and 343 morphological characters in Table 1.

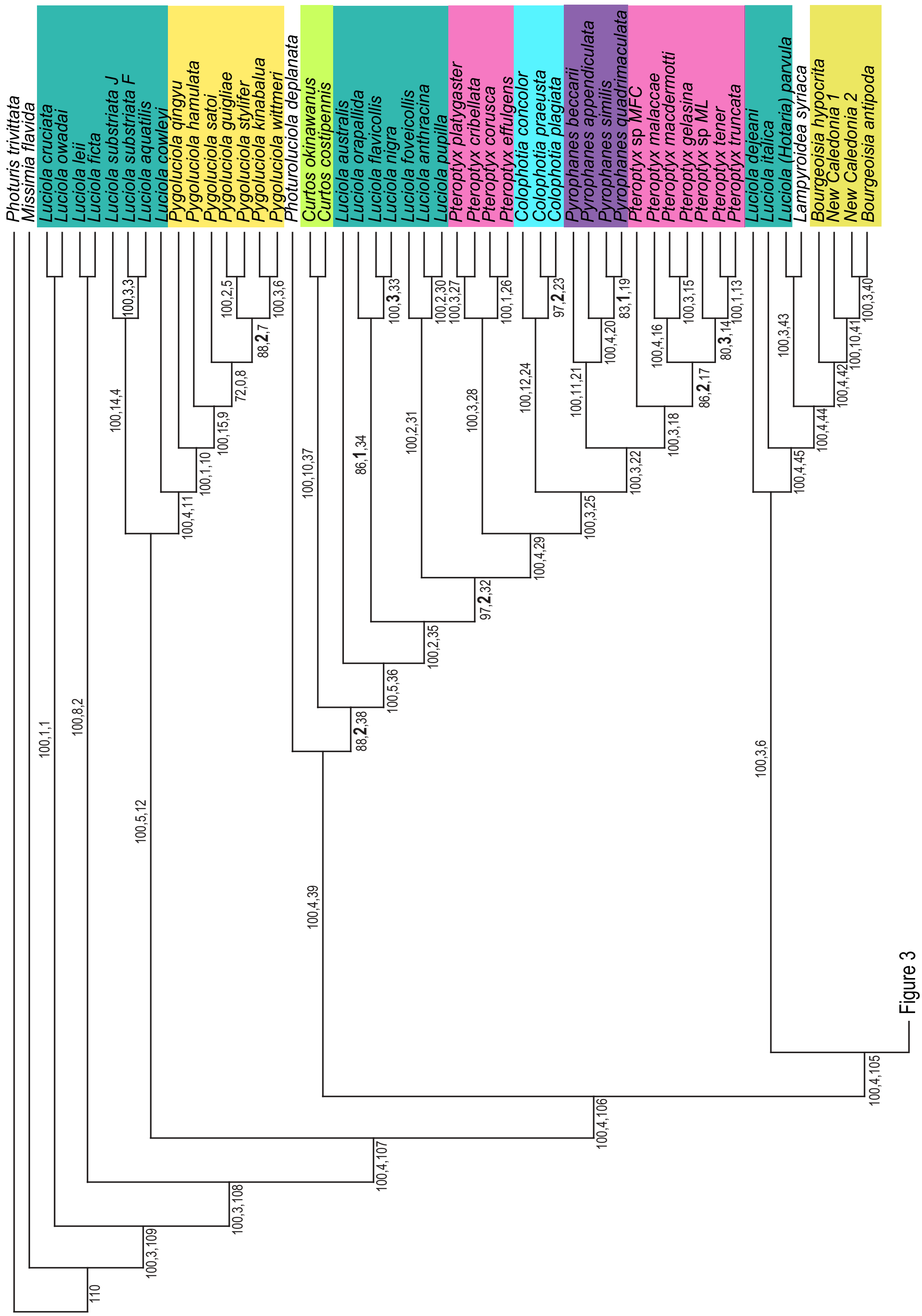


**FIGURE 2.** Preferred MPT equivalent to majority rule consensus of 739 most parsimonious trees of length 3387 from phylogenetic analysis of 112 taxa and 343 morphological characters in Table 1. % of MPTs with the node, BS (bold), and node numbers along the branches. Where TreeRot v.2 was unable to find the shortest MPT, the BS is not bold. Part 1.

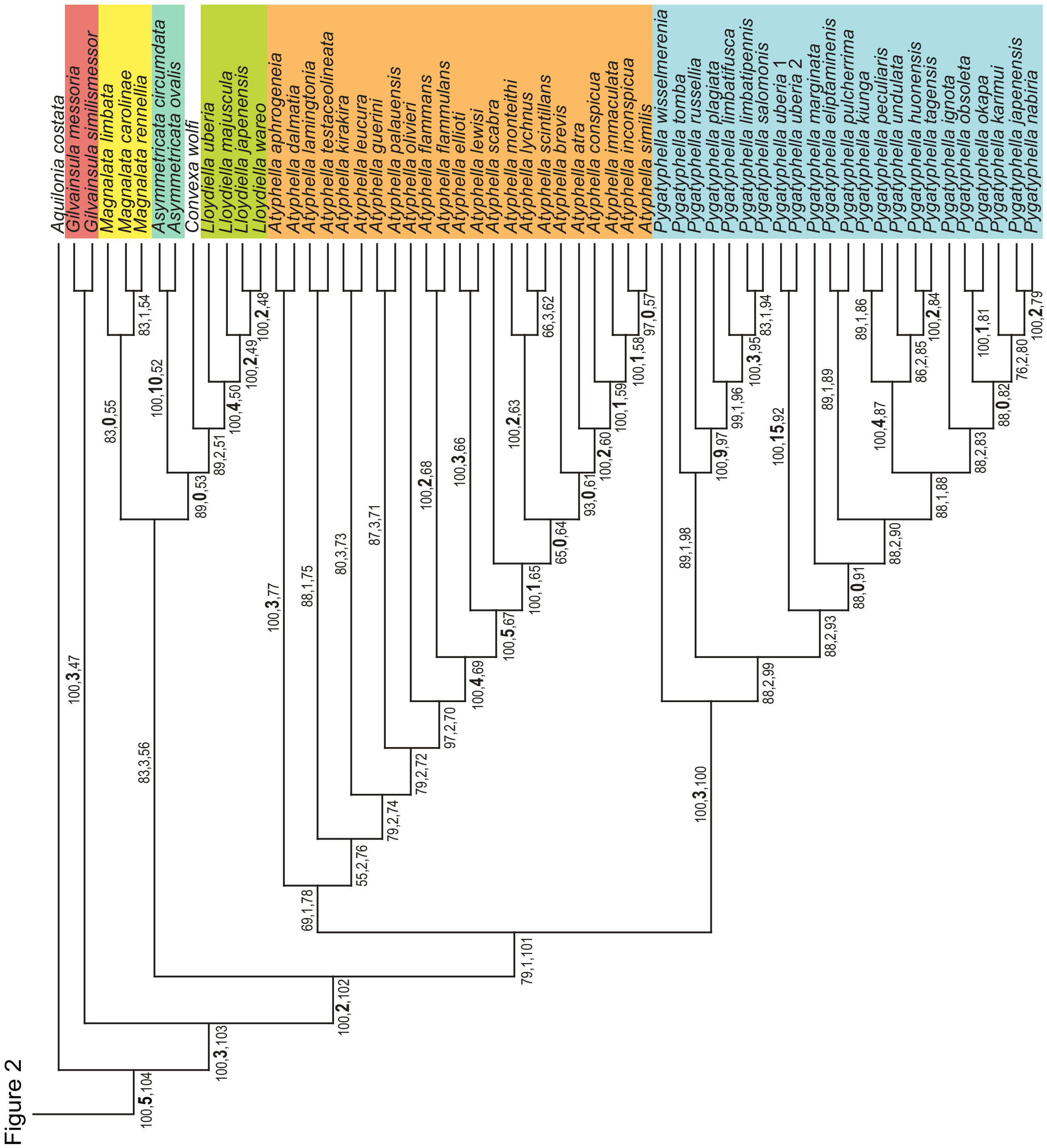


**FIGURE 3** Preferred MPT equivalent to majority rule consensus of 739 most parsimonious trees of length 3387 from phylogenetic analysis of 112 taxa and 343 morphological characters in Table 1. % of MPTs with the node, BS (bold), and node numbers along the branches. Where TreeRot v.2 was unable to find the shortest MPT, the BS is not bold. Part 2.

Ballantyne (1968) erected *Luciola* (*Pygatyphella*) for eight species of New Guinean fireflies, which were distinguished by a striking dorsal colour pattern, and features of the terminal abdomen. Ballantyne and Lambkin (2000, 2001, 2006) assigned three species; *huonensis*, *obsoleta* and *undulata* to *Atyphella*, but no formal actions were taken concerning the status of the subgenus *Pygatyphella* and the remaining five species therein. The possibility existed of a series of cryptic species in *Atyphella obsoleta* and Ballantyne (1968) described a range of colour variations and highlighted the distinctiveness of specimens from Wisselmeren. The phylogenetic analysis provides strong support for a separate clade (Fig. 3, node 100, BS=3, PBS♂ genitalia=2.74) of *Pygatyphella* as a distinct genus of 23 species, as sister to *Atyphella*. The redefined *Pygatyphella* includes *huonensis*, *obsoleta* and *undulata*, and the new species *wisselmerenia* clearly distinct from *obsoleta*. *Pygatyphella eliptaminensis* (Ballantyne), *Pygat. marginata* (Ballantyne), *Pygat. peculiaris* (Olivier) and *Pygat. pulcherrima* (Ballantyne) are transferred from *Luciola* (*Pygatyphella*) Ballantyne. *Pygat. tagensis* (Ballantyne), *Pygat. hounensis* (Ballantyne), *Pygat. obsoleta* (Olivier), and *Pygat. undulata* (Pic) are transferred from *Atyphella* Olliff. *Pygatyphella ignota* (Olivier) and *Pygat. salomonis* (Olivier) are transferred from *Luciola* Laporte. *Pygatyphella limbatipennis* (Pic) is transferred from *Atyphella salomonis* var *limbatipennis* Pic, and *Pygat. plagiata* (Blanchard) is transferred from *Luciola*. Ten new species are described; *Pygat. japenensis* **sp. n.**, *Pygat. karimui* **sp. n.**, *Pygat. kiunga* **sp. n.**, *Pygat. limbatifusca* **sp. n.**, *Pygat. nabiria* **sp. n.**, *Pygat. okapa* **sp. n.**, *Pygat. russellia* **sp. n.**, *Pygat. tomba* **sp. n.**, *Pygat. uberia* **sp. n.**, and *Pygat. wisselmerenia* **sp. n.** with *uberia* representing specimens known in previous analyses as 'Sisiak'.

Strong support for a clade (Fig. 3, node 50, BS=4, PBS♂ colour=1.99) of four species leads to the erection of the new genus; *Lloydiella* for *Ll. majuscula* (Lea) transferred from *Atyphella*, and three new species; *Ll. japenensis* **sp. n.**, *Ll. uberia* **sp. n.**, and *Ll. wareo* **sp. n.**

The majority rule consensus tree of the phylogenetic analysis indicates in 89% of the MPTs that *wolfi* (Olivier) is most closely related to *Lloydiella* and not supported as part of *Atyphella* and therefore the monotypic *Convexa* **gen. n.** is erected for *C. wolfi*.

Two SE Asian species of *Luciola* form a very strongly supported clade (Fig. 3, node 52, BS=10, PBS♂ genitalia=10.15) sister to the clade of *Lloydiella* and *Convexa* and are placed in the new genus *Asymmetricata* **gen. n.** as *As. ovalis* (Hope) and *As. circumdata* (Motsch.).

The majority rule consensus tree indicates in 83% of the MPTs that three species form a clade, sister to *Asymmetricata*, *Lloydiella*, and *Convexa* and they are placed in a new genus, *Magnalata* **gen. n.** for *M. limbata* (Blanchard) transferred from *Luciola*, *M. carolinae* (Olivier) transferred from *Atyphella* and a new species *M. rennellia* **sp. n.** While there is little support for this clade, there is no support for the inclusion of any of these three species in any other existing or new genus.

*Gilvainsula* **gen. n.** is described for a well-supported clade (Fig. 3, node 47, BS=3, PBS♂ genitalia=3.86) sister to *Asymmetricata*, *Lloydiella*, *Convexa*, *Atyphella*, and *Pygatyphella* for *G. messoria* (Olivier), transferred from *Atyphella* Olliff and a new species *G. similismessoria* **sp. n.**

*Aquilonia* **gen. n.** is described for the distinct, single species, *Aq. costata* (Lea), which is transferred from *Atyphella* Olliff, to which it clearly does not belong.

The *Atyphella* complex (Fig. 3, node 104, BS=5) containing *Aquilonia*, *Gilvainsula*, *Magnalata*, *Asymmetricata*, *Lloydiella*, *Convexa*, *Atyphella*, and *Pygatyphella* is strongly supported in the phylogenetic analysis, as distinct from the clade *Luciola* represented by the type species *L. italica*.

While the relationships in the *Luciola* clade are not dealt with in this study, the opportunity is taken to deal with supported relationships within several other of the outgroup clades in this, our most comprehensive, phylogenetic analysis. The monotypic *Missimia* **gen. n.** is erected for four specimens dealt with in previous phylogenetic analyses as 'Mt Missim', and assigned to the distinct *M. flavida* **sp. n.**

The monotypic *Photuroluciola* (Pic) for the species *Photuro. deplanata* Pic is raised to generic status from a subgenus of *Luciola* from which the analysis shows it is clearly distinct, and only distantly related.

*Pygoluciola* is clearly distinct and separate from *Atyphella*. The genus *Pygoluciola* (node 1 Fig. 2) receives very high Bremer support in this analysis of the Luciolinae.

## Taxonomy

### Key to genera of Luciolinae using males

This key reflects the results obtained in the phylogenetic analysis herein (see Figs 1–3) and is expanded from Fu and Ballantyne (2008). Certain *Luciola* species may not key to a genus here and are highlighted in the Discussion.

1. Clypeolabral suture absent; labrum well sclerotised, inflexible, inflexibly joined to rest of head; in specimen held horizontally and viewed from beneath humerus visible, not covered by epipleuron; posterolateral corners of pronotum very acute and pointed (Figs 21, 22, 27, 29, 30, 32–34)............ *Missimia* **gen. n.**
   Clypeolabral suture present (Figs 28, 31), labrum not well sclerotised, flexible, junction between rest of head and labrum flexible; in specimen held horizontally and viewed from beneath humerus not visible, is covered by epipleuron; posterolateral corners of pronotum not very acute and pointed........................... 2
2. When viewed from the side midlateral margins of pronotum elevated (appear sinuate from side); asymmetrical ML of aedeagus with acute apex, finely serrate along dorsal edges, bearing infolding flaps behind apex; left LL with preapical flap (right LL lacking flap); from beneath LL just visible at sides of ML, both apices not usually visible in same plane, separated in apical 1/3 only; aedeagal sheath sternite posterior to tergite articulations subparallel-sided in basal 1/3, then unevenly emarginated on both sides and narrowing to a slender obliquely truncate apex (Figs 38–55); Fu & Ballantyne, 2008 Figs 41–55........................
   .............................................................................................................................. *Photuroluciola* Pic
   When viewed from the side midlateral margins of pronotum not elevated; if ML of aedeagus asymmetrical then lacking apex as above; no serrations along ML apex nor infolding flaps behind apex; neither LL with preapical flap; viewed from beneath LL either concealed behind ML at their apices or widely visible at the sides of the ML; aedeagal sheath subparallel-sided in basal portion or laterally emarginate; if subparallel-sided not emarginated on both sides towards its apex nor narrowing to an obliquely truncate apex (Figs 35, 36, 37)............................................................................................................................ 3
3. Eyes with strong posterior emargination; LO absent in V7 in *B. hypocrita*; very dark almost black dorsal colouration (Fig. 59)............................................................................... *Bourgeoisia* Olivier <u>Partim</u>[1]
   Eyes lacking strong posterior emargination; LO present in V7 (may be entire or bipartite); dorsal colouration variable, seldom as above.................................................................................................... 4
4. LL of aedeagus widely visible at sides of ML when aedeagus viewed from beneath; pronotum wider than or subequal to humeral width, rarely less than (Figs 35, 73, 76)............................................................ 5
   LL of aedeagus not visible at sides of ML when aedeagus viewed from beneath; pronotum always narrower than humeral width (Figs 36, 75) ........................................................................................ 16
5. Elytral humeral carina absent; elytral punctation not conspicuous, not evenly spaced, not as wide and deep as that of pronotum; MPP short, squat, barely produced; aedeagus with LL as wide at their bases as at their apices; LL bearing elongate slender flattened lobes along inner (ventral) margins; ML strongly laterally compressed, curving ventrally with preapical point (as in Fig. 514) (Ballantyne, 1968 Figs 162c, 169)
   .................................................................................................................................. *Luciola* <u>Partim</u>[2]
   Elytral humeral carina present (Figs 57, 58) or absent; elytral punctation either not conspicuous, not evenly spaced, not as wide and as deep as that of pronotum, or conspicuous, evenly spaced and similar in size to that of pronotum (Figs 57, 58); MPP always obviously developed, sometimes L>W with apex inclined dorsally (Figs 60, 61); aedeagal LL always narrower at apices than at bases; LL lacking elongate slender flattened lobes on inner (ventral) margins; ML not strongly laterally compressed nor with preapical point ...................................................................................................................................... 6
6. Elytral humeral carina developed; punctation of elytra conspicuous, evenly spaced, as wide and deep as

that of pronotum; LL of uneven length (Figs 57, 58)................................................*Curtos* Motschulsky
Elytral humeral carina not developed, punctation of elytra not any larger and deeper than that of pronotum, usually smaller and narrower; LL of even length.............................................................................. 7

7. MPP of V7 elongate and inclining dorsally; median posterior margin of T8 narrowly produced and inclining ventrally where it may envelop the MPP (Ballantyne & Lambkin, 2006 Figs 25, 26) (Fig. 60) ........... ............................................................................................................ *Pygoluciola* Wittmer Partim[3]
MPP developed, may be elongate (L>W), not inclining strongly dorsally unless terminated by paired hooks (Figs 98–100); median posterior margin of tergite 8 not narrowly produced and inclining ventrally ........................................................................................................................................ 8

8. Aedeagal sheath sternite with narrow elongate anterior portion and expanded posterior area; lateral arms of tergite widely visible at sides of sheath sternite and extending forward; aedeagus with strongly asymmetrical bilobed basal piece; MPP scarcely produced; V7 almost entirely occupied by LO; posterolateral corners of T8 very narrowly pointed, and slightly down turned (Fu & Ballantyne 2008 Figs 17, 19; Ballantyne 2008 Fig. 9) ...................................................................... *Pygoluciola* Wittmer Partim[3]
Aedeagal sheath sternite lacking narrow elongate portion and expanded posterior area; if lateral arms of tergite visible at sides of sternite then close to sternite margins or not developed as above; aedeagus with basal piece not usually bilobed or asymmetrical ........................................................................ 9

9. Pronotum wider than width across elytral humeri; often with small indentation along posterolateral margin, near corner (Fig. 64); anterior hypomeron never strongly flattened, often delimited from posterior hypomeron by sloping area especially if head can be withdrawn into prothoracic cavity; posterior area of hypomeron widely flattened and closely adpressed; elytra never with ridge continuing around apex (Figs 69–71); dorsal colouration often with median dark pronotal mark, dark markings on either or both of MS and MN, and at elytral base dark markings either of triangular form adjacent to MS or restricted to basal half of suture only (Figs 64, 69–71); apical segment of labial palpi like a wide flattened triangle with 3 or more teeth on inner margin; posterior half of V7 usually arched, sometimes swollen (Figs 61, 62) (not arched in *Pygat. wisselmerenia*); MPP always developed, usually longer than wide, with apex rounded, or squarely or obliquely truncate; LO usually retracted into anterior half or less of V7 (except in *Pygat. wisselmerenia* where it occupies most of V7), sometimes bipartite; tergite 8 symmetrical, not narrowed in posterior half, posterior margin thick and down turned and engulfing the MPP in *undulata* only (Figs 504–506).......................................................................................... *Pygatyphella* (Ballantyne)
Pronotum wider than, or subequal to, width across elytral humeri, lateral margin lacking small indentation along posterolateral margin near corner; anterior hypomeron often strongly flattened, if not flattened then not obviously delimited from posterior hypomeron by sloping area (Fig. 84); posterior area of hypomeron narrowly to widely flattened and often closely adpressed; elytra often with ridge continuing around apex (Fig. 83); dorsal colouration variable, rarely as described above; apical segment of labial palpi variable, either like a narrow to wide flattened triangle with 2 or more teeth on inner margin, or inner margin irregular not dentate, or ovoid, inner margin lacking teeth; posterior half of V7 not arched, or swollen; MPP short, or longer than wide, apex rounded, usually symmetrical, may be medianly shallowly emarginated; LO entire or bipartite, occupying most of the area of V7 or retracted into anterior half or less; tergite 8 usually symmetrical, may be asymmetrical and partially engulfing MPP from above (Figs 6, 7, 108–111) ...................................................................................................................................... 10

10. Tergite 8 strongly asymmetrical; V7 LO bipartite, or entire with anterior median emargination (Figs 6, 7, 108–111) ........................................................................................... *Asymmetricata* **gen. n.**
Tergite 8 symmetrical, not strongly emarginated on right side; LO bipartite or entire, if entire lacking anterior median emargination.............................................................................................. 11

11. Pronotum wider than width across elytral humeri; pronotal punctation small sparse, intervening areas very smooth and shiny; elytral margins convex-sided; ML constricted just behind apex (Figs 12, 13, 73, 74) ...

.......................................................................................................................... *Convexa* **gen. n.**

Pronotum wider than or subequal in width to width across elytral humeri (Figs 76, 77); pronotal punctation not small and sparse; elytral margins convex or parallel-sided; ML not constricted just behind apex .......................................................................................................................................... 12

12. Dorsal colouration pale, yellowish or very pale brown, with elytral apices often dark brown (Fig. 4)..... 13

Dorsal colouration never as above; pronotum orange with or without a median dark mark; elytra very dark brown to black, often with lateral and sutural margins orange, or elytra brown with paler stripes corresponding at least in part to interstitial lines ....................................................................................... 14

13. Pronotum parallel-sided, margins straight or pronotum slightly wider across middle than elsewhere; pronotal width subequal to humeral width; elytra parallel-sided with 2 well–defined interstitial lines (1,2); apical segment of labial palp with inner margin with 2 teeth (Fig. 4)............................. *Aquilonia* **gen. n.**

Pronotum not subparallel-sided, lateral margins diverge with rounded convergence in posterior area (pronotum wider across posterior 2/3 than elsewhere); pronotal width subequal to or greater than humeral width; elytra convex-sided, 2 interstitial lines well–defined or not; apical segment of labial palpi with inner margin irregular, not dentate (Figs 15, 16)........................................................ *Gilvainsula* **gen. n.**

14. Pronotal width subequal to humeral width; anterior hypomeron not flat to neck; 2–3 interstitial lines; antennae longer than GHW; apical segment of labial palpi dentate and laterally flattened, 2 or more teeth; median longitudinal trough sometimes present on ventral surface of T8 (Ballantyne & Lambkin, 2000 Fig. 3L); anterior prolongations of T8 usually longer than posterior entire portion, narrow and expanded vertically; aedeagus with LL/ML wide; LL do not diverge along their median dorsal length and are narrower at their apex than ML; BP hooded (Figs 19, 20, 76, 80–82) ............................................... *Lloydiella* **gen. n.**

Pronotal width subequal to or greater than humeral width; anterior hypomeron sometimes flat to neck; 0–4 interstitial lines; antennae less than, subequal to or >GHW; apical segment of labial palpi either laterally flattened with inner margin having 2 or more teeth, or lacking teeth with inner margin irregular, or ovoid, with inner margin entire; median longitudinal trough on ventral surface of T8 absent; anterior prolongations of T8 never longer than posterior entire portion, may be very short or absent; aedeagus with LL/ML moderate; LL may diverge along their median dorsal length and at their apex subequal to or sometimes narrower than ML; BP not hooded ........................................................................................... 15

15. Pronotum wider across posterior margin than rest, never subparallel-sided (Fig. 77); posterolateral corners rounded and extending beyond median posterior margin; anterior hypomeron flat to neck in *rennellia* only; flattened posterior strongly adpressed except in *limbata*; pronotal with/GHW from beneath 1.6 or greater; epipleuron not continuing around apex as ridge; antennal sockets never contiguous; frons-vertex junction rounded, never angulate; mouthparts functional; apical segment of labial palpi strongly flattened, like a narrow to wide triangle, with inner margin either irregular not dentate, or dentate with 2 teeth; dorsal colouration often orange pronotum with dark brown elytra having lateral margin orange (Figs 17, 18, 77) .............................................................................................................. *Magnalata* **gen. n.**

Pronotum often wider across posterior margin than rest (Figs 9–11, 78, 79, 84) sometimes subparallel-sided; posterolateral corners rounded or angulate, sometimes extending beyond median posterior margin; anterior hypomeron flat to neck in Australian species (Figs 9, 10 78, 79, 84, 85) and *A. scabra*; flattened posterior area strongly adpressed; pronotal width/GHW from beneath 1.6 or less; epipleuron may continue around apex as a ridge; antennal sockets sometimes contiguous; frons-vertex junction rounded, or angulate; Mouthparts functional or not; apical segment of labial palpi often strongly flattened, of form of narrow to wide triangle, with inner margin either dentate or irregular, not dentate in *A. guerini* and *A. palauensis* only; if dentate then usually more than 2 teeth; apical segment of labial palpi often ovoid entire ......................................................................................................................... *Atyphella* Olliff

16. Deflexed elytral apices present (*Pteroptyx* Olivier[4]) (Fig. 96) ............................................................. 17

Deflexed elytral apices absent ........................................................................................ 18

17. Metafemoral comb present; aedeagal sheath with paraprocts (Ballantyne 1987a Fig. 4a–d); Figs 86–89, 94, 95) ........................................................................................................ *Pteroptyx* A Partim[4]
    Metafemoral comb absent; aedeagal sheath lacking paraprocts (Ballantyne 1987a Fig. 4e–h) (Figs 90–93); LO entire or bipartite; entire LO often with paired cuticular strips on dorsal surface in V7 (Fig. 97) ......... ........................................................................................................ *Pteroptyx* B Partim[4]
18. Median carina on V7 between LO halves present; aedeagal sheath at least 4 times as long as wide, usually longer; antennae with apical 3 segments shortened; T8 with very long anterolateral arms (Figs 101–105) ........................................................................................................ *Colophotia* Olivier[5]
    Median carina absent; aedeagal sheath never very long and slender; antennal segments not shortened; T8 anterolateral arms not conspicuously elongated ........................................................................ 19
19. Incurving hairy lobes and pointed projections present along posterior margin of V7; MFC present; aedeagal sheath with paraprocts (Figs 106, 107) ........................................................ *Pyrophanes* Olivier[6]
    Incurving hairy lobes and pointed projections along posterior margin of V7 absent; MFC absent; aedeagal sheath lacking paraprocts .......................................................................... *Luciola* Partim[7]

1. Part of *Luciola* s. str. clade (see Table 4). *Bourgeoisia* is distinguished. *Lampyroidea syriaca* is keyed in couplet 4, as the eye excavation is not visible when the head is retracted, unlike *Bourgeoisia*. *Luciola cowleyi* Blackburn with strongly emarginate eyes will key to *Pygoluciola* in couplet 7.
2. *Luciola* s. str. Three species of *Luciola (italica, dejeani* and *parvula)*, and *Lampyroidea* spp. are distinguished.
3. This analysis confirms an expanded definition of *Pygoluciola* (Fu & Ballantyne, 2008).
4. *Pteroptyx* is composed of two elements, A=*Pteroptyx* s str., B=New Guinean *Pteroptyx* which will require a new generic name (Ballantyne & Lambkin work in progress).
5. This key distinguishes those species of *Colophotia* Olivier with a median carina between LO halves on V7, consistent with the type species *C. praeusta* Erichs.
6. All known species of *Pyrophanes* have the same arrangement of lobes and projections along the posterior margin of V7.
7. The *Luciola* keyed here are several species of Australian (see Ballantyne & Lambkin 2000) and New Guinean *Luciola* (Ballantyne & Lambkin in prep.); their morphology is inconsistent with that of *Luciola* s. str.

## ***Aquilonia* gen. n.**
(Fig. 4)

**Type species:** *Atyphella costata* (Lea) by monotypy.

**Diagnosis**. *Aquilonia* is distinguished most obviously by its dorsal colour pattern, which is approached in the study area by two species of *Gilvainsula* **gen. n.**, and *Pygatyphella russellia* **sp. n.** It differs from *Gilvainsula* **gen. n.** by the parallel-sided elytra and pronotum, and the toothed apical segment of labial palpi, and from *Pygat. russellia* by the absence of an arched V7 posterior to the LO, and tergite 8 lacking any median ridges. It differs from most *Atyphella* by its distinctive dorsal colour, the subparallel-sided pronotum, pronotal width subequal to that of elytral humerus, [two features it shares with *A. inconspicua*], and it shares with most species of *Lloydiella* **gen. n.** an aedeagal complex pattern with lateral lobes not divergent along their dorsal length and their inner preapical margins obliquely truncate, while differing in the colour pattern

**Male.** Pronotum (Ballantyne & Lambkin 2000:Fig. 1h) dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate. Pronotum subparallel-sided; pronotal width subequal to humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half subparallel-sided; lateral margins in posterior half subparallel-sided; lateral margins lacking indentation at mid-point, or sinuousity in either horizontal or vertical plane; subparallel-sided margins straight; lacking indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners rounded obtuse; posterolateral corners project as far as median posterior margin and separated from it by shallow emarginations.

Hypomera closed. Median area of hypomeron not elevated in vertical direction; anterior area of hypomeron not flat, posterior area flat, closely adpressed or not; pronotal width/ GHW index 1.4–1.5.

Elytron punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extend beyond mid-point, almost to apex but not as ridge around apex, neither thickened in apical half; 2 interstitial lines (1, 2) not exceeding suture; elytral carina absent; in horizontal specimen viewed from below epipleuron at elytral base wide, covering humerus, viewed from above epipleuron arises anterior to posterior margin of MS; epipleuron developed as a lateral ridge along most of length; sutural margins approximate along most of length in closed elytra; lateral margins parallel-sided.

Head moderately depressed between eyes; well exposed in front of pronotum, not capable of complete retraction within prothoracic cavity; eyes moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum moderately separated; frons-vertex junction rounded, lacking median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous, separated by up to ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when head viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non-lunate, strongly flattened, of form of wide triangle, with inner edge dentate (2 teeth). Antennae 11 segmented; length>GHW to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Ballantyne & Lambkin 2000 Fig. 3 d, e) lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment; LO in V7 entire occupying more than half V7, reaching to sides but not posterior margin [Ballantyne & Lambkin (2000 Fig 3g) illustrated V 7 withdrawn beneath V 6 thus the full extent of V7 and lateral margins of LO not fully visible]; posterior half of V7 not arched or swollen, muscle impressions not visible in this area; neither anterior nor posterior margin of LO emarginate; LO present in V6, occupying almost all V6. MPP present, symmetrical, apex rounded, entire, not laterally compressed, L=W, not inclined dorsally nor engulfed by T8 apex, lacking dorsal ridge, median longitudinal trough. V7 lacking median carina, median longitudinal trough, anteromedian depression on face of LO, PLP, incurving lobes or pointed projections, median ‘dimple’, or reflexed lobes. T7 lacking prolonged posterolateral corners. T8 not strongly sclerotised, symmetrical, W=L, visible posterior area not narrowing abruptly, lacking prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally nor engulfing posterior margin of V7 nor MPP, not extending conspicuously beyond posterior margin of V7; T8 ventral surface lacking flanges, lateral depressed troughs, median longitudinal trough, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 very short, not laterally emarginated before their origins, not expanded dorsoventrally, lacking bifurcation of inner margin and ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath never > 4 times as long as wide; lacking paraprocts; asymmetrical in posterior area where sheath sternite emarginated on right from point of attachment of tergite; sternite not angulate on L or R sides, not subparallel-sided, posterior margin entire, rounded, not emarginated on either side preapically, apex rounded; anterior half of sternite broad, apically rounded; tergite lacking lateral arms extending anteriorly at sides of sheath sternite; tergite not subdivided, lacking projecting pieces along posterior margin of tergite 9, anterior margin lacking transverse band.

Aedeagus L/W 3/1 or shorter; subparallel-sided; LL lack lateral appendages; LL visible from beneath at sides of ML, LL/ML wide to moderate; LL of equal length, slightly shorter than ML, not diverging along inner dorsal margins, separated there by > half their length; LL base width not = LL apex width which is narrower than that of ML; LL apices not expanded in horizontal plane; dorsal base of LL symmetrical, not excavated, median margin prolonged, broadly rounded; LL lacking lateral hairy appendages along their outer ventral margins, not produced preapically nor narrowly on inner apical margin, obliquely truncate along preapical inner margins; apices of LL not inturned, nor out–turned; lacking projection on left LL; inner margins lacking slender leaf-like projection; ML symmetrical, lacking paired lateral teeth and tooth to left side, not strongly arched, apex not shaped like arrowhead, not bulbous, not inclined ventrally; BP not very narrow, not strongly sclerotised, not hooded, not strongly emarginated along anterior margin.

**Female.** Macropterous and observed in flight. Pronotum lacking irregularities in posterolateral areas; punctation moderate to dense; pronotum subequal to humeral width; lacking indentation of lateral margin, irregularities at posterolateral corner; outline similar to that of male. Elytral punctation not as large as that of pronotum, nor evenly spaced; 2 interstitial lines; elytral carina absent. No legs or parts thereof swollen and /or curved. LO in V6 only, lacking any elevations or depressions or ridges on V7.

**Larva** not associated.

**Etymology**. *Aquilonia* (feminine, from aquilonius Latin, northern) describes the northerly distribution in Australia of the single known species.

**Remarks**. *Aquilonia* **gen. n.** is known from one Australian species, which is unusual in its distribution (restricted to the northern tropical areas in open forest), and its colour. While the dorsal colour pattern of light brown to yellow/orange, often with elytral apices black, is widespread in Asia, it is rare in Australia and New Guinea and seen only in this species, two species of *Gilvainsula* **gen. n.**, and *Pygatyphella russellia* **sp. n.** No Asian species with this colouration investigated thus far (Ballantyne work in progress) conforms with *A. costata*.

### *Aquilonia costata* (Lea)
(Fig. 4)

*Luciola costata* Lea, 1921b:66.
*Luciola (Luciola) costata* Lea. McDermott, 1966:102. Calder, 1998:178.
*Atyphella costata* (Lea). Ballantyne & Lambkin, 2000:31.

**Holotype**. Male. **AUSTRALIA**: Northern Territory: 14.44S 131.08E, Flora River, IX.1912, Spencer (MV).

**Material examined**. **AUSTRALIA**: Northern Territory: 14.30S, 132.15E, 3 km SSW Katherine, 12.XI.1979 T Weir, 2 males (ANIC).

**Diagnosis**. Males 7.7–9.7 mm long; the only reliably recorded Australian firefly with dorsal yellow/ orange colouration and black elytral apices. *Luciola dejeani* Gemminger has similar colouration but is probably not Australian and appears close to *Luciola chinensis* (Ballantyne & Lambkin, 2000:59). Larvae unknown.

### *Asymmetricata* gen. n.
(Figs 5–8, 108–114)

**Type species:** *Luciola circumdata* (Motsch.)

**Diagnosis**. Dorsal surface, especially shape of pronotum, similar to many *Atyphella*; colour very like *C. wolfi* from above; distinguished from all other Luciolinae by the asymmetrical tergite 8 which is emarginate on its right side (Fig. 7).

**Male.** Pronotum (Fig. 5) dorsal surface lacking irregularities in posterolateral areas, longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate.

Pronotum wider across posterior area than rest, pronotal width greater than humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent; lateral margins in posterior half diverge then converge with rounded convergence; lacking indentation at mid-point, or sinuousity in either horizontal or vertical plane; lacking indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners rounded; rounded corners obtuse, posterolateral corners project as far as or beyond median posterior margin, separated from it by shallow emargination.

Hypomera closed. Median area of hypomeron not elevated vertically; anterior area of hypomeron not flattened, posterior area of hypomeron widely flattened and strongly adpressed; pronotal width/ GHW index 1.6.

Elytron (Fig. 5) punctation dense, not linear, not as large as pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extending beyond mid-point almost to apex, not extending as ridge around apex; no expansion of epipleuron or sutural ridge in apical half; 2 interstitial lines, inner two do not exceed suture; elytral carina absent; in horizontal specimen viewed from beneath epipleuron at elytral base wide, covers humerus; viewed from above arises anterior to posterior margin of MS; epipleuron developed as lateral ridge along most of length; sutural margins approximate along most of their length in closed elytra; lateral margins convex–sided.

Head (Fig. 6) moderately depressed between eyes; moderately exposed in front of pronotum, not capable of complete retraction within prothoracic cavity; eyes moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum close to moderately separated; frons-vertex junction rounded, with no median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous and separated by < ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when head viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non-lunate, strongly flattened, wide triangular shape with inner edge dentate. Antennae 11 segmented; length > GHW to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel; in very short antennae FS may be subequal in length and width.

Legs (Fig. 6) with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Figs 6, 7, 108–111) lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment; LO in V7 entire or bipartite, reaching to sides but not to posterior margin; both entire and bipartite LO occupying most of V7; anterior margin of entire LO in V7 narrowly medially emarginate; posterior half of V7 not arched or swollen, muscle impressions not visible here; LO present in V6, occupying almost all V6. MPP present, symmetrical or asymmetrical; medially shallowly emarginate or not; non-emarginate MPP apex rounded, entire; not laterally compressed, short or L=W, slightly inclined dorsally, sometimes engulfed by T8 apex, lacking dorsal ridge, dorsal median longitudinal trough. V7 lacking median carina, PLP, incurving lobes or pointed projections, median 'dimple', or reflexed lobes; V7 with median longitudinal trough between halves of bipartite LO, anteromedian face of entire LO with narrow longitudinal depression. T7 lacking prolonged posterolateral corners. T8 strongly sclerotised, asymmetrical, emarginated on right side, L>W, visible posterior area not narrowing abruptly, lacking prolonged posterolateral corners, median posterior emargination, median posterior projections; inclining ventrally, engulfing MPP, not extending conspicuously beyond posterior margin of V7. T8 ventral surface lacking flanges, lateral depressed troughs, median longitudinal trough, asymmetrical projections, median posterior ridge; T8 with concealed anterolateral arms as long as visible posterior portion of T8, narrow in horizontal plane and expanded dorsoventrally, not laterally emarginated before their origins, apices lacking bifurcation of inner margin and bases lacking ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath (Figs 115–117) never > 4 times as long as wide; lacking paraprocts; symmetrical in posterior area where sheath sternite subparallel-sided along length; sternite not angulate on L or R sides, posterior area not evenly emarginated on either side preapically, posterior margin of sternite broadly and slightly asymmetrically emarginated; anterior half of sternite broad, apically rounded; tergite lateral arms extending narrowly anteriorly to sides of sheath sternite; tergite not subdivided, lacking projecting pieces along posterior margin of tergite 9, anterior margin of tergite darker than rest with lateral margins narrowly darker (wider and slightly longer on right side).

Aedeagus (Figs 112–114) L/W 3/1; LL lacking lateral appendages, visible from beneath at sides of ML, LL/ML wide; LL of equal length, slightly shorter than ML, diverging along inner margins, separated there by > half their length; LL base width not = LL apex width; LL apex width subequal to ML width; LL apices not expanded horizontally; dorsal base of LL asymmetrical, not excavated, anterior margin prolonged to left; LL lacking lateral hairy appendages along outer ventral margins, margins not produced preapically nor narrowly on inner apical margin, not obliquely truncate along preapical inner margins; apices of LL not inturned, or out–turned; lacking projection on left LL only; inner margins lacking slender leaf-like projection; ML symmetrical, lacking paired lateral teeth, tooth to left side; not strongly arched, apex not shaped like arrowhead, not bulbous, not inclined ventrally; BP hooded, not very narrow, not strongly sclerotised, not strongly emarginated along anterior margin.

**Female.** Macropterous in *As. ovalis* (Fig. 14), assumed capable of flight. Pronotum lacking irregularities in posterolateral areas; punctation moderate to dense; pronotum > humeral width; indentation of lateral margin, irregularities at posterolateral corner, absent; outline similar to male. Elytral punctation not as large as pronotum nor evenly spaced; 2 interstitial lines; elytral carina absent. No legs or parts thereof swollen and/or curved. LO in V6 only, V7 lacking any elevations, depressions or ridges.

Larva not associated.

**Etymology**. *Asymmetricata* is a feminine noun latinised from the English word asymmetrical. If the last two syllables (at-a) are pronounced with the first ‘a’ sounded ‘ay’ (as in hay), then the generic name aptly evokes the distinguishing feature of an asymmetrical tergite 8.

**Remarks**. Ballantyne included representatives of all recognised species groups within the Luciolinae for this analysis, including these species. The *Atyphella* complex was shown to be paraphyletic, with the clear separation of these two species from *Atyphella*. This new genus is however based on a very restricted treatment and hindered by lack of specimens, and Ballantyne’s inability to borrow type material of *L. ovalis*. Ballantyne (1987b) described the asymmetrical T8 in males in *Luciola circumdata* and suggested the aedeagus would have to be extracted dorsally. This feature is doubtless more widespread than this restricted treatment allows, and it is probable that *L. impressa* Olivier and *L. humeralis* Walker belong here.

### Key to species of *Asymmetricata* gen. n. using males

1. LO in V7 entire ........................................................................................*circumdata* (Motsch.)
   LO in V7 bipartite ........................................................................................ *ovalis* (Hope)

### *Asymmetricata circumdata* (Motsch.)
(Figs 5, 6, 8, 108, 109, 112–117)

*Luciola circumdata* Motschulsky, 1854:50 (female). Lacordaire, 1857:338. Olivier, 1885:364 (Male, female); 1902:84. Bourgeois, 1890:184. McDermott, 1964:44; 1966: 101. Ballantyne, 1987b:181, Fig. 1.

**Holotype**. Female. ‘Indes orientales’ [A. N. Severtzov Institute of Animal Morphology, Moscow] (examined by, and abdomen drawn by Mrs E. Davydova).

**Material examined. THAILAND**: 8.59N, 99.06E, nr Ban Bang Pla, off Rt 8091, SW Kathun Baen, 29.vi.1980, J E Lloyd, S Wing, male (T8043) (Lloyd). 9.57N, 98.38E, Ranong, Queen Sirikit Park, 10.v.1997, P. Sommartya, 3 males (ANIC). 13.32N, 100.16E, Samut Sakhon rt 35 just W jct 3097, 7.viii.1980, J E Lloyd, male (T8062) (Lloyd). 15.42N, 100.08E, Nakhon Sawan Bung Boraphet, 11.vi.1997, S. Divasiri, male

(ANIC). Chomlong, 18.v.1961, K. Iwata, male (ANIC). **CAMBODIA**: Cheko, 13.iii.1965, K Yoshikawa, 2 males (ANIC).

**Diagnosis**. One of two *Asymmetricata* species with orange pronotum, and dark brown elytra with orange margins; distinguished from the similar *A. ovalis* by the entire LO in V7 (that of *ovalis* is bipartite). Very similar in colouration and dorsal facies to that of *Convexa wolfi*, distinguished by the asymmetrical tergite 8 (that of *C. wolfi* is symmetrical).

**Male redescription.** 11.2–12.2 mm long; 4.5–5.2 mm wide; W/L 0.4. Colour: (Figs 5, 6) Pronotum, MS, MN and sutural, apical and lateral margins of elytra orange, rest of elytra, head, antennae and palpi dark brown; irregular retraction of fat body under pronotum may confuse interpretation of colour; ventral surface of thorax, and legs, orange except for dark brown tibiae and tarsi; abdominal V2–5 very dark brown, LO white; MPP slightly yellow; tergites 7, 8 yellow, semitransparent, rest mottled mid-brown. Pronotum: 2.2–2.7 mm long, 4.0–4.7 mm wide; W/L 1.7–1.8; area between anterior and posterior hypomeron slightly angulate. Elytra: convex-sided, 9.0–9.5 mm long, 4 interstitial lines visible, inner two approach suture in height, outer two not as well–defined. Head: GHW 2.4–2.5mm; SIW 0.4–0.5 mm; SIW/ GHW 1/5–1/6; ASD subequal to ASW; frons-vertex junction rounded, frons about 1 x ASW high. Abdomen: (Figs 6, 108, 109) narrow antero-median depression of LO in V7 not visible in some pinned specimens where segments have contracted lengthwise; fine median longitudinal depression along anterior ¾ length of ventral face of LO in Cheko, Chomlong and Ranong males; LO entire in V6, 7; apex of MPP slightly asymmetrical, entire, appears broadly truncate from beneath.

**Remarks**. Published accounts of association of males to this species have been unreliable, and identification of these specimens as *circumdata* is based on the distinctive colour pattern, and the difference in LO structure from *L. ovalis* (where it is bipartite). Motschulsky (1854) described a female from 'Indes orientales'. Mrs E Davydova, late of the Severtzov Institute Moscow, examined the type (and single specimen) of *L circumdata*, indicated the size (12mm), and her drawing (with LB) of the terminal abdominal ventrites confirmed a female. Olivier (1885) assigned a single male (from 'Birmanie'), which he associated with a similarly coloured female. He did not describe the V7 LO shape, but his description of the two terminal ventrites as 'blanc de cire' probably indicated an entire LO. Bourgeois (1890) assigned a male (without a LO description), and female and indicated a wide range (Burma, Thailand and Cambodia). McDermott (1964:44) considered the last ventral segment of the abdomen 'cleft' in *L. ovalis* (probably a reference to the bipartite light organs) but not so "in the very similar *L. circumdata* Motsch." The possibility that some form of gradation from entire to at least partially bipartite LO could be investigated when more specimens are available (the median depression on V7 in some specimens gives the impression that the LO is bipartite when it is not).

### *Asymmetricata ovalis* (Hope)

(Figs 7, 110, 111)

*Lampyris ovalis* Hope, in Gray, 1831:26.
*Luciola ovalis* (Hope). McDermott, 1964:44; 1966:111 Partim.
? *Luciola ovalis* (Hope). McDermott, 1962:24, Fig. 21.
*Nec Luciola ovalis* (Hope). Gorham, 1880:99, 103 (= *L. circumdata* Motsch); 1895:303. Olivier, 1891:595–604.

**Holotype.** Male. 'Nepaul' (NHML).

**Material examined**. **INDIA**: 27.04N, 88.28E, Western Bengal, Kalimpong, Bombasti area, vii–viii.1992, R. Kumar male, female (ANIC).

**Diagnosis.** Most obviously distinguished from the similarly coloured *A. circumdata* by the bipartite LO.

**Male redescription.** 11.9 mm long; 5.0 mm wide; W/L 0.4. Colour: Pronotum, MS, MN, sutural, apical and lateral margins of elytra orange, rest of elytra dark brown except for slightly lighter brown interstitial line 2; irregular retraction of fat body under pronotum may confuse interpretation of colour; head, antennae and palpi dark brown; ventral surface of thorax, and legs orange except for dark brown tibiae, tarsi; V2–5 very dark brown, LO white except for slightly yellow area between LO halves; MPP yellow; T 7, 8 yellow, semi-transparent, rest mottled mid-brown. Pronotum: 2.1 mm long, 4.2 mm wide; W/L 2.0; area between anterior and posterior hypomeron slightly angulate. Elytra: convex-sided, 9.8 mm long, 4 interstitial lines visible, inner two approach suture, outer two not as well–defined. Head GHW 2.4 mm; SIW 0.3 mm; SIW/ GHW 1/8; ASD less than ASW, sockets close not contiguous; frons-vertex junction rounded, frons about 1 x ASW high. Abdomen: (Figs 7, 110–111) LO bipartite; apex of MPP narrowing slightly and rounded.

**Female.** (Fig. 8) Macropterous. 11.8 mm long; coloured as for male except for creamy white (LO) V6 and yellowish, semitransparent V7, 8. Pronotal outline as for male. Head of winged female form. V7 depressed transversely across median area (may be post–mortem effect) and posterior margin mainly straight except for broad shallow median emargination; V8 with shallow median emargination; T8 with rounded posterior margin.

**Remarks.** Hope's (1831) five word description indicated dorsal colouration consistent with that described here for both *Asymmetricata* species. The type series of *L. ovalis* was examined by LB in 1993, the LO in V7 confirmed as bipartite and length of specimens slightly shorter (9–10 mm. long). It has not been possible to reexamine the type series for this study. If we accept that males of *L. circumdata* have an entire LO in V7 then Gorham (1880) incorrectly synonymised *ovalis* with *circumdata*. He also incorrectly attributed V7 (with median longitudinal 'cleft') to the segment in front, and thought the area posterior to the LO, including the prolonged MPP, was another segment. He recorded the species from India. Gorham (1895) indicated an even wider range (NW India to Burma and Sumatra) and confirmed his original identification. Since Olivier (1890–91) also synonymised *ovalis* and *circumdata* it is probable that this reference to *ovalis* is actually to *circumdata*. McDermott (1962:24, Fig. 21) briefly described and figured male terminal abdomen of *L. ovalis* with clearly bipartite LO in V7, but did not indicate any asymmetry of tergite 8. McDermott (1964) described the last ventral segment in *L. ovalis* as 'cleft' and was probably referring to the bipartite LO.

Clearly this preliminary treatment with few specimens highlights the need for further investigation to confirm these identifications, and to clarify whether the LO is so variable that it exists in a range from entire with median cleft through to totally bipartite.

### *Atyphella* Olliff, 1890
(Figs 9–11, 35, 78, 79, 83–85, 118–179)

*Atyphella* Olliff, 1890:645. Lea, 1909:110. Olivier, 1909b:lxxxii (Partim); 1910b:40; 1911:171; 1913:417 (Partim). Ballantyne, 1987b:172, 175–77, 181, 183–5. Calder, 1998:176 (Partim). Ballantyne & Lambkin, 2000:22 (Partim); 2006 (Partim):30.
*Luciola* (*Luciola*) Laporte. Sensu McDermott, 1964:45; 1966:99.
*Luciola (Atyphella*) (Olliff). Ballantyne, 1968:108. Ballantyne & McLean, 1970:23.

**Type species**. *Atyphella lychnus* Olliff, 1890.

**Diagnosis**. Males of Australian species, and *A. scabra*, with anterior hypomeron flat to neck, and posterior area flattened and strongly adpressed; non-Australian species lack the flat anterior hypomeron; epipleuron either continuing around elytral apex as a ridge (Figs 9–11, 79, 83, 118, 119, 122–125, 127–129, 169, 170) or not; frons-vertex junction rounded, or angulate (Figs 84, 85); mouthparts functional or not; apical segment of labial palpi either strongly flattened, with inner margin dentate, or ovoid with inner margin entire; aedeagal sheath with posterior area of sternite emarginate on its right side from attachment of tergite. Distinguished most obviously from *Aquilonia* and *Gilvainsula* by their distinctive pale dorsal colouration; lacking the asymmetrical tergite 8 of *Asymmetricata*; differing from *Convexa* and *Magnalata* which have distinctive dark elytra often with pale margins; lacking the dorsal colour pattern, shape of aedeagus and hooded basal piece of *Lloydiella*, and lacking the arched V7 with LO retracted to anterior half or less characteristic of *Pygatyphella*. Females (Figs 130–136) either macropterous or exhibiting varying degrees of brachelytry. Larvae with laterally explanate tergal margins concealing laterotergites from above.

**Male**. Pronotum dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate.

Pronotum (Figs 9, 11, 84, 85, 118, 122–129, 137–139, 142, 144, 147, 150–152, 154, 157–159,166–169, 177, 178) usually wider across posterior area than rest, subparallel-sided in *inconspicua*, some *immaculata*; pronotal width usually greater than humeral width, subequal to humeral width in *aphrogeneia*, *guerini*, *inconspicua*, *lewisi* and *similis*. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent, or subparallel-sided in *inconspicua* (Fig. 125*)*; lateral margins in posterior half either subparallel-sided in *inconspicua* and some *immaculata* (Fig. 127), or diverge along their length in *similis* some *dalmatia* **sp. n.** (Fig. 147) and some *immaculata*, or diverge then converge with rounded convergence ((Figs 78, 84, 123, 129, 147, 158, 159, 166, 169, 177); lacking indentation at mid-point, or sinuousity in either horizontal or vertical plane; subparallel-sided margins straight; lacking indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners rounded or angulate; rounded corners obtuse, < 90°; in *dalmatia* **sp. n.**; angulate corners approximately 90° and inclined at right angles, or obliquely, to median line; posterolateral corners either not projecting as far as median posterior margin ( *aphrogeneia*), or projecting as far as or beyond it and separated from it by a shallow emargination except in some *aphrogeneia.*

Hypomera closed. Median area of hypomeron not elevated vertically; anterior, and posterior areas of hypomeron narrowly to widely flat to side of head in Australian species and *A scabra* (Fig. 84, 178); anterior area of hypomeron not flattened in remainder; posterior area of hypomeron widely flattened in remainder (Fig. 84) except for some *aphrogeneia and inconspicua* where it is narrow; flattened areas closely adpressed except for some *aphrogeneia*; pronotal width/ GHW index 1.6 except for *inconspicua* (1.2), and 1.4–1.5 in some *aphrogeneia* and *immaculata*.

Elytron punctation usually dense (Figs 123, 125, 126–129, 137, 138, 144, 150, 153, 154, 167, 177), sparse in *aphrogeneia* (Fig. 118); punctation not linear, not as large as pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extend beyond mid-point, may extend as ridge around apex without any further expansion of either, or apical half of both epipleuron, sutural ridge, and elytral apex expanded in *aphrogeneia*; ridge around apex of elytron may be visible from beneath; 0, 2, 3 or 4 interstitial lines, inner two exceed height of suture in *scabra* only; elytral carina absent; in horizontal specimen viewed from beneath epipleuron at elytral base wide, covers humerus from below; in specimen viewed from above arises anterior to posterior margin of MS; epipleuron developed as lateral ridge along most of length; sutural margins approximate along most of their length in closed elytra except in *aphrogeneia* where they diverge in apical half; lateral margins parallel-sided or convex.

Head moderately to strongly depressed between eyes; moderately exposed in front of pronotum, not capable of complete retraction within prothoracic cavity except in *lychnus*, *monteithi* and *scintillans*; eyes close to moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum close (moderately separated in some *dalmatia* **sp. n.**,); frons-vertex ‘junction’ rounded or acute (Fig. 84), with median elevation in *conspicua* only (Ballantyne & Lambkin 2000 Fig. 2f); posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, contiguous or separated by up to ASW; ,clypeolabral suture present, flexible, not in front of anterior eye margin when head viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional or not; apical segment of labial palpi non–lunate, either strongly flattened, shaped either like a wide to narrow triangle, with inner edge irregular (*guerini*) or dentate; or narrow triangle with L>W; or not flattened and ovoid, as long as or longer than wide. Antennae 11 segmented, sometimes less; length subequal to GHW – twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel; in very short antennae FS may be subequal in length and width.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

**TABLE 3.** Current species identifications for species identified by Ballantyne in Lloyd (1973b) by code names or numbers (*Luciola* species 4, 7, 8, 10, 11, 13, 14 will be addressed elsewhere.)

| Current species identification | Species identification used in Lloyd, 1973b | Code name/ number used in Lloyd 1973b | References | Specimens in JELC |
|---|---|---|---|---|
| *Pygatyphella limbatipennis* (Pic) | *Luciola (Atyphella)salomonis* var *limbatipennis* Pic | *Luciola* Species 1 | Lloyd, 1973b:992 | G649–52, 654, 655, 657, 658, 660–62. |
| *Magnalata limbata* (Blanchard) | *Luciola (Luciola) wolfi*( Olivier) | *Luciola* species 2 | Lloyd, 1973b: 992 | G 653, 656, 659 |
| | *Luciola rubiginosa*. The three larval specimens included here by Lloyd (1973b) were loaned and have not been relocated. | *Luciola* Species 3 | Lloyd 1973b | G664 |
| *Pygatyphella peculiaris* (Olivier) | *Luciola (Atyphella) peculiaris* Olivier | *Luciola* species 5 | Lloyd, 1973b: 992; 1977:178–9 | G 316, 319, 321, 324, 331, 351, 354, 565, 566, 583, 584, 587, 589, 596, 604, 616 |
| *Pygatyphella huonensis* (Ballantyne) | *Luciola (Pygatyphella) huonensis* Ballantyne | *Luciola* species 6 | Lloyd, 1973b: 995; 1977:178–9. | G 609, 612 |
| *Atyphella testaceolineata* Pic | *Luciola (Atyphella) testaceolineata* (Pic) | *Luciola* species 9 | Lloyd, 1973b: 995 | G 619 – 620. |
| *Pygatyphella uberia* **sp. n.** | *Luciola (Luciola)* sp. | *Luciola* species 12 | Lloyd, 1973b: 995. Ballantyne, 1987b:177, 185, Fig.2, c–f | Lloyd: G 320, 353 (paratypes) |

Abdomen lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment; LO in V7 usually entire, bipartite in *scabra* (Fig. 178, 179; restricted to anterolateral plaques), *kirakira* **sp. n.** (Fig. 142, 143), and possibly *lewisi* where it is not possible to determine its extent; either reaching both to sides and posterior margin in *olivieri* and *testaceolineata*, or reaching only sides; entire LO in V7 occupies most of V7; bipartite LO occupies > half V7; neither anterior nor posterior margin of entire LO in V7 emarginate; posterior half of V7 not arched or swollen, muscle impressions not visible in this area; LO present in V6, entire and occupying almost all V6 except in *scabra* where it is restricted to anterolateral plaques. MPP present, symmetrical, apex rounded, (except narrow and pointed, or rounded in *scabra*), entire, not laterally compressed, short, not inclined dorsally nor engulfed by T8 apex, lacking dorsal ridge and median longitudinal trough. V7 lacking median carina, median longitudinal trough, anteromedian depression on face of LO, incurving lobes, pointed projections, median 'dimple', or reflexed lobes and PLP (inconsistent development of this area in *scabra* could be postmortem change). T7 lacking prolonged posterolateral corners. T8 not strongly sclerotised, often subparallel-sided, symmetrical, W=L or W>L, visible posterior area does not narrow abruptly, lacking prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally nor engulfing posterior margin of V7 nor MPP, extending conspicuously beyond posterior margin of V7 in *scabra* only; T8 ventral surface lacking flanges, lateral depressed troughs, median longitudinal trough, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 either absent (in *scabra*), or very short and narrow, or elongate but not as long as visible posterior portion of T8, and narrow; not laterally emarginated before their origins, not expanded dorsoventrally, apices lacking bifurcation of inner margin, bases lacking ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

**TABLE 4.** Generic categories in the Luciolinae (nodes are numbered from the majority rule tree Figs 2, 3).

| Ballantyne and Lambkin 2000, 2001, 2006 | Present composition |
|---|---|
| Luciolinae | Luciolinae |
| *Luciola* s str. (Clade 1) includes: | *Missimia* **gen. n.** |
| • *L. italica* (type species) | **Presently unassigned** (Node 1 *Luciola* ***cruciata –L. owadai*****)** |
| • *L. dejeani* | **Presently unassigned (Node** 2 L**.** ***leii –L. ficta*****)** |
| • *Lampyroidea* sp. | **Presently unassigned** (Node 4 *L. substriata* J –*L. substriata* A) |
| • *Bourgeoisia* sp. | *Pygoluciola* Wittmer (Node 9 *Pyg hamulata–Pyg wittmeri*) |
| • *L. (Hotaria) parvula* | *Photuroluciola* Pic |
| *Luciola* (Clade 2) | *Curtos* Motschulsky (Node 37 *okinawanus–costipennis*) |
| • *Luciola* sp. (Australian species) | **Presently unassigned** (Node 35 *L. australis–L. pupilla*) |
| • *Pteroptyx* | *Pteroptyx* Olivier sensu latu ( Node 28 *P. platygaster–P effulgens*) |
| • *Pyrophanes* | *Colophotia* Dejean (Node 24 *concolor–plagiata*) |
| • *Colophotia* | *Pyrophanes* Olivier (Node 21 *beccarii–quadrimaculata*) |
| *Atyphella* Olliff | *Pteroptyx* s. str. (Node 18 *L. sp MFC–truncata*) |
| *Pygoluciola* Wittmer | *Luciola* Laporte s str. (Node 6 *dejeani – antipoda*) |
| *Curtos* Motschulsky | *Aquilonia* **gen. n.** (Node 5 *costata*) |
| | *Gilvainsula* **gen. n.** (Node 47 *messoria–similismessoria*) |
| | *Magnalata* **gen. n.** (Node 55 *carolinae – rennellia*) |
| | *Asymmetricata* **gen. n.**. (Node 52 *circumdata–ovalis*) |
| | *Convexa* **gen. n.**. (Node *51* ***wolfi*****)** |
| | *Lloydiella* **gen. n.** (Node 50 *uberia–wareo*) |
| | *Atyphella* Olliff (Node 78 *aphrogeneia–similis*) |
| | *Pygatyphella* (Ballantyne) (Node 3 *wisselmerenia–nabiria*) |

Aedeagal sheath (Figs 121, 145, 148, 170, 171, 181–183) never > 4 times as long as wide; lacking paraprocts; asymmetrical in posterior area where sheath sternite emarginated on right side from point of attachment of tergite; sternite not angulate on L or R sides, not subparallel-sided, posterior margin apically entire and rounded except for short rounded median projection in *scabra* (Figs 182, 183); not emarginated on either side preapically; anterior half of sternite broad, apically rounded; tergite lacking lateral arms extending anteriorly at sides of sheath sternite; tergite not subdivided, lacking projecting pieces along posterior margin of tergite 9; anterior margin tergite 9 lacking transverse band.

Aedeagus (Ballantyne & Lambkin 2000 Fig. 5 in part) Figs 120, 145, 146, 148, 149, 160–165, 172–174, 184, 185) L/W 3/1 or shorter; LL lack lateral appendages, visible from beneath at sides of ML, LL/ML moderate; LL of equal length, subequal to or slightly longer or shorter than ML, diverging or not along inner margins, separated there by > half their length; LL base width not = LL apex width which is subequal to or narrower than ML; LL apices not expanded horizontally; dorsal base of LL symmetrical, not excavated, if median margin prolonged then either broadly rounded, broadly truncate, pointed entire, or pointed, medially emarginate; LL lacking lateral hairy appendages along outer ventral margins, which are not produced preapically, nor narrowly on inner apical margin, and not obliquely truncate along their preapical inner margins except for *palauensis* and *dalmatia* **sp. n.**; apices of LL not inturned, may be out–turned with apex rounded; lacking projection on left LL only; inner margins lacking slender leaf-like projection. ML symmetrical, lacking paired lateral teeth and tooth to left side, not strongly arched, apex not shaped like arrowhead, not bulbous, not inclined ventrally; BP not very narrow, not strongly sclerotised, not hooded, usually in two pieces and not strongly emarginated along anterior margin.

**TABLE 5.** Current species composition of Luciolinae genera treated here.

| Composition of *Atyphella* Olliff as in Ballantyne and Lambkin, 2000 | Current composition *Atyphella* Olliff | *Pygatyphella* gen. n. | *Lloydiella* gen. n. | *Magnalata* gen. n. |
|---|---|---|---|---|
| *aphrogeneia* Ballantyne, 1979[1]<br>*atra* Lea 1921<br>*brevis* Lea 1909<br>*carolinae* (Olivier, 1911)<br>*costata* (Lea, 1921b)<br>*conspicua* Ballantyne, 2000<br>*ellioti* Ballantyne, 2000<br>*flammans* Olliff, 1890<br>*flammulans* Ballantyne, 2000<br>*guerini* Ballantyne, 1988<br>*huonensis* (Ballantyne 1968)<br>*immaculata* Ballantyne, 2000<br>*inconspicua* (Lea, 1921)<br>*leucura* (Olivier *1906*)<br>*lewisi* Ballantyne, 2000<br>*lychnus* Olliff, 1890<br>*majuscula* (Lea, 1915)<br>*marginipennis* (Guerin 1830)<br>*monteithi* Ballantyne, 2000<br>*obsoleta* Olivier, 1911<br>*olivieri* Lea, 1915<br>*scintillans* Olliff, 1890<br>*similis* Ballantyne, 2000<br>*undulata* Pic, 1929<br>*wolfi* (Olivier) | *aphrogeneia* Ballantyne, 1979[1]<br>*atra* Lea 1921<br>*brevis* Lea 1909<br>*dalmatia* **sp. n.**<br>*conspicua* Ballantyne, 2000<br>*ellioti* Ballantyne, 2000<br>*flammans* Olliff, 1890<br>*flammulans* Ballantyne, 2000<br>*guerini* Ballantyne, 1988<br>*immaculata* Ballantyne, 2000<br>inconspicua (Lea, 1921)<br>*kirakira* **sp. n.**<br>*lamingtonia* **sp. n.**<br>*leucura* (Olivier, 1906)<br>*lewisi* Ballantyne, 2000<br>*lychnus* Olliff, 1890<br>*monteithi* Ballantyne, 2000<br>*olivieri* Lea, 1915<br>*palauensis* Wittmer, 1958<br>*scabra* Olivier, 1911<br>*scintillans* Olliff, 1890<br>*similis* Ballantyne, 2000<br>*testaceolineata* Pic, 1939 | *eliptaminensis* (Ballantyne, 1968<br>*huonensis* (Ballantyne, 1968)<br>*ignota* (Olivier, 1911)<br>*japenensis* **sp. n.**<br>*karimui* sp. n<br>*kiunga* sp. n<br>*limbatipennis* (Pic, 1911)<br>*limbatifusca* sp. n<br>*marginata* (Ballantyne, 1968)<br>*nabiria* sp. n<br>*obsoleta* (Olivier, 1911)<br>*okapa* sp. n<br>*peculiaris* (Olivier, 1909)<br>*plagiata* (Blanchard, 1853)<br>*pulcherrima* (Ballantyne, 1968)<br>*russellia* sp. n<br>*salomonis* (Olivier, 1911)<br>*tagensis* (Ballantyne, 1968)<br>*tomba* sp. n<br>*uberia* sp. n<br>*undulata* (Pic, 1929)<br>*wisselmerenia* sp. n | *japenensis* **sp. n.**<br>*majuscula* (Lea, 1915)<br>*uberia* **sp. n.**<br>*wareo* **sp. n.** | *carolinae* (Olivier, 1911)<br>*limbata* (Blanchard, 1853)<br>*rennellia* **sp. n.** |
| *Aquilonia* **gen. n.** | *Gilvainsula* **gen. n.** | *Missimia* **gen. n.** | *Asymmetricata* **gen. n.** | *Convexa* **gen. n.** |
| *costata* (Lea, 1921b) | *messoria* (Olivier, 1913)<br>*similismessoria* **sp. n.** | *flavida* **sp. n.** | *circumdata* (Motsch. 1854)<br>*ovalis* (Hope, 1831) | *wolfi* (Olivier, 1910a) |

**TABLE 6.** Voucher specimens used for phylogenetic analysis and interpretation of morphology.

| Species | Authority for identification | Reference | Collection |
|---|---|---|---|
| *Atyphella similis* Ballantyne | LB | Ballantyne & Lambkin 2000:53 | Lawrence/ ANIC |
| *Colophotia concolor* Olivier | LB | Ballantyne, 1993; work in progress | USNM |
| *C plagiata* Erichs. | LB | Ballantyne, 1993; work in progress | USNM |
| *C. praeusta* Eschsch. | LB | Ballantyne, 1993; work in progress | USNM |
| *Curtos okinawanus* (Matsumura) | Ohba | Jeng *et al*. 1998:331 | ANIC |
| *C. costipennis* (Gorham) | Ohba | Jeng *et al*. 1998:331 | ANIC |
| *Luciola anthracina* Olivier | E. Olivier | | MNHN |
| *Luciola aquatilis* Thancharoen | Thancharoen | Thancharoen *et al*. 2007:55 | ANIC |
| *L. cruciata* Motsch. | N. Ohba | | ANIC |
| *L. foveicollis* Olivier | E. Olivier | | MNHN |
| *L* sp. MFC unidentified *Luciola* | LB | | ANIC |
| *L. owadai Sato & Kimura* paratype | N. Ohba | Jeng *et al*. 2003:543 | ANIC |
| *L. pupilla* Olivier | L B comparison with type | Ballantyne, 1987a: 164; Ballantyne & McLean 1970:268. | ANIC |
| *Luciola substriata* J and F (Taiwan J and mainland China F) | LB | Fu & Ballantyne work in progress | ANIC |
| New Caledonia 1, 2 | Unidentified, New Caledonia | | QM |
| *Photinus pallens* F. | J Lloyd | Ballantyne work in progress | JEL |
| *Photuris trivittata* Lloyd & Ballantyne | LB | Lloyd & Ballantyne 2003:464 | JEL |
| *Pteroptyx corusca* Ballantyne | LB | Ballantyne 1987:137 | ANIC |
| *P. effulgens* Ballantyne | LB | Ballantyne 1987:141 | ANIC |
| *P. gelasina* Ballantyne | LB | Ballantyne, 2001: 64. | ANIC |
| *P. tener* Olivier type and other specimens | LB | Ballantyne 2001: 74; Ballantyne & Menayah 2002:323. | MNHN; ANIC |
| *Pt* sp ML unidentified *Pteroptyx* species | LB | | ANIC |
| *P. truncata* Ballantyne | LB | Ballantyne, 2001: 77. | ANIC |
| *Pygoluciola* sp. S | LB | *Pygoluciola satoi* Ballantyne; 2008:1 | Raffles |
| *Pygoluciola* sp. Q | LB | *Pygoluciola qingyu* Fu & Ballantyne 2008 | |
| *Pyrophanes appendiculata* Olivier | LB | Ballantyne work in progress | USNM |
| *P. quadrimaculata* Olivier | LB | Ballantyne work in progress | USNM |
| *P. similis* Olivier | LB | Comparison with type in MNHN | USNM |

**Female** (Figs 130–136, 155, 156). Pronotum lacking irregularities in posterolateral areas; punctation moderate to dense, sparse in *lewisi* and *conspicua*; pronotum > humeral width in macropterous females; lacking indentation of lateral margin, and irregularities at posterolateral corner. Elytral punctation not as large as pronotum nor evenly spaced. *Atyphella* females of four forms (Figs 130–136): 1. Macropterous, capable of flight; head of winged female form. 2. Fore wings cover most if not all of (gravid) female abdomen; hind wings shortened, may be about ¾ as long as fore wings (*flammans* and *lychnus*) (Figs 130, 131), head of wingless female form, pronotum with laterally divergent margins in at least anterior half. 3. Fore wings cover body but hind wings absent (*atra*); head, eyes and pronotal shape as for 2. 4. Brachelytral females with very short or vestigial hind wings (Figs 132–136), head and eyes same form as 2, pronotum subparallel-sided in *conspicua, inconspicua* and *lewisi*, pronotal margins diverge posteriorly in *scintillans* and *similis*. 0, 2, 3 or 4 interstitial lines (0, 2 or 4 in macropterous females; 3 in *atra* which lacks hind wings); elytral carina absent. No legs or parts thereof swollen and/or curved. LO in V6 only, lacking any elevations or depressions or ridges on V7.

**Larva** (Ballantyne & Lambkin 2000 Figs 7, 12, 15). Terrestrial; tergal plates sclerotised to margins, lateral tergal margins explanate, finely margined or thickened, may be ridge-like, covering laterotergites from above; arrangement of plates on ventral aspect of thorax and abdomen like that described (Ballantyne & Lambkin, 2000; Ballantyne & Menayah, 2002). Protergum L=W or W>L in *aphrogeneia* and *guerini*; tubercles sometimes present along anterior margin, posterolateral corners rounded; median line sometimes with ridged margins; lateral margin of protergum thickened in *olivieri*, *guerini;* punctures in anterior half of terga 2–10 sometimes larger than rest; posterolateral corners of terga 1–8 rounded entire, of tergum 12 either produced narrowly or not; median posterior margins of terga 1–11 lacking either rounded or pointed projections; lacking brush of hairs from apex of tibiotarsus; mandibles lacking inner teeth; antennal segment 3 short, sense cone adjacent to segment 3 short, wide; terrestrial, with laterosternites on abdominal segments 1–8 bearing spiracles.

**Remarks.** *Atyphella* was restored to generic level by Ballantyne (in Calder 1998), its status confirmed by cladistic analysis, and revised and redescribed from its Australian examples by Ballantyne and Lambkin (2000). The internal composition was further expanded in Ballantyne and Lambkin (2001, 2006).
Ballantyne and Lambkin (2000) included 23 species in *Atyphella* Olliff, 16 Australian and seven from the island of New Guinea. *Atyphella* s. str. as defined here comprises 24 species mainly from Australia and includes 14 of those 16 Australian species, and one of the New Guinean species (*leucura*), and is expanded to include A. *testaceolineata*, and two new species. Its present composition and the new assignments for species removed from *Atyphella* are shown in Table 4.

As Australian species# were dealt with in detail in Ballantyne and Lambkin (2000) they are treated here in an abbreviated fashion.

**List of species of *Atyphella***

# = Australian species
*aphrogeneia* (Ballantyne, 1979)
*atra* Lea 1921a#
*brevis* Lea 1909#
*dalmatia* **sp. n.**
*conspicua* Ballantyne, 2000#
*ellioti* Ballantyne, 2000#
*flammans* Olliff, 1890#
*flammulans* Ballantyne, 2000#
*guerini* Ballantyne, 1998
*immaculata* Ballantyne, 2000#
*inconspicua* (Lea, 1921)#
*kirakira* **sp. n.**
*lamingtonia* **sp. n.**
*leucura* (Olivier, 1906)

*lewisi* Ballantyne, 2000#
*lychnus* Olliff, 1890#
*monteithi* Ballantyne, 2000#
*olivieri* Lea, 1915#
*palauensis* Wittmer, 1958
*scabra* Olivier, 1911
*scintillans* Olliff, 1890#
*similis* Ballantyne, 2000#
*testaceolineata* Pic, 1939

**Key to species of *Atyphella* Olliff using males**

1. Pronotum orange with no darker markings; Australian; apical segment of labial palp fusiform (Fig. 127). ........ *immaculata* Ballantyne
   Pronotum always with some darker markings especially in median area ........ 2
2. LO in V7 divided (Figs 142, 143, 178, 179) ........ 3
   LO in V7 entire ........ 5
3. LO in V6 subdivided; interstitial lines 1 and 2 wider and higher than sutural ridge; MPP pointed (Figs 177–187) ........ *scabra* Olivier
   LO in V6 entire; interstitial lines 1 and 2 not wider and higher than sutural ridge; MPP not pointed ........ 4
4. Solomon Islands; elytra dark brown; MPP produced, longer than wide and often oblique at tip (Figs 142–146, 148, 149) ........ *kirakira* **sp. n.**
   Australia; elytra striped, not concolourous; MPP not longer than wide, apex rounded (Fig. 130) ........ *lewisi* Ballantyne
5. Elytra dark brown with lateral and sutural margins and apex pale cream (Figs 131, 132) ........ *olivieri* Lea
   Elytra not as above ........ 6
6. Elytra striped (Figs 11, 123, 125, 150, 151, 153) ........ 7
   Elytra not striped........ 13
7. Frons-vertex junction acute (Figs 84, 85)........ 8
   Frons-vertex junction rounded........ 10
8. Elytra with 2 well-defined interstitial lines; frons high ........ *flammulans* Ballantyne
   Elytra with 3 well-defined interstitial lines; frons low to high ........ 9
9. Elytra convex-sided when closed (Fig 122); antennal sockets contiguous or almost so; mouthparts small may be non-functional, apical segment of labial palp fusiform ........ *brevis* Lea
   Elytra parallel-sided when closed; antennal sockets not contiguous; mouthparts functional ........ *similis* Ballantyne (<u>Partim</u>)
10. Australian; 4 interstitial lines; head covered by pronotum and retracted within prothoracic cavity in repose; antennal sockets not contiguous but close; apex labial palpi fusiform (Figs 11, 78, 79)........ *lychnus* Olliff
    3–4 interstitial lines; head not covered nor so retracted in repose; antennal sockets contiguous; apex of labial palpi laterally flattened and dentate ........ 11
11. Elytra with 4 interstitial lines; elytra with additional stripes due to lines of fat body (Fig. 150, 151); LO does not reach posterior margin of V7 ........ *lamingtonia* **sp. n.**
    Elytra with 2 or 3 interstitial lines; no additional stripes due to lines of fat body; LO often reaches posterior margin of V7 ........ 12
12. Australian; small (< 4 mms long); elytra with 2 interstitial lines; mouthparts probably non–functional; api-

cal segment of labial palpi fusiform; (Fig. 130) ............................................................ *ellioti* Ballantyne

New Guinean; larger (never as small as 4 mms or less); elytra with 3 interstitial lines (Fig. 153); mouthparts functional, apical segment of labial palpi flattened with inner margin dentate ...... *testaceolineata* Pic

13. Median area of frons-vertex elevated; pronotum not subparallel-sided, wider than humeral width ............ ........................................................................................................................ *conspicua* Ballantyne

Median area of frons–vertex junction not elevated; pronotum either subparallel-sided or not ................ 14

14. Pronotum subparallel-sided; subequal in width to humeral width (Fig. 125) .................... *inconspicua* Lea

Pronotum not subparallel-sided; usually wider than humeral width ...................................................... 15

15. Antennal sockets contiguous; mouthparts probably non–functional; pronotum wide, W/L 2(Fig. 10) ........ ........................................................................................................................................ *atra* Lea

Antennal sockets not contiguous; mouthparts functional; pronotum narrower, W/L 1.8............................. ....................................................................................................... *similis* Ballantyne (Partim)

### *Atyphella aphrogeneia* (Ballantyne, 1979)
**(Figs 118–121)**

*Luciola (Luciola) aphrogeneia* Ballantyne, in Ballantyne & Buck, 1979:119. Case, 1984:201.
*Atyphella aphrogeneia* (Ballantyne). Ballantyne & Lambkin, 2000:15; 2001:374, 2006:30.

**Holotype.** Male. **PAPUA, NEW GUINEA**: Madang Pr., 4.59S, 145.40E, Cape Croisilles, Madang District (ANIC).

**Other material examined. PAPUA, NEW GUINEA**: Madang Pr., 4.59S, 145.40E, Madang, B. Challis, male (SAM). **VANUATU (**New Hebrides**):** 16.19S, 167.30E, Malakula (Atchin Island), L. Cheesman, iii.1930, 2 males; vi. 1929 male (NHML). Rana Island, 30.v.1903, male (AMS).

**Diagnosis.** Dorsal colouration of dark brown elytra and pronotum with median dark markings is similar to that of some *Magnalata carolinae*; distinguished by the apical expansion of the male elytra, which are not contiguous dorsally in apical half, taper towards their thickened apices, where the apical ¼ of both epipleuron and sutural ridge and elytral apex are wider than remainder (Figs 118, 119); females macropterous and capable of flight; larva dorsally black with lateral yellow markings on all but terminal two terga (Ballantyne & Buck, 1979, Figs 28, 29).

**Remarks.** *Atyphella aphrogeneia* occurs in the salt spray zone of coral outcrops near Madang, Papua New Guinea (Ballantyne & Buck, 1979), where, during the premating exchange of light signals, the female is sessile (but not wingless, see Case, 1984:202) and the male ‘patrols a narrow strip between the surf spray zone and the jungle’ (Case, 1984:201). It also occurs on island locations in Vanuatu. It is only the second firefly species known from such an unusual habitat (the other is a Jamaican firefly larva, McDermott, 1953). The larva is neither aquatic nor apparently semiaquatic. Ballantyne (1987b:175) suggested that the elytral apex thickening might contribute towards a means of securing mating pairs in an otherwise precarious position on coral outcrops, and the narrowing of the elytral apices afford the abdomen more flexibility. This has not been substantiated by observation.

### *Atyphella atra* Lea, 1921
(Figs 9, 10, 83–85)

*Atyphella atra* Lea, 1921a:198. Ballantyne *in* Calder 1998: 177 (comb. rev.) Ballantyne & Lambkin, 2000: 25; 2001: 374, 2006: 30.
*Luciola (Luciola) atra* (Lea). McDermott, 1966: 99.
*Luciola (Atyphella) atra* (Lea). Ballantyne & McLean, 1970: 281. Moore, 1989: 136.

**Holotype.** Male. **AUSTRALIA:** 28.19S, 153.05E, Lamington National Park (C2290 QM).

**Diagnosis.** Males distinguished from most other *Atyphella* by the acute frons-vertex junction, the small (probably non–functional) mouthparts, the contiguous antennal sockets, the brown – dark brown parallel-sided elytra; females pale coloured with fully developed elytra and vestigial hind wings; paler male specimens very like *A. similis*, which has angulate posterolateral pronotal corners, separated antennal sockets, well developed mouthparts and flightless brachelytral females. Ballantyne and Lambkin (2000) distinguished *atra* and *similis* most obviously by their distinctive females.

### *Atyphella brevis* Lea, 1909

(Fig. 122)

*Atyphella brevis* Lea, 1909:111; 1921a:197; 1929:345. Olivier, 1910b:46. Tillyard, 1926:212. Ballantyne *In* Calder, 1998:177 (comb. rev). Ballantyne & Lambkin, 2000:29; 2001:364, 2006:30.
*Luciola (Luciola) brevis* (Lea). McDermott, 1966: 100.

**Lectotype**. Male. **AUSTRALIA:** 17.16S, 145.29E, Atherton, designated by Ballantyne & Lambkin, 2000 (SAM).

**Diagnosis.** One of six Australian species with striped elytra; Ballantyne & Lambkin (2000:29) distinguished *brevis* by a combination of characters including the convex–sided elytra, the poorly developed mouthparts and the acutely margined frons–vertex junction. Female, larva not associated.

### *Atyphella conspicua* Ballantyne, 2000

*Atyphella conspicua* Ballantyne in Ballantyne & Lambkin, 2000:30; 2001:364, 2006:30.

**Holotype.** Male. **AUSTRALIA**: 16.42 S, 145.13 E, Stewart Creek (QMT61017).

**Diagnosis.** Males with brown elytra and pale pronotum with medial dark marking, distinguished from *A. inconspicua* by the divergent lateral margins of the pronotum, and the median elevation of the acute frons-vertex junction (Ballantyne & Lambkin 2000 Fig.2f); brachelytral females with vestigial hind wings are tentatively associated.

### *Atyphella dalmatia* sp. n.

(Figs 137–141, 147)

**Holotype.** Male. **PAPUA NEW GUINEA**: 6.35S, 147.51E, Morobe Pr., Finschhaven (*sic*), Wareo, L. Wagner (SAM).

**Paratypes** (24). Same locality, collector, as holotype, males (SAM).

**Diagnosis.** Distinguished from all other *Atyphella* by the scattered small pale spots on the brown to dark brown elytra.

**Male description.** 7.1–8.8 mm long; 2.8–3.4 mm wide; W/L 0.4. Colour: Pronotum largely yellow, usually with small paired median brown areas (20/25) (Fig. 147), median brown area occupying about half surface area and widening posteriorly (3/25) or occupying more than half of the whole area (2/25); MS, MN yellow; elytra dark brown (24/25, pale brown in one paratype), with paler spots which are concentrated in the inner (sutural) half (Figs 137–138), minimum of 3 pale spots on left elytron (1/25) to maximum of 18 spots on each elytron; 4 males with spots mostly concentrated around inner two interstitial lines; head, antennae and palpi mid-brown; ventral aspect of pro and mesosterna yellowish to light brown, metasternum dark brown; all legs yellow with tibiae and tarsi dark brown; V2–5 very dark brown, 6 and 7 white; tergites dark brown, T7 pale and slightly darker mottled, T8 pale. Pronotum: (Fig. 147) 1.5–1.8 mm long, 2.5–3.2 mm wide; W/L 1.6–1.7; lateral margins divergent posteriorly along their length (21/25) with slight rounded convergence in 4/25; posterolateral corners < 90°, rounded, projecting beyond median posterior margin; anterior half of hypomeron not flat but approaching closely, posterior area widely flat and closely adpressed. Elytron: parallel-sided; 5.6–7.0 mm long; 3 well-defined interstitial lines; epipleuron and suture continue around apex (visible both from above and beneath) neither further thickened in apical half. Head: cannot be retracted into prothoracic cavity; GHW 1.5–2.0 mm; SIW 0.25–0.3 mm; SIW/GHW 0.15–0.16; ASD<ASW (sockets close but not contiguous); frons-vertex junction not defined, this area rounded. Antennae slightly longer than GHW up to almost twice GHW; 11 segmented. Mouthparts functional; apical segment of labial palpi ovoid, longer than wide. Abdomen, ventrites (Fig. 139): LO entire in V6 and V7, in V7 LO reaching sides but not posterior margin (LO closely following posterior outline and disposition in fresh specimen may be interpreted differently). MPP short, rounded. Tergites: T8 as wide as long; anterolateral prolongations narrow, not as long as posterior exposed portion, not obviously expanded vertically. Aedeagal sheath (Figs 140, 141): lacking rounded projection along posterior margin of sternite. Aedeagus (Figs 140, 141): L/W<3/1; LL/ML moderate; LL not divergent along most of length dorsally and slightly shorter than ML; apices of LL rounded, not out–turned, width subequal to that of ML; inner apical area of LL obliquely truncate; base of LL produced, rounded.

**Female, Larva.** Unknown.

**Etymology**. The specific name is latinised from the name of the spotted dog (dalmatian) and is a play on words to highlight the 'spotted' nature of the dorsal surface.

### *Atyphella ellioti* Ballantyne, 2000

*Atyphella ellioti* Ballantyne, in Ballantyne & Lambkin, 2000:33; 2001:364, 2006:30.

**Holotype.** Male. **AUSTRALIA:** 19.16 S, 146.49 E, Mt Elliot National Park (QMT61104).

**Diagnosis**. One of the six Australian species with striped elytra and the smallest Australian *Atyphella* (< 4 mms long); elytra with two interstitial lines, and brown pronotum with median darker area; female, larva not associated.

### *Atyphella flammans* Olliff, 1890
(Figs 125, 130, 131)

*Atyphella flammans* Olliff, 1980:651. Lea, 1909:111; 1921b: 68. Olivier, 1910b:46. Ballantyne in Calder, 1998:176 (comb. rev). Ballantyne & Lambkin, 2000:35, 2001:364, 2006:30.
*Luciola (Luciola) flammans* McDermott, 1966:104.

**Lectotype.** Male. **AUSTRALIA**: 20.42 S, 140.30 E, Cloncurry (K33979, AMS) designated by Ballantyne & Lambkin, 2000:35.

**Diagnosis**. The largest of the six Australian species with striped elytra (8–13 mm long); distinguished from the very similar *A. flammulans* Ballantyne by the number of pale interstitial lines (4) and the rounded frons-vertex junction. Female (Figs 130, 131) with fully developed elytra and shortened hind wings (see Discussion on female aptery); coloured as for male or paler; Ballantyne and Lambkin, 2000:35 characterised the larva.

**Remarks.** The probability of mislabelling of the type specimen was discussed (Ballantyne & Lambkin, 2000:35).

### *Atyphella flammulans* Ballantyne, 2000

*Atyphella flammulans* Ballantyne in Ballantyne & Lambkin, 2000:38, 2001:364, 2006:30.

**Holotype.** Male. **AUSTRALIA**: 17.56 S, 145.56 E, Boulder Creek via Tully (QMT 61110).

**Diagnosis.** One of the six Australian species with striped elytra, most similar to *A. flammans*, distinguished by the acute frons-vertex junction, the smaller size (< 9 mm long) and the presence of two well–defined interstitial lines. Female, larva not associated.

### *Atyphella guerini* (Ballantyne, 2000)
(Fig. 126)

*Luciola guerini* Laporte, 1833:151. Masters, 1886:288; 1888:327. McDermott, 1966:105 (Partim); Nomen nudum**.**
*Lampyris australis* F. (misid.). Boisduval, 1835:125. Motschulsky, 1854:53 (Partim).
*Lampyris australis* Guérin-Méneville, 1838:74. *Nec* Fabricius, 1775:201; 1787:162; 1792:102; 1801:104.
*Luciola australis* Guérin-Méneville. Lacordaire, 1857:337.
*Luciola australis* (F.). Olivier, 1883:330; 1885:362; 1902:74; 1907:52; 1909b: lxxxi; 1913:417. Lea, 1909:108 (Partim); 1921a:197. Misidentification.
*Luciola (Luciola) australis* (F.) McDermott, 1966:105 (Partim).
*Luciola guerini* Ballantyne, 1988:164.
*Atyphella guerini* (Ballantyne). Ballantyne, 2000: 117.

**Type.** Not located.

**Material examined. PAPUA NEW GUINEA***:* New Ireland Pr., New Ireland: 6.00S, 147.00E, No other data, identification label ''*Lampyris australis*'' authority obscured, male (MNHN). 3.13S, 151.56E, Kandan, 1.i.1960, W. W. Brandt, male (BPBM). Gilingil Plantation, 2 m, VII.4.1956, E. J. Ford jnr, male (BPBM). **SOLOMON ISLANDS**: Western Pr., New Georgia: 8.25S, 157.60E Munda, 30.VIII.1965, Tilley (Roy. Soc. Exped. BM 1966–1) male (NHML). **INDONESIA:** 1.68S, 127.88E Halmahera, Djilolo, ex Standinger, male (MNHN).

**Diagnosis.** One of three species from this study area with uniformly orange pronotum and dark brown elytra; distinguished from *Pygat. salomonis* and *Ll. majuscula* as follows (extended from Ballantyne, 2000):

*A. guerini:* basal abdominal ventrites mid-brown; V5 very dark brown; all abdominal tergites pale; V7 with MPP apically rounded, not considerably prolonged; aedeagus with basal piece not hooded, median lobe lacking pointed projection at sides of ejaculatory orifice; elytral interstitial lines 1, 2 as well–defined as suture; LO occupies more than half V7, area posterior to LO in V7 not arched or swollen; ventral face of T8 lacks median longitudinal groove or posterior asymmetrical curved ridge; not Australian.

*Pygat. salomonis:* basal abdominal ventrites pale; V5 very dark brown; all abdominal tergites pale brown; V7 with median posterior projection considerably prolonged, parallel-sided, and apically truncate, often obliquely; aedeagus lacking hooded basal piece, median lobe with pointed projections at sides of ejaculatory orifice; elytral interstitial lines faint, not as well–defined as suture; LO occupies about half or less of V7; area posterior to LO in V7 somewhat arched; ventral face of T8 with single curved ridge to left of median line; not Australian.

*Ll. majuscula*: all abdominal ventrites (except for pale LO in 6 and 7) very dark; all abdominal tergites dark except for pale tergites 7, 8; V7 with median posterior projection moderately produced, apically rounded, not parallel-sided; aedeagus with basal piece hooded; all 4 elytral interstitial lines as well–defined as suture; LO occupies most of V7; area posterior to LO small, not arched; ventral surface of T8 with median longitudinal groove; Australian.

**Remarks.** Ballantyne (1988) resolved the identities of *Luciola australis* F. and *L. guerini* Laporte, which was treated as a *nomen nudum*. While *guerini* was not part of Ballantyne and Lambkin's (2000) cladistic analysis, Ballantyne (2000) indicated that it differed from *A. majuscula* in only one male character and its position is confirmed here. Ballantyne (2000) assigned *guerini* to *Atyphella* and described 31 males and two possible larvae (associated only by similarity of label data), from New Ireland. The single male from New Georgia is in poor condition and covered in mould and is a tentative association only, as is the Halmahera male, which was not dissected.

### *Atyphella immaculata* Ballantyne, 2000

(Fig. 127)

*Atyphella immaculata* Ballantyne in Ballantyne & Lambkin, 2000:38, 2001:364, 2006: 30.

**Holotype**. Male. AUSTRALIA: 15.49 S, 145.17 E, Mt Finnigan (QMT 61139).

**Diagnosis.** One of only two Australian species with orange pronotum and very dark elytra [the other is *Lloydiella majuscula*]. Distinguished most obviously by its smaller size, parallel-sided elytra and lack of a hooded basal piece on the aedeagus. Female, larva not associated.

### *Atyphella inconspicua* (Lea)

(Fig. 125)

*Luciola inconspicua* Lea, 1921a:197.
*Luciola (Luciola) inconspicua* Lea. McDermott, 1966:106.
*Atyphella inconspicua* (Lea) comb. n. Ballantyne in Calder, 1998: 177. Ballantyne & Lambkin, 2000: 38, 2001: 364, 2006: 30.

**Lectotype.** Male. **AUSTRALIA:** 16.55 S, 145.46 E, Cairns district, designated by Ballantyne & Lambkin, 2000 (QM).

**Diagnosis**. A relatively small species (< 8 mm long) with brown elytra and pronotum with a median dark mark; similar to *A. conspicua,* distinguished by the parallel-sided pronotal margins, and pronotal width not exceeding humeral width; females brachelytral, elytra contiguous in mid-line, hind wings absent. Larva not associated.

### *Atyphella kirakira* sp. n.

(Figs 142–146, 148, 149)

**Holotype.** Male. **SOLOMON ISLANDS**: Makira Pr., 10.30S, 161.49E, San Cristobal Island, Kira Kira, 0–50m, 10.xi.1964, RS (BPBM).

**Paratypes** (4). **SOLOMON ISLANDS**: Same locality as holotype, 2 males. Central Pr., Florida Group, Tulagi, 6.IX.1960, COB, male. Guadalcanal Pr., 9.35S, 160.12E Guadalcanal, Lame, near Mt Tatuve, 300m, COB, male (BPBM).

**Diagnosis**. A small species (< 7 mm long) with uniformly dark brown elytra and orange pronotum with median dark area, LO apparently bipartite in V7, and MPP in V7 short, rounded; distinguished from other *Atyphella* with bipartite LO by the uniformly coloured elytra and the entire LO in V6.

**Male.** 6.6–6.9 mm long; 3 mm wide; just over twice as long as wide. Colour: (Figs 142, 144) Pronotum yellowish orange, semitransparent with fat body showing through cuticle, median dark marking not reaching either anterior or posterior margins, marking almost black in Lame male; MN yellow, MS slightly dingy pale brown; elytra moderately dark brown; head dark brown, antennae and palpi mid-brown; in 2 Kira Kira males all legs pale, abdominal ventrites pre LO mid-brown; one Kira Kira male legs pale with tibiae and tarsi light brown, and abdominal ventrites pre LO moderately dark brown; tergites light brown semitransparent, T8 yellowish; LO in anterolateral areas of V7 closely and narrowly adpressed to dorsal surface , separated between by diffuse fat body extending posteriorly almost to MPP (LO interpreted as bipartite). Pronotum: 1.5–1.6 mm long; 2.3–2.5 mm wide; W/L 1.5–1.6; ¼ as long as body; lateral margins diverge with rounded convergence; posterolateral corners rounded obtuse, projecting a little behind median posterior margin; anterior portion of hypomeron not flat; posterior portion of hypomeron flat, closely adpressed. Elytron (Fig. 144): margins slightly convex-sided; 5.1–5.3 mm long; 2 defined interstitial lines slightly better defined at their bases than in their apical half in 2/5; epipleuron and suture not continuing around apex as a ridge and neither thickened in apical half. Head: not able to be retracted into prothoracic cavity; GHW 1.6 mm; SIW 0.2 mm; SIW/GHW 1/8; ASD<ASW, antennal sockets close but not contiguous; frons-vertex ‘junction’ rounded not well–defined, frons 3 X as high as ASW. Antennal length longer than GHW; 11 segmented. Mouthparts well developed, probably functional; apical segment of labial palpi laterally compressed, like an elongate narrow triangle, with inner longer margin bearing paired elongate teeth at apex only in 3, and 1 apical and 2 subapical teeth in one. Abdomen, ventrites (Figs 142, 143): LO occupying all of V6; LO in V7 interpreted as bipartite (no information about light production exists and this is a morphological, not functional interpretation), reaching sides but not posterior margin, adpressed areas occupying less than half V7; at least half of V7 posterior to adpressed areas of LO filled with fat body; MPP short, broad. Tergites: T8 as wide as long; anterior prolongations of T8 very short and narrow. Aedeagal sheath (Figs 145, 148): with posterior margin of ventrite rounded, lacking projection. Aedeagus (Figs 145–149): L/W 2/1, LL/ML 3.5; LL very slightly shorter than ML, apices rounded, not out-turned, narrower than width of apex of ML; LL diverge along their length, apices well–separated; base of LL broadly truncate, scarcely produced.

**Female, Larva.** Not associated**.**

**Etymology**. The specific name is considered a noun in apposition, and reflects not only the type locality but the use of the name twice highlights the apparently bipartite LO

### ***Atyphella lamingtonia*** **sp. n.**

(Figs 150–152, 160–161)

**Holotype.** Male. **PAPUA NEW GUINEA:** Northern Pr., 9.02S, 148.2E, Mt Lamington, 1200–1500 feet, C T McNamara (SAM).

**Paratypes** (4)**. PAPUA NEW GUINEA:** same as for holotype, males (SAM).

**Diagnosis.** One of eight species from New Guinea and Australia with striped elytra; the only species with additional lines of fat body in elytra giving appearance of extra longitudinal stripes; lacking flat anterior portion of hypomeron and ridge around elytral apices characteristic of Australian *Atyphella*.

**Male description**. 5.6–6.6 mm long, 2.6–2.8 mm wide, W/L 0.4. Colour (Figs 150–152): pronotum pale whitish yellow, semitransparent and paler in areas of fat body clusters; median dark marking extending to and expanding narrowly at both anterior and posterior margins; MN pale; MS and base colour of elytra light brown; elytra with 4 pale interstitial lines with irregular deposition of fat body within lines, and 2 additional fine lines between suture and interstitial line1, and lines 1 and 2; elytra (Figs 150, 151) with pale lateral margin not reaching interstitial line 4, narrowly pale around apex, suture with pale apical 1/3 (fat body), anterior 2/3 light brown; head between eyes, metathoracic sternum, tibiae and tarsi of all legs, abdominal ventrites 2–5 and tergites 2–6 very dark brown, rest dingy slightly paler brown except for pale semitransparent tergites 7, 8 and whitish LO. Pronotum: 1.1 mm long; 2.0–2.2 mm wide; W/L 2–2.2; 1/5–1/6 as long as total body length; lateral margins divergent posteriorly with rounded convergence; posterolateral corners rounded obtuse, projecting a little behind median posterior margin; anterior hypomeron not flat; posterior area widely flattened and closely adpressed. Elytron (Figs 150, 151): margins slightly convex-sided; 4.5–5.0 mm long; with 4 defined interstitial lines; epipleuron and suture not continuing around apex as ridge and neither thickened in apical half. Head: GHW 1.3 mm; SIW 0.1 mm; SIW/GHW 1/13; ASD<ASW, antennal sockets very close, not contiguous; frons-vertex 'junction' rounded not well–defined. Antennal length longer than GHW and < 2 x GHW; 11 segmented. Mouthparts functional; apical segment of labial palpi laterally compressed, like a fairly wide triangle, with inner longer margin bearing 3 elongate teeth. Abdomen, ventrites: LO occupying most of V6; LO in V7 reaching sides but not posterior margin, MPP short and broad. Tergites: T8 as wide as long; anterior prolongations of T8 narrow, not as long as posterior entire half. Aedeagal sheath: with posterior margin of sternite rounded, lacking projection. Aedeagus (Figs 160–161): L/W<3/1, LL/ML moderate; LL diverging along their length in apical half only, and slightly shorter than ML; apices of LL rounded, not outturned, width subequal to that of ML; base of LL broadly rounded.

**Female, Larva.** Not associated.

**Etymology.** The species is named for its type locality.

### *Atyphella leucura* (Olivier, 1906)

(Figs 166–176)

*Luciola leucura* Olivier, 1906:157; 1907:53; 1911:172.
*Atyphella leucura* (Olivier). Olivier, 1910b:46; 1913:417. Ballantyne &Lambkin, 2000:15, 2001:364, 2006:30.
*Luciola (Luciola) leucura* Olivier. McDermott, 1966:108.

**Holotype.** Male. **PAPUA NEW GUINEA**: New Britain Pr., labelled 1. (printed) LIX Nelle-Bretagne; 2. (printed) Nouv.-Bretagne LIX–1889; 3. (handwritten) leucura Ern. Oliv. (MNHN).

**Other material examined. PAPUA NEW GUINEA**: New Britain Pr.: 4.21S, 152.02E, Kerevat: 10.ii.1966, G. Monteith, 2 males (UQBA); Lowl Exp. Stn., 23.v.1954, J. Szentivany, male (DAPM). Gazelle Peninsula: 4.26S, 152.05E. Gaulim 120–140m, 19–28.XI.1962, 3 males, JS (BPBM); Mt Sinewit, 1100–1200 m, 15–16.XI.1962 JS, male; 4.29S, 152.08E, Upper Warangoi Illugi 230m 12–30.XII.1962, JS, 2 males (BPBM).

**Diagnosis.** Dorsally pale with a large median dark area on pronotum, a dark area on each elytron adjacent to MS and lighter brown markings in apical half. Similar in colouration to many *Pygatyphella* spp., differs in extent of LO in V7 and lack of arching of V7. Distinguished by its restricted occurrence on New Britain.

**Male redescription.** 8.8–10.0 mm long; 4.0–4.3 mm wide, just over twice as long as wide. Colour Figs 166–169): Pronotum dingy very pale yellowish brown with wide median darker brown area extending from anterior to posterior margin, wider across posterior 1/3, with mottled darker areas (dark brown and reddish brown) outlining darker pattern within (Fig. 166, 169); in type semitransparent areas indicate retraction of fat body along anterior margin and at sides of median dark area; MN light brown with median darker area; MS entirely light brown (in 2 Gaulim males), or light brown with an anteromedian darker area not reaching sides or posterior margin; elytra pale dingy yellowish, with darker markings, semitransparent with underlying fat body evenly dispersed in small clumps except less in posterior darker area; narrow basal darker brown area running obliquely from interstitial line 2 to inner edge of suture, adjacent to MS, not assuming subtriangular shape here; suture in basal 1/5 pale yellowish brown, suture in next ½ length slightly darker brown; brown band extending irregularly across elytron from anterior margin of darker sutural band, covering most of posterior half of elytron except for lateral margin, and about 1/7 of sutural apex; head, antennae and mouthparts mid–brown; ventral surface of prothorax yellowish, of meso and metathorax brown with metepipleural plates yellow; legs medium brown except for paler brown coxae 1, 2, all trochanters and bases of femora, and darker brown coxae 3; abdomen dingy pale yellowish brown with edges of V3 and 4 more darkly marked, and V6 with irregular dark markings across posterior margin; T 2–4 yellowish in middle, brown at sides, T 5, 6 mottled yellowish brown, T 7, 8 yellowish semitransparent. Pronotum: 1.6–2.0 mm long; 2.7–3.6 mm wide; W/L 1.6–1.8; dorsal surface densely punctate, punctures contiguous over most of surface; lateral margins divergent posteriorly with rounded convergence; posterolateral corners rounded obtuse, projecting little behind median posterior margin, separated by shallow emarginations; anterior portion of hypomeron not flat; posterior portion of hypomeron flat, closely adpressed. Elytron: margins convex–sided; 6.9–8.0 mm long; 4 faintly defined interstitial lines; epipleuron and suture not continuing around apex as a ridge, neither thickened in apical half. Head: not able to be retracted into prothoracic cavity completely; GHW 2.0–2.2 mm; SIW 0.2–0.25 mm; SIW/GHW 1/10; ASD<ASW, antennal sockets close, not contiguous; frons-vertex ‘junction’ rounded, frons not defined. Antennal length greater than GHW less than twice GHW; 11 segmented. Mouthparts well developed, functional; apical segment of labial palpi laterally compressed, subtriangular, inner longer margin dentate, with 3 elongate slender teeth. Abdomen, ventrites (figs 168, 175): LO occupying all of V6; LO in V7 entire; reaching sides but not posterior margin, occupying most of V7. MPP short apically rounded. Tergites: T8 as wide as long; anterior prolongations very short and narrow. Aedeagal sheath (Figs 170, 171): posterior margin of sternite rounded, lacking projection. Aedeagus (Figs 172–174): L/W<3/1, LL/ML 2.4; LL diverging along length, well–separated at apices; apices rounded, slightly out-turned, narrower than width of apex of ML; LL a little shorter than ML, base of LL produced anteriorly symmetrically, relatively acutely, sometimes appearing medianly emarginate.

**Female.** Not associated.

**Larva**. Not reliably associated. A single larva taken at Kerevat by Monteith (UQIC) with two males of this species has laterally explanate tergal margins.

**Remarks.** Olivier (1906) highlighted the glossy apunctate margins to the pronotum, and the ‘mucronate’ last abdominal segment. The lateral margins of the pronotum of specimens listed here are punctate. The colour is similar to that of several mainland New Guinea *Pygatyphella* species. All other New Britain fireflies have orange pronotum and dark brown elytra (Ballantyne, 1987a; Ballantyne obs.).

### *Atyphella lewisi* Ballantyne, 2000
(Fig. 130)

*Atyphella lewisi* Ballantyne in Ballantyne & Lambkin, 2000: 41, 2001: 364, 2006: 30.

**Holotype.** Male. **AUSTRALIA**: Mt Lewis Road, via Julatten (ANIC).

**Diagnosis**. One of the six Australian species with striped elytra; small (<6 mm long); similar to *A. brevis* and *A. ellioti*, distinguished by its size, convex frons-vertex junction, 2 interstitial lines and the apparently bipartite LO in V7; probable female brachelytral, hind wings absent, elytra do not approach in mid-line. Larva not associated.

***Atyphella lychnus*** **Olliff, 1890**
(Figs 11, 78, 79)

*Atyphella lychnus* Olliff, 1890:647, 1297 (female). Olivier, 1910b:47; 1911:172. Lea, 1909:111; 1921c:7. Tillyard, 1926:213. Ballantyne in Calder, 1998: 177 (comb. rev.). Ballantyne &Lambkin, 2000: 43, 2001: 364, 2006: 30. *Nec* Lea, 1929:345.
*Luciola (Luciola) lychnus* (Olliff). McDermott, 1966:109. Moore, 1989:136, Fig. 188. Lawrence and Britton, 1991: Fig. 35.38, C & D (adult).
*Luciola (Atyphella) lychnus* (Olliff). Moore, 1989:136.

**Lectotype**. Male. **AUSTRALIA**: Mt Wilson, designated by Ballantyne & Lambkin, 2000 (AMS).

**Diagnosis**. One of the six Australian species with striped elytra; 4 interstitial lines. Female with fully developed elytra and shortened hind wings. Ballantyne and Lambkin, 2000: 43 characterised the distinctively coloured larva.

***Atyphella monteithi*** **Ballantyne, 2000**

*Atyphella monteithi* Ballantyne in Ballantyne & Lambkin, 2000: 47, 2001: 364, 2006: 30.

**Holotype.** Male. **AUSTRALIA**: Crystal Cascades via Cairns (QMT62709).

**Diagnosis.** Known from three specimens from Cairns; orange pronotum with median dark mark; elytra brown, slightly convex-sided, with three well–defined interstitial lines.

***Atyphella olivieri*** **Lea, 1915**
(Figs 128, 129)

*Atyphella olivieri* Lea, 1915:494; 1921a:197; 1921c:7. Ballantyne in Calder, 1998:177 (comb. rev.). Ballantyne & Lambkin, 2000:48, 2001:364, 2006:30.
*Atyphella Olivieri* Lea. Olivier 1910b:47; 1911:172.
*Luciola (Luciola) oliveris* (Lea). McDermott, 1964:16. Unnecessary Nom. Nov.
*Luciola (Luciola) olivierius* (Lea). McDermott, 1966:110. Unnecessary name change or probable misspelling for *L. oliveris* McDermott 1964.

**Lectotype.** Male. **AUSTRALIA:** Cairns, designated by Ballantyne & Lambkin, 2000 (QM).

**Diagnosis**. Known from its conspicuous dorsal colouration; pronotum very pale cream with median dark mark; elytra dark brown with broad cream lateral, sutural and apical borders. Female macropterous coloured as for male. Ballantyne and Lambkin (2000:50) described larvae taken in the vicinity of flying males.

***Atyphella palauensis*** **Wittmer, 1958**
(Figs 154–157, 159, 162–163)

*Atyphella carolinae* subspecies *palauensis* Wittmer, 1958: 68.

**Holotype.** Male. **REPUBLIC OF PALAU:** 7.0N, 134.0 E, Pelelieu Is. E coast 27.i.1948 (BPBM).

. **Other specimens examined**. **REPUBLIC OF PALAU**: 7.0N, 134.0 E Pelelieu Is: E coast, 27.i.1948, H Dybus, paratype male; 27.vi.1985, 2 males; 27.vi.1983, no collector, 2 males; Peliliou (sic), Garyuoka, 21.i.1938, Shiro Mirakami 1 male paratype, 1 female paratype. Babelthaup hill NW of Seabee camp, 6.50–7.10 pm, M Jess, 2 males 1 female (BPBM).

**Diagnosis**. Distinguished most obviously by its small size, locality and largely pale dorsal colouration with darker markings across elytral base and at apex.

**Male redescription.** 5.6–7.0 mm long; 2.6–3.0 mm wide; W/L 0.4. Colour: Pronotum (Fig. 159) yellow, semitransparent, underlying fat body clearly visible and faint trace of median dark marking (4/6 Pelelieu, Garyuoka and Babelthaup), or pronotum dingy yellow over whole of surface (2/6 Pelelieu) with most of median area diffusely slightly darker (1/6), or faint median mark restricted to small area (1/6), pronotum of a Pelelieu male with dark marking beginning at mid-point and expanding across median half of posterior margin; MN pale light brown, MS very pale; elytra (Figs 154, 157) semitransparent, underlying hind wings confuse colour interpretation; elytra light brown with base and apex narrowly slightly darker brown; head reddish to dark brown, antennae and palpi paler brown; venter of thorax pale except for midbrown metasternum (pale brown in one Babelthaup male); legs pale brown with apical half or all of tibiae, and all of tarsi brown; basal abdominal ventrites pale mottled with darker brown; V5 mostly brown; basal abdominal tergites brown, T7, 8 pale yellow. Pronotum (Fig. 159): 1.1–1.5 mm long; 2.0–2.4 mm wide; W/L 1.6–1.8; lateral margins diverging posteriorly with rounded convergence; posterolateral corners rounded obtuse, projecting beyond median posterior margin; anterior half of hypomeron not flat; posterior half widely flat, closely adpressed. Elytron (Figs 154, 157): slightly convex-sided; 4.5–5.5 mm long; with 2 reasonably well–defined interstitial lines; epipleuron and suture not continuing around apex, not thickened in apical half. Head: cannot be retracted into prothoracic cavity; GHW 1.4–1.8 mm; SIW 0.2; SIW/GHW 0.1–0.14; ASD<ASW, sockets not contiguous; frons-vertex junction not well–defined, rounded. Antennae longer than GHW, not reaching 2 x GHW; 11 segmented. Mouthparts functional; apical segment of labial palp flattened, like a wide triangle with inner edge irregular, bearing either no teeth or 2 teeth. Abdomen, ventrites: LO entire in V6 and V7 reaching sides but not posterior margin. MPP rounded, short. Tergites: T8 as wide as long; anterolateral prolongations very short. Aedeagus (Figs 162, 163): elongate, may appear subparallel-sided; L/W 3.5/1; LL/ ML 2.8; LL diverging or not along their length dorsally, slightly shorter than ML; apices of LL slightly out–turned and rounded, width at tip equal to that of ML; inner apical area of LL obliquely truncate; base of LL produced and rounded.

**Female.** (Figs 155, 156) 7.0 mm long. Elytra fully developed and cover body, hind wings ¾ length of elytra and female probably incapable of flight. Colour: dorsal colouration approaches that of male except paratype pronotum has no median darker markings; Babelthaup female with very pale pronotum with median brown area, and very pale elytra with basal and apical darker markings; elytra semitransparent and appear slightly mottled; abdominal ventrites light brown. Pronotal outline as for male. Head of wingless female form; head can be completely retracted within prothoracic cavity. V7 with median posterior margin broadly emarginated; acute junction between sides of median emargination and remainder of obliquely truncate posterior margin. T8 with lateral margins converging gently posteriorly and posterior margin rounded.

**Larva**. Not associated.

### *Atyphella scabra* Olivier, 1911
(Figs 177–185)

*Atyphella scabra* Olivier, 1911, p. 173; 1913, p. 417.
*Luciola (Luciola) scabia* (Olivier). McDermott, 1966, p.112 (Mis-spelling).

**Holotype**. Male. **PAPUA NEW GUINEA**: Pawarin labelled (Fig. 180): 1. (HW) male symbol; 2. (HW) Pawarin Juin, 1903; 3. typed Nieuw Guinea Expeditie 1903; 4. pink label, (HW) *Atyphella scabra* Ern Oliv. (MNHN).

**Other material examined. PAPUA NEW GUINEA**: Pawarin Male labelled as for type except lacking identification label. **PAPUA NEW GUINEA**: 3.17S, 142.35E, Torecella Mt, Sea Falls near Afua, 1700 ft, 1939, P G Moore, 2 males (BPBM).

**Diagnosis.** Distinguished from all other *Atyphella* by the widely bipartite LO in both V6 and V7, the pointed MPP, the considerable extension of T8 beyond the margin of V7, and the strong elevation of interstitial lines 1, 2 exceeding that of the suture.

**Male redescription.** 7.8–9.0 mm long; 3.2–3.9 mm wide; W/L approx. 2.5. Colour: (Figs 177, 178). Pronotum: dingy orange, median half darker brown and extending to anterior and posterior margins (punctures here ringed in darker brown); elevations above eyes appearing paler in Sea Falls males; head dark brown, antennae and palpi light brown; MN yellow, MS brown not as dark as mid-brown elytra (type elytra slightly darker in anterior half and along interstitial lines 1, 2); narrow area of epipleuron in type male slightly paler brown than rest; ventral thorax pale brown, except for darker brownish semitransparent metasternum; legs pale brown; basal ventrites brown; V6 and 7 semitransparent, areas of LOs yellowish, whitish fat body continuous between LO halves in Sea Falls males, not continuous in type; tergites dingy yellow and semitransparent, ventral surface of T8 orange yellow. Pronotum: 1.6–1.8 mm long; 3.1–3.5 mm wide; W/L 1.9–2.1; dorsal surface smooth, densely punctate, punctures contiguous over most of surface; lateral margins divergent posteriorly with rounded convergence; posterolateral corners rounded obtuse, projecting little behind median posterior margin; anterior portion of hypomeron flat; posterior portion of hypomeron flat, both areas closely adpressed (Fig. 178). Elytron (Fig. 177): convex-sided; 2 well–defined interstitial lines (1, 2) more strongly elevated than, and 1.5 to 2 X as thick as sutural ridge; basal edges of line 2 and inner margin of line 1 bearing single line of punctures larger than rest, irregular in shape and size; epipleuron and suture continue around apex as a ridge, not thickened in their apical half. Head: not able to be retracted within prothoracic cavity; GHW 1.8–2.3 mm; SIW 0.15–0.2 mm; SIW/GHW 1/9–1/11; ASD<ASW, antennal sockets very close not contiguous; frons-vertex junction not defined, this area rounded. Mouthparts well developed, probably functional; apical segment of labial palpi ovoid, longer than wide. Antennal length subequal to GHW or slightly less; 11 segmented. Abdomen (Figs 178, 179): LO in V6 and V7 restricted to small anterolateral plaques occupying less than half area of each ventrite. MPP short, narrow, apically acute; posterolateral corners short, slightly angulate, horizontal (appear to project slightly posteriorly in pinned specimens, after soaking in water or ethanol are round, not projecting). Tergites: T8 (Figs 178, 179) as wide as long; posterior half as wide as anterior half, projecting for about half its width beyond posterior margin of V7; posterior margin of T8 bisinuate; anterior prolongations of T8 not developed. Aedeagal sheath (Figs 181–183): posterior margin of sternite rounded, with short rounded medial projection (arrow in Figs 182, 183). Aedeagus (Figs 35, 184–185): L/W 2.5/1, LL/ML 2.2; LL diverge along their length and are widely separated at their rounded apices; LL slightly shorter than ML, apices rounded, out-turned and narrower than apex and base of ML; base of LL produced anteriorly and broadly rounded (appears slightly asymmetrical, interpreted here as symmetrical); ML broad, apically rounded.

**Female and larva**. Unknown.

**Remarks.** Olivier (1911) described the median dark mark wider along the anterior margin than posterior, a distinction not now obvious on the type. Olivier also described the brown elytra as finely pale margined laterally; he keyed *scabra* using ''elytra <u>black</u>''. The margins on the type do not appear paler than the rest.

### *Atyphella scintillans* Olliff, 1890
(Figs 129, 132)

*Atyphella scintillans* Olliff, 1890:650. Lea, 1909:111; 1921a:198 (female). Ballantyne in Calder, 1998:177 (comb. rev.). Ballantyne & Lambkin, 2000: 51, 2001: 364, 2006: 30.
*Luciola decora* Olivier, 1902:77; 1907:51; 1910b:47. Lea, 1909:111 (synonymy).
*Luciola (Atyphella) scintillans* (Olliff). McDermott, 1964:44.
*Luciola (Luciola) scintillans* (Olliff). McDermott, 1966:112.

**Lectotype.** Male. **AUSTRALIA**: Ash Island, Upper Hunter River designated by Ballantyne & Lambkin, 2000 (AMS).

**Diagnosis**. Male with yellow pronotum with median dark markings; dark brown elytra with 4 interstitial lines; head can be retracted into prothoracic cavity; antennae 9 segmented. Female brachelytral, elytra meet in mid-line, hind wings vestigial. Ballantyne and Lambkin, 2000: 51 characterised the distinctively coloured larva.

### *Atyphella similis* Ballantyne, 2000

*Atyphella similis* Ballantyne, in Ballantyne & Lambkin, 2000:53, 2001:364, 2006:30.

**Holotype.** Male. **AUSTRALIA:** Lamington National Park (QMT62936).

**Diagnosis.** Similar to both *A. lychnus* and *A. atra*, distinguished by a combination of male, female and larval characters (Ballantyne & Lambkin, 2000: 54).

### *Atyphella testaceolineata* Pic, 1939
(Figs153, 158, 164–165)

*Atyphella testaceolineata* Pic, 1939:370; Wittmer, 1939:127
*Luciola (Luciola) testaceolineata* (Pic). McDermott, 1966, p.114.

**Holotype.** Male (head and prothorax missing) INDONESIA: Maluku Islands, 3.24S, 126.40E, Buru Island (Zoology Museum, Amsterdam).

**Other material examined. PAPUA NEW GUINEA**: Morobe Pr., 8.24S, 147.05E, Erume, 2000 m, 6.viii.1974, T. Fenner, 4 males (DAPM). Morobe Dist., 7.20S, 146.42E. 4.5 mi w Wau: Edie Cr. Rd, at Namie Cr. Elev. C 4500'', November 17 1969, J.E. Lloyd, 1 male (G620), 1 female (G619) (JELC), 1 male (G621) (ANIC); 7.20S, 146.42E. Wau, 1600–1700 m, 28.xii.1961, JS, 1 male (BPBM).

**Code name.** *Luciola* 9 (Lloyd, 1973b)

**Diagnosis.** One of eight *Atyphella* spp. with striped elytra; distinguished from *lewisi*, *brevis*, *ellioti* and *lychnus* by the flattened and dentate apical palpomere (the other species have an ovoid entire apical palpomere), from *flammans* and *flammulans*, which have contiguous antennal sockets, by the separated antennal sockets, and from the only other New Guinean species, *lamingtonia*, by lacking additional pale lines of fat body between the pale interstitial lines.

**Male redescription.** 6.6–8.3 mm long; 3.1–3.8 mm wide; W/L 0.4. Colour (Fig. 153): Pronotum (Fig. 158) pale clear yellow, semitransparent in areas, with median dark brown area reaching anterior margin, and almost to posterior margin; fat body irregularly retracted beneath cuticle leaving paler areas; MS and MN pale cream; elytra brown with suture, lateral margin including elytral apex and 3 interstitial lines yellow; lateral elytral margin semitransparent, extending to and covering weakly developed interstitial line 4; head very dark reddish brown, antennae and palpi brown, labrum pale brown; ventral aspect of thorax brown; all legs brown except for paler coxae 1 and 2 and trochanters 1, 2 and 3, tibiae and tarsi darker brown than remainder; basal abdominal ventrites black; V6 and 7 uniformly pale cream; all abdominal tergites light brown except for pale yellow T8. Pronotum (Fig. 158): 1.2–1.5 mm long; 2.3–2.9 mm wide; W/L=1.9; punctures broad, moderately deep, contiguous; lateral margins diverge posteriorly with rounded convergence; posterolateral corners rounded, obtuse, projecting beyond median posterior margin and separated by shallow emarginations; anterior hypomeron not flat to neck; posterior hypomeron flat to neck strongly adpressed. Elytron: convex-sided, bearing 3 moderately elevated interstitial lines. Head: not able to be retracted completely into prothoracic cavity; GHW 1.4–1.6 mm; SIW 0.2mm; SIW/GHW 1/7–1/8; ASD<ASW; antennal sockets very close not contiguous, frons-vertex junction rounded. Mouthparts functional; apical segment of labial palpi laterally compressed, like a wide triangle, inner margin dentate with basal wide tooth and 3 narrower teeth, one at apex. Antennal length slightly longer than GHW; 11 segmented. Abdomen, ventrites: LO occupying V6 completely,

in V7 extending to all margins including posterior margin. MPP short, broad and rounded. Tergites: T8 as wide as long; anterolateral prolongations of T8 not as long as posterior (entire) portion, narrow, not expanded vertically. Aedeagal sheath: posterior margin of ventrite rounded, lacking short rounded medial projection. Aedeagus (Figs 164, 165): L/W<3/1, LL/ML moderate; LL divergent along their length dorsally; LL slightly shorter than ML, apices rounded, not out-turned and narrower than apex ML; LL narrow and parallel-sided in apical half when viewed from above; base of LL produced anteriorly and broadly rounded or truncate.

**Female**. Associated by similarity of label data only. 6mm long. Fully developed fore wings, hind wings absent; flightless. Only differences from the male are noted: one elytron present, paler than male, with paler interstitial lines still visible (this could be due to absence of hind wings); elytron not covering abdomen completely (T8 protrudes); head not examined; ventral aspect of body blotchy cream, semitransparent; paler LO material apparently restricted to lateral areas of V6; V7 very shallowly and narrowly emarginated along posterior margin; median posterior margin of V8 appears entire, as is that of T8.

**Remarks.** The incomplete holotype male of *A. testaceolineata* was not dissected. Specimens assigned here are considered to approach most closely the elytral pattern of the type specimen but are tentative assignments only. Pic's (1939) 9mm long specimens were from Buru Island, with elytral suture, lateral margins and interstitial lines pale, suggestive to Pic of *Luciola olivierius* McDermott. If this is a correct association, then this species, and a possible Halmahera record of a male of *A. guerini*, are the only species of *Atyphella* known from west of the island of New Guinea. Lloyd's (1973b) *Luciola* 9 are tentatively assigned here. Lloyd (1973b:995) described the flashing pattern as "single, short flashes each 1 sec. Occasionally a dim flash was interposed between the bright flashes".

## *Convexa* gen. n.

(Figs 12–14, 73, 74, 186–191)

**Type species**. *Atyphella wolfi* (Olivier).

**Diagnosis**. Similar to many *Atyphella* especially in outline of pronotum, distinguished by its dorsal colouration of orange pronotum and dark brown elytra with pale orange lateral margins, pale apex and part of suture; male pronotum wider than width across elytral humeri, hypomeron not strongly adpressed in anterior half; pronotal punctation small, sparse, areas between punctures very smooth and shiny; elytra convex-sided. Aedeagus with ML constricted preapically and apex thus appearing slightly bulbous. Female macropterous, coloured as for male; larva not associated.

**Male.** Pronotum (Figs 12, 186, 187) dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation small and widely separated. Anterior margin not explanate. Pronotum wider across posterior area than rest, pronotal width greater than humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent posteriorly; lateral margins in posterior half diverge then converge with rounded convergence; lateral margins lacking indentation at mid-point, or sinuousity in either horizontal or vertical plane, indentation near posterolateral corner, and irregularities at corner; posterolateral corners rounded obtuse; posterolateral corners projecting beyond median posterior margin and separated by shallow emargination.

Hypomeron closed. Median area of hypomeron not elevated in vertical plane, lateral margins not sinuate from above; anterior area of hypomeron not flat to side of head, posterior area widely flat and strongly adpressed; anterior raised area of hypomeron sloping smoothly to posterior flat area; pronotal width/ GHW index 1.6.

Elytron (Figs 12, 13, 186) with punctation dense, not linear, not as large as pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extending beyond mid-point of elytron, not extending as ridge around apex, not thickened in apical half; 0 or 2 interstitial lines, none exceeding suture; elytral carina absent; viewed from beneath with specimen horizontal epipleuron at elytral base wide, covering humerus, viewed from above epipleuron arising anterior to posterior margin of MS; epipleuron a ridge along most of length; sutural margins approximate along most of length in closed elytra; lateral margins convex.

Head (Fig. 13) moderately depressed between eyes; moderately exposed in front of pronotum, not capable of complete retraction within prothoracic cavity; eyes moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum close; frons-vertex junction rounded, no elevation in median area; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous, separated by < ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non-lunate, strongly flattened, like a wide triangle, inner edge dentate, with 2 elongate 'teeth'. Antennae 11 segmented; length greater than GHW to twice GHW; no segments shortened, flattened or expanded; pedicel not produced; FS1 not shorter than pedicel; all FS longer than wide.

Legs (Fig. 13) with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Fig. 13) lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins, nor with anterior margins extending into emarginated posterior margin of anterior segment; LO in V7 entire, occupying half V7, sometimes less; LO reaching to sides but not posterior margin; neither anterior nor posterior margin of LO medially emarginated; posterior area of V7 behind LO not arched or swollen, muscle impressions not visible in this area; LO in V6 entire occupying almost all V6. MPP present, symmetrical, apex rounded, entire, not laterally compressed, short or L=W; MPP not inclined dorsally nor engulfed by T8 apex; lacking dorsal ridge, ventral longitudinal trough. V7 lacking median carina, median longitudinal trough, narrow anteromedian depression on anterior face of LO, lacking PLP, incurving lobes or pointed projections, median 'dimple' or reflexed lobes. T7 lacking prolonged posterolateral corners. T8 symmetrical, wider than long in visible posterior area with lateral margins rounded, never subparallel-sided; visible posterior area not narrowing abruptly, lacking median posterior emargination, median posterior projections, not inclining ventrally nor engulfing posterior margin of V7 nor MPP, not extending conspicuously beyond median posterior margin of V7; T8 ventral surface lacking flanges, lateral depressed troughs, asymmetrical projections, median posterior longitudinal ridge, median longitudinal trough; concealed anterolateral arms of T8 longer than visible posterior portion, narrow horizontally, expanded dorsoventrally, not laterally emarginated before origins, apices lacking bifurcation of inner margin and bases lacking ventrally directed pieces; lateral margins of T8 not enfolding sides of V7; transverse band of darker cuticle across posterior ventral margin appears ridge like.

Aedeagal sheath (Figs 190, 191) never > 4 times as long as wide; lacking paraprocts; asymmetrical in posterior area where sheath sternite emarginated on right side from point of attachment of tergite; sheath not angulate on R or L sides; not subparallel-sided, not evenly emarginated on either side preapically, anterior half of sheath sternite broad, apically rounded, usually with slight median depression; tergite lacking lateral arms extending anteriorly and widely to sides of sternite; tergite not subdivided, lacking lateral projecting pieces along posterior margin of tergite 9; anterior margin of tergite 9 lacking transverse band; with curved pointed slightly sclerotised cuticular piece projecting on left side only (Figs 190, 191) and attaching to muscles arising from anterior portion of T8.

Aedeagus (Figs 188, 189) L/W<3/1; LL lacking lateral appendages, visible from beneath at sides of ML; LL/ML wide; LL of equal length; slightly shorter than ML; LL diverging along inner margins and separated there by > half their length; LL base width not =LL apex width which is subequal to ML, apices not expanding horizontally, not out–turned; dorsal base of LL symmetrical, not excavated, median margin prolonged, broadly rounded; LL lacking hairy appendages along outer ventral margins; apices of LL not out–turned nor inturned; lacking projection on left lateral lobe; inner margins lack slender leaf–like projection; short length of preapical inner margin of LL obliquely truncate, lacking strongly developed tooth at anterior end of emargination. ML symmetrical, lacking paired lateral teeth, single tooth to left side, not strongly arched, apex not in arrowhead shape, apex bulbous, not inclined ventrally. BP not very wide, not strongly sclerotised, not strongly emarginated along anterior margin, not hooded.

**Female**. (Fig. 14) Macropterous and assumed capable of flight. Pronotum lacking irregularities in posterolateral areas of dorsal surface; punctation small widely separated, not as large as elytron; pronotum always wider across posterior margin; lacking indentation of lateral margin and irregularities at posterolateral corner; pronotal width > humeral width; outline as for male. Elytral punctation not as large as pronotum, nor evenly spaced; interstitial lines 0 or 2; elytral carina absent; convex-sided. Head with eyes smaller than male, of winged female form, can be retracted within prothoracic cavity; antennae on head between eyes; clypeolabral suture present and flexible. No legs or parts thereof swollen and /or curved. LO in V6 only, lacking any elevations or depressions or ridges on V7.

**Larva** not associated.

**Etymology.** *Convexa* is a feminine noun latinised from the English word convex, highlighting the convex–sided elytra.

**Remarks**. Previous analyses have hinted at the distinctiveness of this species. Ballantyne and Lambkin (2000) grouped this species with a *marginipennis, costata* and *majuscula* complex, separate to most of the Australian *Atyphella*, and (2006) with a *flammans – olivieri* (Australian) complex.

### *Convexa wolfi* (Olivier, 1910)

(Figs 12–14, 73, 74, 186–191)

*Luciola wolfi* Olivier, 1910a:343; *in* Heyden, 1915:167.
*Luciola (Luciola) wolfi* (Olivier). McDermott, 1966:114.
*Atyphella wolfi* (Olivier). Ballantyne & Lambkin, 2000: 87.

**Holotype.** Female. **SOLOMON ISLANDS** (Museé Senckenberg, Frankfurt).

**Other material examined**. **PAPUA NEW GUINEA:** North Solomons Pr., Bougainville: 5.40S, 154.56E Mutahi 18 km SE Tinputz, 900 m 1–7.iii.1968, RS, 1 male; 1100m in malaise trap, ii.1968, Tawi, 2 males (BPBM). 5.40S, 154.56E Torpanos, 200m, 6 km W of Tinputz, malaise trap, 22 –29.ii.1968, RS, 6 males (BPBM). 5.55S, 154.59E, Togerao, 18–21.iv.1965 RS, 2 males (BPBM). 5.59S, 154.59E Kukugai village, 150m, x–xii.1960, W. Brandt, 4 females, 6 males. 5.59S, 154.59E Kokure, near Crown Prince Range, 900m, 11.vi.1956, JS, male. 6.44S, 155.40E Konga village (Buin), 6.ii–21.iii.1961, W. Brandt, male (ANIC). **SOLOMON ISLANDS:** Western Pr., Choiseul: 7.10S, 156.95E Kitipi R 80m, malaise trap, 13.iii.1964, PS, 3 males (BPBM); Malangona, 10m, malaise trap, 8.iii.1964, PS, 1 male. Kolombangara 7.95S, 157.05E, Kolombangara R 80m, malaise trap, 20.iii.1964, PS, 3 males (BPBM). Isabel Pr., Santa Isabel: 8.23S, 159.48E SE Tatamba 0–50m, 5–15.ix.1964 RS, 1 male (malaise trap), 1 female (BPBM). Central Pr., 9.08S, 160.25E, Florida Group, Nggela Is: Haleta, 0–300m, 4.x.1964, RS, 2 males, 1 female (BPBM). Guadalcanal Pr., 9.35S, 160.12E Guadalcanal: Lavoro Plantation, 1924, C. Hart, male (AMS); Poha River, 22.viii.1954, E. Brown, female (NHML). Lame near Mt Tatuve, 300m 18.v.1960, COB, male (BPBM). Sol Is Lunga R (bridge) 4.ix.1960 COB 2 males; Poha R 5 m, 2.vii.1956 JLG, male; Suta, 500–1200 m 27.vi.1956, JLG 2 males, female (female in light trap) (BPBM).

**Diagnosis.** Males are associated here. This is one of four similarly coloured species from the Solomons. *Pygat. limbatipennis* and *Pygat. limbatifusca* have LO retracted into anterior half of V7 and posterior area of V7 arched, MPP often obliquely truncate, posterior area of T8 venter with curved ridge slightly to one side of middle, and ML of aedeagus with paired lateral teeth. *M. limbata* has a black MS, lacks the flattened posterior area of the hypomeron and the pronotal punctures are close.

**Male redescription.** 9.9–13.2 mm long; 4.8–6.3 mm wide; W/L approximately 2/1. Colour (Figs 12–14, 73): Pronotum bright, shiny orange yellow, (semitransparent where fat body is retracted); MS, MN yellow; elytra dark brown, lateral margin broadly yellow, extending around apex, suture narrowly yellow in at least apical 1/3; head, antennae, palpi dark brown; ventral aspect of thorax pale yellow–brown, legs yellow–dingy orange with tibiae yellow or brown, tarsi brown; basal abdominal ventrites yellow, V5 very narrowly brown across posterior margin; LO creamy in V6, 7; posterior ½ or more of V7 semitransparent, yellow; tergites yellow (7, 8 paler than rest); T7 narrowly dark along posterior margin. Pronotum: 2.1–3.0 mm long; 3.8–4.8 mm wide; W/L 1.6–1.7; surface of pronotum very smooth and shiny; punctures very small, shallow, separated by 1–2 X width of puncture. Elytra: 7.5–10.3 mm long; interstitial lines not as well–defined as suture, 4 lines usually visible (except for Kukugai–1, Mutuhi–1, Togerao–2, Torpanos–1, and Choiseul–3, where only the inner one or two lines approach the suture). Head: GHW 2.1–2.8 mm; SIW 0.2–0.3 mm; SIW/GHW 0.09–0.12; ASD<ASW, sockets close not contiguous; frons 5 x ASW, frons-vertex junction rounded. Mouthparts with apical segment of labial palpi flattened, like a wide triangle, pattern of teeth varying sometimes from L to R palp and within and between different island locations (base of palp with broad blunt tooth, median narrower tooth and apical broad bluntly rounded tooth on both palpi from Kukugai, Mutahi, Togerao, Choiseul, Poha, Santa Isabel, Malangona, Haleta, Suta and Lame; left palp entire or with one incision, right palp with 3 teeth as described above in some Kukugai, Torpanos; right palp entire, left palp with 2 teeth in Mutahi; right palp with 3 teeth, left palp with 2 in some Torpanos; right and left palp with one broad preapical incision appearing as two teeth, basal one very broad in some Choiseul, Haleta; left palp with 3, right palp as above in some Choiseul). Aedeagal sheath: (Figs 190, 191) lacking median depression of anterior margin of sternite in Guadalcanal (Lunga R) and Santa Isabel male.

**Female**. (Fig. 14) Macropterous. 13–15 mm long (usually longer and wider than males). Coloured as for male except for pale V7, 8. V7 with median posterior margin broadly and shallowly emarginated and postero-lateral corners broadly rounded; median posterior margin of V8 narrowly emarginated; T8 with lateral margins converging gently posteriorly and posterior margin rounded.

**TABLE 7.** Distribution of species with pale margined elytra in the Solomon Islands.

| Locality | *M. limbata* | *C. wolfi* | *Pygat. limbatifusca* | *Pygat. limbatipennis* |
|---|---|---|---|---|
| Bougainville | | + | | + |
| Choiseul | | + | | + |
| Vella Lavella | | | | |
| Gizo | | | | |
| Kolombangara | | + | | + |
| Santa Isabel | + | + | | + |
| New Georgia | | | | + |
| Florida Group | + | + | | + |
| Russell Is | + | | | |
| Guadalcanal | + | + | | + |
| Malaita | + | | | + |
| San Cristobal | + | | + | |
| Rennell | + | | | |

**Remarks**. Assignment of males to this species is supported by the colouration, the distinctively shiny pronotum with small and well–separated punctures, and the very convex-sided elytra, all consistent with the type female, as well as the geographical location. Four species (*M. limbata*, *C. wolfi*, *Pygat. limbatipennis* and *Pygat. limbatifusca* **sp. n.**) with similar dorsal colouration of pale margined elytra, occur in the Solomon

Islands (see Table 7). Only *C. wolfi* has elytra margined along three sides, and it occurs in the more northerly part of the range from Bougainville, to Choiseul, through Gizo and Kolombangara to Santa Isabel with the most southerly records from Guadalcanal. With the exception of Vella Lavella and Malaita its distribution parallels that of *Pygat. salomonis*, which lacks the pale margined elytra.

### *Gilvainsula* gen. n.

(Figs 192–203)

**Type species:** *Atyphella messoria* Olivier.

**Diagnosis.** One of only two genera of the *Atyphella* 'complex' with pale dorsal colouration, and elytral apices pale or dark. Distinguished from *Aquilonia* by its geographic location (*Aquilonia* is restricted to Australia), the divergent lateral margins of the pronotum that converge in the posterior area with rounded convergence, and the paler colour.

**Male.** Pronotum (Figs 15, 196) dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate.

Pronotum (Fig. 196) wider across posterior area than rest; pronotal width subequal to or > humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent posteriorly, lateral margins in posterior half diverge then converge with rounded convergence; lacking indentation at mid-point, or sinuousity in either horizontal or vertical plane; lacking indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners rounded; rounded corners obtuse, posterolateral corners project beyond median posterior margin and separated by shallow emargination.

Hypomera closed. Median area of hypomeron not elevated vertically; anterior area of hypomeron not flat to side of head, posterior area flat but not closely adpressed; pronotal width/ GHW index 1.6.

Elytron punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extend beyond mid-point, do not extend as a ridge around apex and without any further expansion of either; 0 or 2 interstitial lines, inner two not exceeding suture; elytral carina absent; viewed from below with specimen horizontal epipleuron at elytral base wide, covers humerus from below, and viewed from above arises anterior to posterior margin of MS; epipleuron developed as lateral ridge along most of length; sutural margins approximate along most of length in closed elytra; lateral margins slightly convex-sided.

Head moderately depressed between eyes; moderately exposed in front of pronotum, not capable of complete retraction within prothoracic cavity; eyes moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum moderately separated; frons-vertex junction rounded, lacking median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, separated by <ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when head viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non–lunate, strongly flattened, in the shape of a wide triangle, with inner edge irregular not dentate. Antennae 11 segmented; length subequal to GHW up to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel; in very short antennae FS may be subequal in length and width.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment; LO in V7 entire, reaching sides but not posterior margin and occupying most of V7; posterior half of V7 not arched or swollen, muscle impressions not visible in this area; LO present in V6, occupying almost all V6. MPP present, apex rounded, entire, not laterally compressed, short, not inclined dorsally nor engulfed by T8 apex, lacking dorsal ridge and median longitudinal trough. V7 lacking median carina, median longitudinal trough, anteromedian depression on face of LO, PLP, incurving lobes or pointed projections, median 'dimple', or reflexed lobes. T7 lacking prolonged posterolateral corners. T8 not strongly sclerotised, symmetrical, W=L, visible posterior area not narrowing abruptly, lacking prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally nor engulfing posterior margin of V7 nor MPP, nor extending conspicuously beyond posterior margin of V7; T8 ventral surface lacking flanges, lateral depressed troughs, median longitudinal trough, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 present, not as long as visible posterior portion of T8, and broad, not laterally emarginated before their origins, not expanded dorsoventrally, apices lacking bifurcation of inner margin and bases lacking ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath never > 4 times as long as wide; lacking paraprocts; asymmetrical in posterior area where sheath ventrite emarginated on right side from point of attachment of tergite; sternite not angulate on L or R sides, not subparallel-sided, posterior margin entire, not emarginated on either side preapically, and rounded; anterior half of sternite broad, apically rounded (with a short median point in specimen standing next to type of *messoria*); tergite lacking lateral arms that extend widely anteriorly at sides of sheath sternite; tergite not subdivided, lacking projecting pieces along posterior margin of tergite 9, a narrow band across anterior margin of tergite 9 may be darker than rest; with pale cuticular piece that projects on left side only and attaches to muscles arising from anterior portion of abdominal T8.

Aedeagus L/W 3/1; essentially subparallel-sided; LL lack lateral appendages, are visible from beneath at sides of ML, LL/ML wide to moderate; LL of equal length, slightly shorter than ML, not diverging along inner margins, and separated there by > half their length; LL base width not=LL apex width which is narrower than that of ML with apices not expanded horizontally; base of LL (from above) symmetrical, not excavated, margin prolonged and pointed entire; LL lacking lateral hairy appendages along their outer ventral margins, which are not produced preapically nor narrowly on their inner apical margin and are obliquely truncate along their preapical inner margins; apices of LL not inturned, nor out–turned; lacking projection on left LL only; inner margins lack slender leaf-like projection; ML symmetrical, lacking paired lateral teeth and tooth to left side, not strongly arched, and apex not in shape of arrowhead, not bulbous, not inclined ventrally; BP not very narrow, not strongly sclerotised, not hooded, and not strongly emarginated along anterior margin.

**Female** (associated by similarity of colour and label data)**.** Macropterous. Pronotum lacking irregularities in posterolateral areas; punctation moderate to dense; pronotum > humeral width; indentation of lateral margin, irregularities at posterolateral corner, absent; outline as for male. Elytral punctation not as large as that of pronotum nor evenly spaced; 2 interstitial lines; elytral carina absent. Head of winged female form. No legs or parts thereof swollen and /or curved. LO in V6 only, lacking any elevations or depressions or ridges on V7.

**Larva** not associated.

**Etymology.** The generic name, a feminine noun, emphasizes the pale dorsal colouration and the island habitat (gilva from gilvus Latin for pale yellow, and insula Latin for island).

### List of species of *Gilvainsula*

*G. messoria* (Olivier)
G. *similismessoria* **sp. n.**

### Key to species of *Gilvalinsula* gen. n.

1. Dorsal colouration entirely pale........................................................................... *messoria* (Olivier)
   Dorsal colour pale with elytral apices black.......................................................... *similismessoria* **sp. n.**

***Gilvainsula messoria*** **(Olivier, 1913)**
(Figs 15, 16, 192, 195, 196, 199–203)

*Atyphella messoria* Olivier, 1913:421.
*Luciola (Luciola) messoria* (Olivier). McDermott, 1966:110.

**Holotype.** Male. **PAPUA NEW GUINEA:** 10.38S, 152.44E. Specimen labelled (Fig. 195) 1. (printed) St Aignan, (=Misima Island) VIII to XI.97 (Meek); 2. (Handwritten on pink paper) 'messoria Ern Oliv.' (MNHN).

**Other specimen examined**. Male, same locality as type (MNHN).

**Diagnosis.** Very similar to *G. similismessoria*, distinguished by the pale dorsal colouration.

**Male redescription.** 10.5–11.4 mm long; 4.0 mm wide; W/L 0.35–0.4. Colour: (Figs 15, 16) Dorsally light brownish yellow; head between eyes, antennae and palpi brown; ventral surface of rest of body light brownish yellow except for dark brown tibiae and tarsi of all legs, brown posterior half of V5 (wider at edges and narrower in middle), pale creamy LO in V6, 7; tergites yellow semitransparent. Pronotum: 2.2–2.4 mm long; 3.5–4.0 mm wide; W/L 1.6; pronotal width subequal to humeral width. Elytron: 8.3–9.0 mm long; interstitial lines not as well developed as suture in type male, lines 1, 2 as well–defined in second male especially in basal half. Head: GHW 2.2–2.3 mm; SIW 0.4; SIW/GHW 0.16–0.18; ASD subequal to ASW. Apical segment of labial palpi with inner edge of right palp bisinuate with a fairly broad truncate basal area, of left palp with a shallow median incision about 1/3 length from tip. Aedeagal sheath (199, 200): median anterior margin of sheath sternite slightly prolonged, very dark coloured, and pointed in non type male.

**Remarks**. This colouration, rarely seen in New Guinea and Australia, is widespread in Asia (Ballantyne obs; Jeng pers. comm.). The analysis distinguishes two species of *Gilvainsula* **gen. n.** from coastal and island localities off the SE coast of Papua New Guinea based on their dorsal colouration. It is very possible they represent the two extremes of one population.

***Gilvainsula similismessoria*** **sp. n.**
(Figs 193, 194, 197, 198)

**Holotype.** Male. **PAPUA NEW GUINEA**: 8.40S, 148.24E, Buna Bay, C T McNamara (BPBM).

**Paratypes (13). PAPUA NEW GUINEA:** 8.40S, 148.24E, Buna Bay, C T McNamara (4 males 4 females SAM; 2 males BPBM). 9.30S, 150.40E, Fergusson Is H K Bartlett, 1 male (SAM). 10.38S, 152.44E, Misima Is (= St Aignan), H K Bartlett, 1 female; R Andrew 1 male (SAM).

**Male.** 9.9–11.7 mm long; 3.0–5.2 mm wide; W/L 0.3–0.4. Colour: Coloured as for *G. messoria* with these differences: apical 1/5 or less of elytral apex dark brown; elytra in Fergusson male light orange brown. Pronotum: 1.9–2.3 mm long; 3.5–4.5 mm wide; W/L 1.8–2.2; pronotal width greater than hypomeral width in 3 males (Fergusson Is, Misima Is and Buna Bay). Elytron: 8.0–9.4 mm long; two inner interstitial lines approach the suture in development. Head: GHW 2.2–2.8; SIW 0.3–0.4; SIW/GHW 0.1; ASD<ASW. Apical segment of labial palpi irregular not dentate, both bisinuate along outer margin (Buna Bay and one Misima Is male), right palp slightly indented preapically with left palp with shallow median indentation (Misima Is male), and very feebly trisinuate in apical area (Ferguson Is). Aedeagal sheath: apex of sheath sternite curved dorsally, broadly pointed, pale coloured; anterior margin of sheath tergite not with darker anterior band, differentiated from posterior area as it is slightly sclerotised; cuticular piece on left side of tergite barely distinguishable.

**Female.** 11–15mm long. Macropterous and assumed capable of flight. Coloured as for male except for pale semitransparent V7, 8. Pronotal outline as for male. Head of winged female form, can be partially retracted within prothoracic cavity. Median posterior margin of V7 broadly and shallowly emarginated, with posterolateral areas of posterior margin straight and very slightly oblique; median posterior margin of V8 narrowly emarginated. Lateral margins of T8 converge posteriorly with posterior margin rounded.

**Larva.** Not associated.

**Etymology**. The specific name (similis Latin alike) emphasizes the similarity of this species to *G. messoria*.

***Lloydiella* gen. n.**
(Figs 204–224)

**Type species.** *Atyphella majuscula* Lea.

**Diagnosis**. Distinguished most obviously among New Guinean species by its strong dorsal colouration of orange pronotum and dark elytra; pronotal width subequal to humeral width; anterior hypomeron not flat to neck; 2–3 interstitial lines; antennae longer than GHW; labial palpi apical segment dentate and laterally flattened, 2 or more teeth; median longitudinal trough may be present on ventral surface of T8; anterior prolongations of T8 longer than posterior entire portion, narrow and expanded vertically; aedeagus with LL/ML wide; LL not diverging along their median dorsal length and narrower at their apex than ML; BP hooded. Known female macropterous and coloured like male. Associated larva with laterally explanate tergal margins concealing laterotergites from above.

**Male.** Pronotum dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate. Pronotum wider across posterior area than rest, never subparallel-sided; pronotal width subequal to humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent posteriorly; lateral margins in posterior half usually diverge then converge with rounded convergence except diverging along length in *japenensis* **sp. n.** and some *wareo* **sp. n.**; lateral margins lacking indentation at mid-point, or sinuosity in horizontal or vertical plane, indentation near posterolateral corner, and irregularities at corner; posterolateral corners rounded or angulate; rounded corners obtuse, or subequal to 90°, angulate corners 90° or less, never very acute, inclined obliquely to median line; posterolateral corners project to or beyond median posterior margin and separated by shallow emargination or not.

Hypomeron closed. Median area of hypomeron not elevated in vertical plane, lateral margins not sinuate from above; anterior area of hypomeron not flat to side of head, posterior area flat and strongly adpressed; median area sloping smoothly from anterior raised area to posterior flat area; pronotal width/ GHW index 1.6.

Elytral punctation dense, not linear, not as large as pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extend beyond mid-point of elytron, not extending as a ridge around apex, not thickened in their apical half; 2 or 3 interstitial lines, none exceed suture; elytral carina absent; in horizontal specimen viewed from beneath epipleuron at elytral base wide, covers humerus, viewed from above arises anterior to posterior margin of MS; epipleuron developed as a ridge along most of its length; sutural margins approximate along most of length in closed elytra; lateral margins parallel-sided or convex.

Head moderately depressed between eyes; moderately exposed in front of pronotum not capable of complete retraction within prothoracic cavity; eyes close to moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum close to moderately separated; frons-vertex junction rounded, no elevation in median area; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous, separated by<ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non–lunate, strongly flattened, like a wide triangle, inner edge dentate, with 2 or more 'teeth'. Antennae 11 segmented; length greater than GHW to twice GHW; no segments shortened, flattened or expanded; pedicel not produced; FS1 not shorter than pedicel; all FS longer than wide.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins, nor with anterior margins extending into emarginated posterior margin of anterior segment; LO in V7 entire, occupying most of V7; entire LO reaching to sides not posterior margin; neither anterior nor posterior margin of LO medially emarginated; posterior area of V7 behind LO not arched or swollen, muscle impressions not visible in this area; LO in V6 entire, occupying almost all V6. MPP present, symmetrical, apex rounded, entire, not laterally compressed, short or L=W; MPP not strongly inclined dorsally nor engulfed by T8 apex; lacking dorsal ridge, ventral longitudinal trough. V7 lacking median carina, median longitudinal trough, narrow anteromedian depression on anterior face of LO, lacking PLP, incurving lobes or pointed projections, median ‘dimple’ or reflexed lobes. T7 lacking prolonged posterolateral corners. T8 usually well sclerotised; symmetrical, sometimes slightly longer than wide in visible posterior area where lateral margins either converge gently posteriorly, or W=L, never subparallel-sided; visible posterior area not narrowing abruptly, lacking median posterior emargination, median posterior projections, not inclined ventrally nor engulfing posterior margin of V7 nor MPP, not extending conspicuously beyond median posterior margin of V7; T8 ventral surface lacking flanges, lateral depressed troughs, asymmetrical projections, median posterior ridge; with obvious elongate, margined, median longitudinal trough in *majuscula* only; concealed anterolateral arms of T8 shorter than, as long as or longer than visible posterior portion, narrow horizontally, expanded dorsoventrally, not laterally emarginated before their origins, apices lacking bifurcation of inner margin and bases lacking ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath never > 4 times as long as wide; lacking paraprocts; asymmetrical in posterior area where sheath sternite emarginated on right side from point of attachment of tergite; sheath not angulate on R or L sides; not subparallel-sided, not emarginated on either side preapically, anterior half of sheath sternite broad, apically rounded; tergite lacking lateral arms that extend anteriorly at sides of sternite; tergite not subdivided, lacking lateral projecting pieces along posterior margin of tergite 9; tergite 9 lacking dark anterior transverse band (a narrow anterior area of sheath tergite often more heavily sclerotised, but not darker, than rest); tergite lacking cuticular projection to left for muscle attachment.

Aedeagus L/W 3/1; LL lack lateral appendages, visible from beneath at sides of ML; LL/ML wide; LL of equal length; slightly shorter than median lobe; LL not diverging along inner margins and separated there by > half their length; LL base width does not=LL apex width which is narrower than ML; LL apices not expanded horizontally, not out–turned; preapical inner and outer margins of LL obliquely truncate; dorsal base of LL symmetrical, not excavated, median margin prolonged, pointed, entire; LL lacking hairy appendages along outer ventral margins; apices of LL not out–turned nor inturned; lacking projection on left lateral lobe; inner margins lack slender leaf–like projection; preapical inner margin of LL obliquely truncate, lacking strongly developed tooth at anterior end of emargination. ML symmetrical, lacking paired lateral teeth, single tooth to left side, not strongly arched, apex not in arrowhead shape, not bulbous, not inclined ventrally. BP not very narrow, not strongly sclerotised, not strongly emarginated along its anterior margin; hooded.

**Female.** Macropterous and assumed capable of flight. Pronotum lacking irregularities in posterolateral areas of dorsal surface; punctation moderate to dense, not as large as elytron; always wider across posterior margin; indentation of lateral margin and irregularities at posterolateral corner absent; pronotal width subequal to humeral width; outline as for male. Elytral punctation not as large as that of pronotum, nor evenly spaced; interstitial lines 2–3; elytral carina absent. Head of winged female form, with eyes smaller than male, can be retracted within prothoracic cavity, lacking any anterior prolongation; antennae on head between eyes; clypeolabral suture present and flexible. No legs or parts thereof swollen and /or curved. LO in V6 only, lacking any elevations or depressions or ridges on V7.

**Larva.** Known only in *Ll. majuscula* (Ballantyne & Lambkin, 2000); terrestrial; tergal plates sclerotised to margins, lateral tergal margins explanate, slightly ridged, hairy and spinose, covering laterotergites which are not visible from above; arrangement of plates in ventral aspect of thorax and abdomen agrees with that described (Ballantyne & Lambkin, 2000; Ballantyne & Menayah, 2002). Protergum wider than long, lacking tubercles along its anterior margin; posterolateral corners acute; median posterior margins of terga 1–11 lacking either rounded or pointed projections, posterolateral corners slightly acute; posterolateral corners of terminal tergum slightly produced; punctures in anterior area of terga 2–11 slightly larger than rest of area; median line extends from anterior to posterior margins in most segments, lacks raised margins; lacking brush of hairs around tarsal claws; mandibles lacking inner teeth; antennal segment 3 short, sense cone adjacent to segment 3 short and wide; with laterosternites on abdominal segments 1–8.

**Etymology.** Although named in honour of a male the generic name is a feminine noun latinised from the English name Lloyd (the most appropriate masculine derivative was already in use).

**Remarks.** I have much pleasure in naming this genus for James Lloyd in appreciation not only of a lifetime dedicated to the pursuit of the elusive firefly and its problems, but also in recognition of his and Dorothy's considerable support and kindnesses to me in my own pursuit.

### List of species of *Lloydiella*

*japenensis* **sp. n.**
*majuscula* (Lea)
*uberia* **sp. n.**
*wareo* **sp. n.**

### Key to species of *Lloydiella* using males

1. Pronotal posterolateral corners rounded; 2 well–defined interstitial lines; MPP well–defined, L=W; T8 lacking any developments on its ventral surface (Figs 204, 208, 210, 220, 224)...................... *uberia* **sp. n.**
   Pronotal posterolateral corners angulate, usually less than 90°; 2–3 well–defined interstitial lines; MPP short, L<W; T8 lacking any developments on its ventral surface; median longitudinal groove present or not ..................................................................................................................................... 2
2. Australian; elytra with 3 well–defined interstitial lines; ventral surface of T8 with median longitudinal groove ............................................................................................................... *majuscula* (Lea)
   New Guinean; elytra with 2 well–defined interstitial lines; ventral surface of T8 lacking longitudinal groove ............................................................................................................................ 3
3. Lateral pronotal margins diverge along the whole of their length; posterolateral pronotal corners < 90° (Figs 205, 209)................................................................................................ *japenensis* **sp. n.**
   Lateral pronotal margins do not diverge along the whole of their length, and converge in posterior area with rounded convergence; posterolateral pronotal corners subequal to 90° (Fig. 207)........... *wareo* **sp. n.**

### ***Lloydiella japenensis*** **sp. n.**
(Figs 205, 209, 212–214, 217–219, 222)

**Holotype.** Male. **INDONESIA IRIAN JAYA**: 1.45S, 136.15E, Japen Is, Mt Baduri, 1000 ft, VIII. 1938 L Cheesman (NHML).

**Paratypes** (3)**.** Same data as for holotype, female, 2 males (NHML).

**Diagnosis**. One of a group of three species that strongly resemble *Ll. majuscula* in colour, size, and shape, distinguished as follows: *Ll. uberia* **sp. n.** has rounded posterolateral corners on the pronotum (the other three have angulate corners); *Ll. majuscula* is Australian, and has a well–defined longitudinal groove on the ventral side of T8 (the other three species lack such a development); *Ll. wareo* **sp. n.** has lateral margins that converge posteriorly, posterolateral corners subequal to 90º, and antennal sockets almost contiguous (*Ll. japenensis* **sp. n.** has lateral pronotal margins that diverge along their length, posterolateral corners less than 90º, and antennal sockets are not contiguous).

**Male.** 10.5–10.6 mm long; 4.3–4.4 mm wide; W/L 0.4. Colour (Figs 205, 209): Pronotum orange, semitransparent, fat body visible in irregular clumps; MS and MN slightly paler; elytra very dark brown; head, antennae, palpi, apical ¼ of femora and tibiae and tarsi of all legs, abdominal V2–5, and tergites 2–6, almost black; ventral aspect of thorax pale yellow; tergites 7, 8 pale yellow. Pronotum: 2.0–2.1 mm long; 3.5 mm wide; W/L 1.6; lateral margins diverge along their length with very slight convergence in 1/3; posterolateral corners angulate, < 90° obliquely inclined to median line and projecting beyond median posterior margin. Elytron: with 2 well–defined interstitial lines (1, 2) and fainter traces of line 3. Head: GHW 2.1–2.3 mm; SIW 0.3; SIW/GHW 0.1; ASD<ASW (sockets close but not contiguous). Apical segment of labial palpi with 2 teeth (developed at base and apex of inner longer edge), basal tooth in 1/3 males with a slight emargination (appears as 2 very short teeth). Abdomen, ventrites (Fig. 222): LO extends to sides and close to posterior margin of V7. MPP short broad and curves slightly dorsally along its length (may be a postmortem effect). Tergites: T8 quite well sclerotised; wider than long in posterior visible area and lateral margins converge slightly posteriorly; ventral surface lacking median longitudinal groove. Aedeagus Figs 213–215. Aedeagal sheath (Figs 218–220) with sheath sternite very broad in posterior half.

**Etymology.** The specific name is Latinised and genitive case from the locality name.

### *Lloydiella majuscula* (Lea, 1915)
(Fig. 223)

*Luciola majuscula* Lea, 1915:495
*Luciola (Luciola) majuscula* Lea. McDermott, 1966:109
*Atyphella majuscula* (Lea). Ballantyne & Lambkin 2000:45.

**Holotype.** Male. **AUSTRALIA:** Coen District. (SAM).

**Diagnosis.** Australian species were distinguished in Ballantyne and Lambkin (2000). This is the only *Lloydiella* in which there is a clear median longitudinal trough in a well sclerotised T8, and 3 fairly well–defined interstitial lines (1–3); MPP short and narrow; aedeagal sheath with posterior area of sternite moderately broad (e.g. like Fig 220). Larva dorsally cream with extensive but irregular brown markings.

### *Lloydiella uberia* sp. n.
(Figs 204, 208, 210, 215, 220, 224)

**Holotype**. Male. **PAPUA NEW GUINEA:** Chimbu Pr., Uberie, 29.ix.1966, R Carver & W Mackay (DAPM).

**Paratypes** (5). **PAPUA NEW GUINEA**: Chimbu Pr., Uberie, 29.ix.1966, R Carver & W Mackay, males (DAPM)

**Diagnosis**. Distinguished by the rounded obtuse posterolateral corners of the pronotum, narrow MPP, dark metasternum and moderately broad posterior area of the aedeagal sheath sternite.

**Male**. 10.0–11.3 mm long; 3.3–4.0 mm wide; W/L 0.3. Colour (Figs 204, 208, 211): Pronotum, MS and MN orange yellow (pronotum is semitransparent and fat body shows through cuticle in clumps); elytra very dark brown almost black; head, antennae and palpi dark brown; ventral aspect of pro and mesothorax yellowish, of metasternum and metepisternal plates dark brown, metepipleural plates yellow; all legs orange yellow except for dark brown apical 1/3 femora and all of tibiae and tarsi; abdominal V2–5 very dark brown as are tergites 2–6; LO creamy white; T 7, 8 pale orange. Pronotum (Figs 204, 208, 210) 2.0–2.4 mm long; 3.3–4.0 mm wide; W/L 1.6; lateral margins diverge posteriorly with rounded convergence; posterolateral corners rounded obtuse, projecting beyond median posterior margin. Elytron: 8.0–8.9 mm long; with 2 well–defined interstitial lines. Head: GHW 2.3–2.6; SIW 0.3; SIW/GHW 0.1. Apical segment of labial palpi with two teeth (one at apex and a slightly wider one at base). Abdomen, ventrites: MPP short narrow prominent, not inclined dorsally along its length. Tergites: T8 with lateral margins rounded; lacking median groove on ventral surface. Aedeagal sheath with sheath sternite moderately broad in posterior half (Fig. 221).

**Etymology.** The specific name is considered a noun in apposition and reflects the type locality.

***Lloydiella wareo* sp. n.**
(Figs 206, 207, 211, 216, 221)

**Holotype**. Male. **PAPUA NEW GUINEA**: Madang Pr., 6.6S, 147.85E, Finschaven (sic), Wareo, L Wagner (SAM).

**Paratypes** (12) **PAPUA NEW GUINEA**: Finschaven (sic), Wareo, L Wagner 11 males, female (missing head and pronotum) (SAM).

**Diagnosis**. Very similar to *Ll. japenensis*, distinguished by its locality, the narrowly separated antennal sockets, and the very narrow posterior half of the aedeagal sheath sternite.

**Male**. 11.0–12.3 mm long; 4.5–5.0 mm wide; W/L 0.4. Colour (Figs 206, 207, 211): Pronotum, MS and MN orange yellow; pronotum with very faint traces of median paired brown marks in 4/12; elytra very dark brown almost black; head and maxillary palpi dark brown, antennae and labial palpi slightly lighter brown; ventral abdomen very dark brown except for white LO; abdominal tergites dark brown, T7, 8 pale, semitransparent, T7 may be faintly mottled in middle. Pronotum: 2.0–2.3 mm long; 3.4–3.9 mm wide; W/L 1.7; lateral margins diverge posteriorly with some slight convergence in posterior area (8/12) or diverge along their length (3/12) with one specimen having divergent left margin and convergent right margin; posterolateral corners angulate, < 90°, and inclined obliquely to the median line. Elytron: 9.0–10.0 mm long; with 2 well–defined interstitial lines (1, 2). Head: GHW 2.1–2.6; SIW 0.3–0.4; SIW/GHW 0.1. Apical segment of labial palpi with 2 teeth (broad basal and more slender apical). Abdomen, ventrites (Fig.211): MPP relatively broad, similar to that of *Ll. Japenensis*, with apex inclining slightly dorsally. Tergites: T8 not heavily sclerotised, lateral margins converge slightly posteriorly, posterior margin broadly rounded, ventral surface lacking median longitudinal groove. Aedeagus (Fig. 216). Aedeagal sheath (Fig. 221) with posterior half of sternite very narrow.

**Female**. Assumed capable of flight. Missing head and pronotum, otherwise coloured as for male except for very pale, whitish and semitransparent V7 and 8. Posterior margin of V7 medially shallowly emarginated, lateral areas broadly rounded; median posterior margin of V8 narrowly emarginated. T8 with lateral margins converging posteriorly and posterior margin rounded.

**Larva**. **Not associated.**

**Etymology**. The specific name is considered a noun in apposition reflecting the type locality**.**

***Magnalata* gen. n.**
(Figs 17, 18, 225–245)

**Type species*: Luciola limbata*** Blanchard

**Diagnosis**. Pronotum wider across posterior margin than rest, never subparallel-sided; anterior hypomeron flat to neck in *rennellia* only; flattened posterior area strongly adpressed except in *limbata*; epipleuron does not continue around apex as a ridge; antennal sockets never contiguous; frons-vertex junction rounded, never angulate; mouthparts functional; apical segment of labial palpi strongly flattened, in the form of a narrow to wide triangle, with inner (longer) margin either irregular not dentate–if dentate then 2 teeth; apical segment of labial palpi never ovoid entire.

**Male.** Pronotum dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate.

Pronotum wider across posterior area than rest; pronotal width greater than or subequal to humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent posteriorly; lateral margins in posterior half diverge then converge with rounded convergence; lacking indentation at mid-point, or sinuousity in either horizontal or vertical plane; lacking indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners rounded, obtuse; posterolateral corners project beyond median posterior margin, separated by scarcely defined emargination in *limbata* or well–defined emargination in remainder. Hypomera closed. Median area of hypomeron not elevated vertically; anterior area of hypomeron not flat to side of head except in *rennellia* **sp. n.**, posterior area of hypomeron widely flat, surfaces approach closely but are strongly adpressed except for *limbata*; pronotal width/ GHW index 1.6.

Elytron punctation dense, not linear, not as large as pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extending beyond mid-point, not extending as a ridge around apex; epipleuron and suture not expanded in apical half; 2–4 interstitial lines, inner two do not exceed suture; elytral carina absent; viewed from beneath with specimen horizontal epipleuron at elytral base wide, covering humerus, viewed from above epipleuron arises anterior to posterior margin of MS; epipleuron a lateral ridge along most of its length; sutural margins approximate along most of length in closed elytra; lateral margins parallel-sided (slightly convex-sided in *carolinae*).

Head moderately depressed between eyes; moderately exposed in front of pronotum, not capable of complete retraction within prothoracic cavity; eyes moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum close; frons-vertex junction rounded, lacking median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous, separated by < ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non–lunate, strongly flattened, like a narrow to wide triangle, with inner edge irregular not dentate, or with 2 inner teeth in some *carolinae*. Antennae 11 segmented; length subequal to GHW up to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel; in very short antennae FS may be subequal in length and width.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen lacking cuticular remnants around aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of more anterior segment; LO in V7 entire, occupying most of V7, reaching sides but not posterior margin; neither anterior nor posterior margin of LO in V7 emarginate; posterior half of V7 not arched or swollen, muscle impressions not visible in this area; LO present in V6, occupying almostV6. MPP present, symmetrical, apex rounded, entire, not laterally compressed, short, not inclined dorsally nor engulfed by T8 apex, lacking dorsal ridge and median longitudinal trough. V7 lacking median carina, median longitudinal trough, anteromedian depression on face of LO, PLP, incurving lobes or pointed projections, median ‘dimple’, or reflexed lobes. T7 lacking prolonged posterolateral corners. T8 not strongly sclerotised, symmetrical, W=L, visible posterior area not narrowing abruptly, lacking prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally nor engulfing posterior margin of V7 nor MPP, not extending conspicuously beyond posterior margin of V7; lateral margins of T8 not enfolding V7 at sides; T8 ventral surface lacking flanges, lateral depressed troughs, median longitudinal trough, asymmetrical projections, median posterior ridge; concealed anterolateral arms of

T8 either very short in *limbata*, or not as long as visible posterior part of T8, narrow horizontally, not laterally emarginated before their origins, not expanded dorsoventrally, apices lacking bifurcation of inner margin and bases lacking ventrally directed pieces.

Aedeagal sheath (Figs 239–241) never > 4 times as long as wide; lacking paraprocts; asymmetrical in posterior area where sheath sternite emarginated on right side from point of attachment of tergite; sternite not angulate on L or R sides, not subparallel-sided in broad anterior or posterior areas, posterior margin entire, not emarginated on either side preapically, rounded; anterior half of sternite broad, apically rounded; tergite lacking lateral arms that extend anteriorly at sides of sheath sternite; tergite not subdivided, lacking projecting pieces along posterior margin of tergite 9, anterior margin of tergite 9 lacking transverse band.

Aedeagus elongate subparallel–sided, L/W 3/1; LL lack lateral appendages, visible from beneath at sides of ML, LL/ML moderate; LL of equal length, slightly shorter than ML, not diverging along inner dorsal margins except in *carolinae*, separated there by > half their length; LL base width not = LL apex width which is subequal to that of ML with apices not expanded horizontally; dorsal base of LL symmetrical, not excavated, median margin prolonged, either acutely entire in *limbata* or rounded entire; LL lacking lateral hairy appendages along outer ventral margins, not produced preapically nor narrowly on inner apical margin, not obliquely truncate along preapical inner margins except in *rennellia* **sp. n.**; a tooth occurs on preapical inner margins in both *limbata* and *rennellia* **sp. n.** and is very strongly developed in the former; apices of LL not inturned, not out–turned except in *carolinae*; lacking projection on left LL only; inner margins lacking slender leaf-like projection; ML symmetrical, lacking paired lateral teeth and tooth to left side, not strongly arched, and apex not in shape of arrowhead, not bulbous, not inclined ventrally; BP not very narrow, not strongly sclerotised, not hooded, and not strongly emarginated along anterior margin.

**Female.** Macropterous and assumed capable of flight. Pronotum lacking irregularities in posterolateral areas; punctation moderate to dense; pronotum > humeral width; indentation of lateral margin, irregularities at posterolateral corner, absent; outline as for that of male. Elytral punctation, not as large as that of pronotum nor evenly spaced; 2 interstitial lines; elytral carina absent. Head of winged female form. No legs or parts thereof swollen and/or curved. LO in V6 only, lacking any elevations or depressions or ridges on V7.

**Larva** not reliably associated, possible association with *limbata* only.

Terrestrial; tergal plates sclerotised to margins, lateral tergal margins explanate, thickened, and covering laterotergites which are not visible from above; arrangement of plates in ventral aspect of thorax and abdomen agrees with that described (Ballantyne & Lambkin, 2000; Ballantyne & Menayah, 2002). Protergum W > L, tubercles absent along anterior margin, posterolateral corners round, and median line with non-ridged margins; median line extends to anterior and posterior margins of most terga; punctures in anterior half of terga 2–10 larger than rest; posterolateral corners of terga 1–8 rounded entire, of tergum 12 produced narrowly; median posterior margins of terga 1–11 lacking either rounded or pointed projections; lacking brush of hairs around tarsal claws; mandibles lacking inner teeth; antennal segment 3 short, sense cone adjacent to segment 3 short and wide; with laterosternites on abdominal segments 1–8.

**Etymology.** *Magnalata* (magna = large, lata = widespread; feminine noun) is so named to emphasize the size of its largest species (*limbata* is the largest of the Solomon Islands firefly fauna) and its wide distribution across the islands.

**List of species of *Magnalata***

*carolinae* (Olivier)
*limbata* (Blanchard)
*rennellia* **sp. n.**

**Key to species of *Magnalata* using males**

1. Elytra dark brown with orange lateral margins not extending around apex; pronotum orange with no darker markings (Figs 17, 228)...................................................................... *limbata* (Blanchard)
   Elytra dark to medium brown, usually lacking paler margins; if lateral margins paler then this band not extending around the apex; pronotum often with darker markings.......................................................... 2
2. Anterior portion of hypomeron flat to neck; elytra parallel-sided; aedeagus with strong tooth on inner preapical margins of LL (Figs 231, 232, 242, 243) *rennellia* **sp. n.**
   Anterior portion of hypomeron not flat to neck; elytra convex-sided; aedeagus lacking strong tooth on inner preapical margins of LL (Figs 225, 226, 233, 234)............................................. *carolinae* (Olivier)

***Magnalata carolinae* (Olivier, 1911)**
(Figs 225, 226, 233, 234, 237)

*Atyphella carolinae* Olivier, 1911:173. Wittmer, 1958:67. Blair, 1940:134.
Ballantyne & Lambkin, 2000:15.
*Luciola (Luciola) carolinae* (Olivier). McDermott, 1966:100. Ballantyne & Buck, 1979:121.

**Holotype.** Male. **REPUBLIC OF PALAU**: labelled (Fig. 237) 1. Type; 2. ♂; 3. Caroline Is., F. W. Christian, 98–200; 4. Lai near Gorgor Point, South Yap; 5. handwritten ‘carolinae Ern Oliv.’ (NHML).

**Other material examined. REPUBLIC OF PALAU**: 9.30S, 138.10E, Yap Island: 3 males, Yap Hill, behind Yap town, 3.xii.1952, 50 m, light trap, JLG (one male no collector or light trap); Balabat, 16.v.1936, Z. Ono, 1 male; 80 (sic). ix.1987, Y Haneda, 1 male (det. W. Wittmer). 7.00S, 134.00E, Angaur Island, 16.iv.1936, Y. Kondo, 3 males (I male det K. G. Blair). (BPBM)

**Diagnosis.** Males exist in three colour variations: 1. Dorsal surface of elytra and pronotum entirely brown to dark brown (Fig 225), or pronotum may be mottled brownish orange (Fig. 226). 2. Pronotum, MS and MN orange with extensive darker brown markings, elytra dark brown. 3. Pronotum MS and MN orange with no darker markings; elytra dark brown. Colour pattern 1 similar to *Bourgeoisia hypocrita* Olivier, which has a black dorsal surface, very shiny elytra (dull in *carolinae*), no flat lateral pronotal areas (posterior half flat in *carolinae*), a pale ventral surface, no apparent LO in V7, paired LOs in V6 (full LOs in both these ventrites in *carolinae*), and posterolateral eye excavations (missing in *carolinae*). Distinguished from *Atyphella aphrogeneia* by the variations in pronotal colouration, the pronotal width/humeral width ratio, and elytral apical modifications in *aphrogeneia*.

**Male.** 8.0–9.2 mm long; 3.0–3.5 mm wide, approximately 3 X as long as wide. Colour (Figs 225, 226): Three colour varieties exist: 1. (Type) entirely very dark brown except for pale LOs and pale tergites 7, 8. 2. Yap Island Yap Hill males (3), Balabat (1) –pronotum orange with overall brown markings (more obvious on margins of punctures), all margins slightly paler dingy orange, median area paler dingy orange in 1/3 males; MN dingy with darker median brown spot; MS coloured like pronotum; elytra mid-brown, dull; head dark brown, antennae, palpi apices and labrum pale brown (except in Balabat male where labial palpi are pale yellow); ventral thorax orange with metasternum brown (semitransparent); legs orange except for brown tibiae, tarsi and coxae 3; tergites dark brown except for 7, 8. 3. Yap Island (Haneda) male, Angaur Island 3 males–pronotum, MS, MN orange, all legs yellow except for dingy brown tips of tibiae and all of tarsi; elytra with lateral margin narrowly light brown and semitransparent; ventral abdomen (except for V6 and V7) yellow with V5 brown. Pronotum. 2.7–3.0 mm wide; 1.4–1.8 mm long; W/L 1.6–1.9; dorsal surface smooth, densely punctate, punctures contiguous over most of surface; posterolateral corners rounded obtuse, projecting a little behind median posterior margin, and separated from it by shallow emarginations; anterior portion of hypomeron not flat; posterior portion of hypomeron flat. Elytron (Figs 225, 226): convex-sided; 5.3–6.3 mm long; 4 well–defined interstitial lines. Head: GHW 1.8–1.9 mm; SIW 0.2 mm; SIW/GHW 1/9; ASD<ASW, antennal sockets very close but not contiguous; frons-vertex junction rounded, frons 2 X ASW. Mouthparts well developed, probably functional; apical segment of labial palpi laterally compressed, subtriangular, inner longer margin irregular in outline, having a basal wide truncate projection, a wide median emargination and a slightly narrow apex. Antennal length subequal to GHW; 11 segmented. Abdomen, ventrites: LO occupying all of V6; LO in V7 entire; reaching sides but not posterior margin, occupying most of the area of V7. Tergites: T8 as wide as long; posterior half as wide as anterior half; anterior prolongations of T8 much shorter than rest of T8, pointed. Aedeagal sheath (Figs 240, 241) with posterior margin of sternite rounded, with no projection. Aedeagus L/W 3/1, LL/ML 2.8; lateral margins subparallel; LL slightly shorter than ML, apices rounded, out-turned and subequal to width of apex of ML, slightly wider than base of ML, and lacking tooth on their preapical inner margins; LL diverge along their length but not widely separated at their apices; base of LL produced anteriorly and broadly rounded.

**Female** and **larva** unknown.

**Remarks.** Ballantyne and Buck (1979) highlighted the colour similarity of this species to *Luciola* (now *Atyphella*) *aphrogeneia*, which is presently known only from coral outcrops along the New Guinea coastline, and is readily distinguished by the elytral characteristics. Blair's (1940) specimens (examined here) were from Angaur and Yap Islands. Nothing is known of the biology and ecology of *M. carolinae*. This study distinguishes Wittmer's subspecies *palauensis* as a distinct species and it is transferred to *Atyphella*.

### *Magnalata limbata* (Blanchard, 1853)

(Figs 17, 18, 227, 228, 229, 230, 235, 236, 238, 239, 244)

*Luciola limbata* Blanchard, 1853:73 Plate VI.
*Luciola* (*Luciola*) *limbata* Blanchard. McDermott, 1966:108.
*Nec Luciola marginipennis* Guérin-Méneville. Olivier, 1902:82. Lacordaire, 1857:337.
*Luciola rubiginosa* Olivier, 1883, p. 329; 1902, p. 85; 1913, p.417 (Synonymy–Partim). McDermott, 1966, p. 112.

**Types.** *Luciola limbata:* **SOLOMON ISLANDS**. Location of holotype unknown.

*Luciola rubiginosa:* 'Patria' (? = New Hebrides, McDermott, 1966). (MNHN).

**Specimens Examined. SOLOMON ISLANDS**: Isabel Pr., 8.00 S, 159.10 E, Santa Isabel, Tatamba, 2–6.x.1965, Roy Soc Exped, village garden, low vegetation, 4 males (NHML); 29.ix.1965, wooded hillside behind rest house, male (NHML). Malaita Pr., 9.00 S, 161.00 E, Malaita: Auki, 2–20 m, 18.ix.1957, JLG, 2 males (BPBM); Malaita, 28.v.1955 E Brown, 6 males (NHML). Central Pr., Florida Group: Big Nggela 9.00S, 160.00E, Takopekope, COB, 12.ix.1960, 2 females, 10 males; Gairava, 14.ix.1960, 2 males. Nggela, Dende, 8.i.1912, 1 male (NHML). Tulagi, R Lever, 2 males (One labelled luminous) (NHML). 9.08S, 160.25E, Small Nggela, Vunuha, 19.ix.1960, COB, light trap, 3 males (BPBM). 9.60 S, 160.20E Guadalcanal Pr., 10 mi NW Honiara at Mavo Bridge, xi.25, 26.1969, J. E. Lloyd, 2 males (G653, 656 flashing data associated), 1 female (G659) (JELC). Makira Pr., San Cristobal: 10.30S, 161.49E, Kira Kira, COB, 24.vii.–1.viii. 1960, 75 males, 2 females (BPBM). Maniate, COB, 6.viii.1960, 5 males (BPBM); Manipwena, Magoha R., 13.viii.1960, COB, 34 males (BPBM); Wugiroga, 8.viii.1960, COB, 1 male (BPBM); Pooma, 0–30m, 16–17.v.1964, JS, 8 males

(BPBM); Huni R mouth, camp 4, Roy. Soc Exped. BM 1966, 12.viii.1965, village garden low vegetation, male (NHML). Central Pr., 11.39S, 160.14E, Rennell: Lavanggu, 19.X.1951, Danish Galathea expedition, 1 male (NHML); Teuhungano, 14.x.1953 J Bodley, 3 males (NHML). Russell Is, R Lever, 2 males (NHML).

**Code name.** *Luciola* 2 (Lloyd, 1973b) (Ballantyne identified this as *L. wolfi* in Lloyd 1973b)

**Diagnosis.** One of four similarly coloured species now known from the Solomons, with dark brown elytra laterally margined with orange, distinguished as follows: *Magnalata limbata*: elytra parallel-sided; MS black; 4 elytral interstitial lines as well developed as suture; pronotal punctures broad, deep, but not contiguous; V4 brown at sides, V5 brown; LO occupying all but a narrow posterior border in V7; MPP about as long as wide, apically rounded, lateral margins converging posteriorly; ML of aedeagus lacking lateral teeth. *Pygatyphella limbatipennis* and *Pygat. limbatifusca* **sp. n.**: pronotum orange (with median dark spots in *limbatifusca*); elytra parallel-sided; MS red; elytral interstitial lines poorly defined; pronotal punctures broad, shallow, contiguous; V4 brown, V5 very dark brown; LO retracted to anterior portion of V7; MPP elongate, apically truncate (sometimes obliquely), lateral margins subparallel; ML of aedeagus with lateral teeth. *Convexa wolfi*: elytra convex-sided; MS red; 4 elytral interstitial lines well–defined; pronotal punctures very small, shallow, separated by 1–2 times their width (surface of pronotum between punctures smooth and shiny); all ventrites yellow except for very narrow brown posterior margin of V5; MPP short apically rounded; ML of aedeagus lacking lateral teeth.

**Male.** Dimensions of the 4 largest populations of this species are distinguished below. Kira Kira 9.7–14.3 mm long; 3.8–5.3 mm wide; W/L 0.4; Maniate 10.4–11.2 mm long; 4.0–4.7 mm wide; W/L 0.4; Pooma 9.2–11.3 mm long; 3.6–4.7 mm wide; W/L 0.4; Manipwena 11.0–12.5 mm long; 4.4–5.0 mm wide; W/L 0.4. Colour (Figs 17, 18, 229–230): Pronotum dingy orange, MN paler orange; irregular retraction of fat body material beneath cuticle leaves darker patches visible; MS very dark brown; elytra very dark brown, almost black, with a moderately wide orange–yellow lateral border narrowing slightly in posterior ¼ and very narrow at apex and not extending to suture; epipleuron orange yellow from beneath; inner half of elytral apex and all suture entirely dark brown; head very dark, antennae, labrum and palpi moderately dark brown; venter of thorax and all legs bright orange yellow except for brown midventral faces of coxae 3 and dark brown tibiae, tarsi of all legs; V2, 3 yellow; V4 yellow medially, laterally brown, entirely dark brown in Auki males; V5 brown, irregularly yellow across anterior margin, entirely dark brown in Auki males; V6, 7 creamy white; all abdominal tergites pale orange yellow. Pronotum (Figs 229, 230): Kira Kira 2.0–2.5 mm long; 3.5–4.7 mm wide; W/L 1.7–1.8; Maniate 2.1–2.3 mm long; 3.9–4.1 mm wide; W/L 1.8; Pooma 1.7–2.3 mm long; 3.3–4.3 mm wide; W/L 1.8–1.9; Manipwena 2.1–2.3 mm long; 3.9–4.2 mm wide; W/L 1.8; dorsal punctures broad, moderately deep, not contiguous over most of disc, subcontiguous laterally. Elytron (Fig. 17): Kira Kira 7.7–11.8 mm long; Maniate 8.3–8.9 mm long; Pooma 7.5–9.0 mm long; Manipwena 8.9–10.2 mm long; parallel-sided; with 2 well–defined and elevated interstitial lines (1, 2). Head: partially retracted beneath PN and into prothoracic cavity in resting position, often scarcely visible from above; GHW Kira Kira 2.2–3.0 mm; SIW 0.4–0.5 mm; SIW/GHW 0.16–0.18; Maniate GHW 2.4–2.5 mm; SIW 0.4; SIW/GHW 0.16; Pooma 2.1–2.8 mm; SIW 0.3–0.4 mm; SIW/GHW 0.14; Manipwena GHW 2.5–2.7 mm; SIW 0.4–0.5; SIW/GHW 0.16–0.18; ASD<ASW; frons 2 X ASW high, frons-vertex junction rounded. Antennae longer than GHW but less than 2 X GHW. Mouthparts functional; apical segment labial palpi laterally compressed, irregularly excised along inner margin (most prevalent situation is listed first): Pooma L and R both with median incision, or L and R entire, or both L and R irregular; Maniate L irregular, R medially emarginated with very short and narrow tooth just anterior to emargination, or L irregular and R medially incised, or both irregular; Pooma L irregular, R medially emarginated, or both irregular, or both entire; Manipwena L and R both medially emarginated, or L emarginated and R irregular, or R emarginated and L irregular, or both irregular. Abdomen, ventrites (Fig. 244): LO entire in V6 and V7 where it reaches sides but not posterior margin, occupying most of V7. MPP moderately broad, apically rounded. Tergites: T8 as wide as long, anterolateral prolongations narrow, not as long as visible posterior portion, and not expanded obviously vertically. Aedeagus (Figs. 235, 236, 238): L/

W>3/1; LL/ML moderate; subparallel-sided; LL not divergent along most of their length dorsally and slightly shorter than ML; apices of LL not out–turned, bearing a tooth on the inner preapical margin; base of LL produced and medially acute.

**Female** (Figs 227, 228). 12.5–16.0 mm long. Coloured as for male except for creamy white LO in ventrite 6 and pale yellow, semitransparent V7, 8. V7 with broad shallow median emargination, lateral areas of posterior margin slightly obliquely truncate; median posterior margin of V8 narrowly emarginate; T8 with lateral margins converging slightly posteriorly, posterior margin rounded.

**Larva**. Associated by similarity of label data only. With laterally explanate tergal margins.

**Remarks.** The very distinctive colour, with black MS, and the size permits a reasonable association in the absence of type material. Olivier (1913) synonymised *L. limbata* and *L. rubiginosa* with *L. marginipennis* Guérin-Méneville; this synonymy is rejected and *marginipennis* is treated as *Incertae Sedis* here. *Luciola limbata* Blanchard (1853) and *Luciola rubiginosa* Olivier (1883) from the Solomons were both described with black MS, and otherwise consistent in colour and geography with specimens described here, while Guérin-Méneville's (1838) *L. marginipennis* had a red MS and was probably from the NW area of the island of New Guinea at Mt Arfak ('Offak'), as was Boisduval's (1835) *Lampyris marginipennis*. This study revealed no fireflies with colour and size that approach either of these two descriptions.

*M. limbata* occurs in the more southerly of the Solomon Islands group (Santa Isabel, Rendova, Russell Is, Nggela, Guadalcanal, Malaita and San Cristobal) where it overlaps in range with *C. wolfi* on Santa Isabel and Guadalcanal, and *Pygat. limbatipennis* on Santa Isabel, the Florida island group and Guadalcanal (Table 7). It and *Pygat. limbatifusca* **sp. n.** are the only firefly species with pale margined elytra presently recorded from San Cristobal.

Lloyd (1973b:992) observed that this species flew at heights of 6–40 feet while *Luciola* species 1 (= *Pygatyphella limbatipennis*) flew just above the ground to a maximum height of 3–4 feet, emitting "single, short, bright flashes,.with a flash period of 0.5 sec". *M. limbata* "emitted single flashes and pairs of flashes with a flash period of 0.5 sec." Lloyd (1973b) identified his 3 larval specimens of '*Luciola* 3' as *Luciola rubiginosa*. These specimens have not been relocated.

### ***Magnalata rennellia* sp. n.**
(Figs 231, 232, 242, 243, 245)

**Holotype.** Male. **SOLOMON ISLANDS:** Central Pr., 11.65S, 160.20E, Rennell, Teavamanga-Lavanggu, 17.x.1951, Danish Galathea expedition; Hutuna, 16.xi.1953, J Bradley (NHML).

**Paratypes** (3). Same locality and data as holotype, males (NHML).

**Diagnosis.** Very similar to *M. carolinae*, distinguished by the flat anterior portion of the hypomeron and the paler pronotum, and the very strongly developed tooth on the inner preapical margins of the LL.

**Male.** 8.7–8.8 mm long; 2.4 mm wide; W/L 0.3. Colour (Figs 231, 232): PN orange (PN of three Rennell males with very pale paired median brown spots coinciding with underlying muscle retraction and interpretation of colour is difficult), MN orange yellow, MS dusky brown, almost as dark as elytra; elytra mid-brown, lateral margin in 4/5 appears narrowly paler (this area semitransparent and interpretation could be a consequence of microscope illumination); in two males the lateral margin of elytra with a narrow line of fat body on inner margin of paler lateral margin, and one male with lateral margins very narrowly pale creamy white, extending narrowly around apex to suture on left but not right side; head very dark reddish brown, antennae (except for paler scape) and palpi brown; venter yellowish except for light brown tibiae and dark red brown tarsi of all legs, dark brown V5, posterior half of V4 and irregular brown markings in lateral areas of V2, 3 and creamy white LO in V6, 7; T7 pale mottled brown, T8 yellow semitransparent, remainder midbrown. Pronotum: 1.8–2.0 mm long; 3.1–3.2 mm wide; W/L 1.6–1.7; anterior half of hypomeron flat, posterior area widely flat and closely adpressed. Elytron (Fig. 232): 6.8–6.9 mm long; 3–4 interstitial lines developed. Head: GHW 2.1 mm; SIW 0.25mm; SIW/GHW 0.1; ASD< ASW; frons-vertex junction rounded, frons about 1 x ASW high. Antennae just > GHW. Mouthparts functional; apical segment of labial palpi like a relatively narrow triangle (longer than wide), with inner (shorter) margin irregular. Abdomen, ventrites (Fig. 245): LO entire in both V6 and V7 reaching sides but not posterior margin and occupying most of V7. MPP short, broad apically rounded. Tergites: T8 about as wide as long; anterolateral prolongations short, narrow, not expanded vertically. Aedeagus (Figs 242, 243): L/W slightly < 3/1; LL/ML moderate; LL not divergent along their length dorsally, and slightly shorter than ML; inner apical area of LL with a strong tooth.

**Female, Larva.** Unknown.

**Etymology**. The specific name *rennellia* is a noun in apposition and seeks to emphasise the restricted locality of this species, which is known only from Rennell Island to the outer SW edge of the Solomon Island complex.

**Remarks**. Within the Solomon Island firefly fauna many fireflies with orange pronota may exhibit paler brown areas in the median pronotal area; in most this is due to the retraction beneath the cuticle of muscle blocks and is not a true colour in the overlying cuticle. It is not possible here to establish the true pronotal colour as the apparent pale brown areas coincide exactly with the area of retraction of muscle beneath the cuticle. Only *Pygat. limbatifusca* **sp. n.** has distinct median dark pronotal markings on an otherwise orange pronotum. Problems with the interpretation of the lateral margin as paler coloured under microscopic examination in this species were also encountered in *Pygat. salomonis* and are discussed further there.

## *Missimia* gen. n.

(Figs 21, 22, 27, 29, 30, 32–34, 246–254)

**Type species**: *Missimia flavida* by monotypy.

**Diagnosis**. Males and females distinguished from all known Luciolinae by the lack of a clypeolabral suture and the heavily sclerotised labrum which is immovably joined to the rest of the head; elongate subparallel-sided body; head exposed; differing from all other genera treated here by the slight and acute prolongation of the posterolateral corners of pronotum and the epipleuron not covering the elytral humerus from below.

**Male.** Pronotum (Figs 21, 22, 34) dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate. Pronotum wider across posterior area than rest; pronotal width less than humeral width; anterolateral corners rounded obtuse; lateral margins in anterior half divergent posteriorly; lateral margins in posterior half sinuate (in horizontal plane), continuing to diverge in posterior 1/4; lateral margins not sinuate in vertical plane, lacking indentation at midpoint, indentation near posterolateral corner, and irregularities at corner; posterolateral corners angulate (pointed); considerably less than 90°, inclined obliquely to median line and may project slightly beyond line of lateral margin; posterolateral corners project as far as median posterior margin, separated from it by shallow emargination.

Hypomera closed. Median area of hypomeron not elevated vertically; anterior area of hypomeron not flat to side of head, posterior area narrowly flattened and closely adpressed; pronotal width/ GHW index 1.3.

Elytron (Figs 21, 22) punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extend beyond mid-point, almost to apex, do not extend as ridge around apex and not expanded in apical half; interstitial lines variable, one (nearest suture) or two (two inner lines nearest suture) almost as well developed as sutural ridge; elytral carina absent; viewed from below in horizontal specimen epipleuron at base (Fig. 33) does not cover humerus, viewed from above arises level with posterior margin of MS; epipleuron developed as lateral ridge along most of length; sutural margins approximate along most of length in closed elytra; lateral margins parallel-sided.

Head (Figs 27, 29, 30, 32) moderately depressed between eyes; moderately exposed in front of pronotum, not capable of complete retraction within prothoracic cavity; eyes widely separated beneath at level of posterior margin of mouthpart complex; eyes above labrum widely separated (GHW 2–3 X SIW); frons-vertex junction rounded, lacking median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets separated by > 3 X ASW, on anterior parallel-sided prolongation of head which is as long as wide; posterior margin of antennal sockets (viewed with 'labrum' horizontal) just in front of anterior eye margins; labrum well marked basally with deep incisions at each side, no clypeolabral suture; area between labrum and rest of head well sclerotised, inflexible; outer edges of labrum reach inner edges of closed mandibles; anterior margin of labrum entire, lacking projections. Mouthparts functional; apical segment of labial palpi lunate, strongly flattened. Antennae 11 segmented; length 3–4 X GHW; FS 2–8 expanded at anteroapical angle; FS elongate slender, 4X longer than wide; pedicel not produced; FS1 not shorter than pedicel.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Figs 249, 250, 253, 254) lacking cuticular remnants in association with aedeagal sheath; no segments with curved posterior margins nor extending anteriorly into emarginated posterior margin of more anterior segment; LO in V7 entire, retracted from all margins and occupying slightly less than half total area; neither anterior nor posterior margin of LO emarginated; posterior half of V7 not arched or swollen, muscle impressions not visible in this area; LO present in V6, occupying most of V6; MPP present, apex rounded, symmetrical, entire, not laterally compressed, L>W, not strongly inclined dorsally nor engulfed by the apex of T8, lacking dorsal ridge and median longitudinal trough. V7 lacking median carina, median longitudinal trough, anteromedian depression on face of LO, incurving lobes or pointed projections along posterior margin, median 'dimple', or reflexed lobes on its dorsal surface. Posterolateral corners angulate, horizontal, appear slightly and narrowly produced in one pinned male. LO in V6 entire and retracted narrowly from all margins. T8 symmetrical, well sclerotised, W=L of visible posterior area which does not narrow abruptly, lacking prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally nor engulfing posterior margin of V7 nor MPP, not extending conspicuously beyond posterior margin of V7; T8 with a median longitudinal trough which is finely margined laterally and symmetrical; T8 ventral surface lacking flanges, lateral depressed troughs, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 present, longer than posterior visible portion, not laterally emarginated before their origins, expanded widely horizontally, not expanded dorsoventrally, apices with bifurcation of inner margin and bases lacking ventrally directed pieces.

Aedeagal sheath (Fig. 252) never > 4 times as long as wide; lacking paraprocts; similar to that of *Atyphella*; asymmetrical in posterior area where sheath sternite emarginated on right side from point of attachment of tergite; sternite not angulate on L or R sides, not subparallel-sided, posterior margin entire, not medially emarginated, not emarginated on either side preapically, and rounded; anterior half of sternite broad, apically rounded; tergite not subdivided, lacking projecting pieces along posterior margin of tergite 9, tergite attaches to sheath sternite at 1/3 its length from anterior end; lacking transverse band; anterior margin of tergite 9 deeply, evenly and widely emarginated.

Aedeagus (Figs 246–248) L/W 3.6/1; subparallel-sided for most of length (apices of LL diverge very slightly); LL lack lateral appendages, visible from beneath at sides of ML, LL/ML wide (3.8/1); LL of equal length, shorter than ML, (0.8 as long as ML), gently diverging along their length dorsally and separated along almost all their length; LL base width not = LL apex width which is wider than that of ML with apices expanded horizontally; dorsal base of LL symmetrical, anteriorly prolonged and pointed; LL lacking lateral hairy appendages along their outer ventral margins, which are not produced preapically nor narrowly on their inner apical margin; inner margins of LL with an elongate narrowly emarginated hair bearing area along ¼ their length; LL obliquely truncate along their preapical inner and outer margins, apices bluntly pointed; apices of LL lacking projection on left LL only; ML symmetrical, very narrow, lacking paired lateral teeth and tooth to left side, not strongly arched, apex not in shape of arrowhead, not bulbous, apex rounded, not further expanded, inclined ventrally and narrower than at base; BP wide, not strongly sclerotised, hooded, not strongly emarginated along anterior margin, apparently in a single piece.

**Female.** Macropterous. Pronotal outline as for male; pronotum lacking irregularities in posterolateral areas, punctation moderate to dense; dimensions C>A or B, pronotal width < humeral width; lacking indentation of lateral margin, irregularities at posterolateral corner. Elytral punctation not as large as that of pronotum nor evenly spaced; two well–defined interstitial lines (1 and 2) visible; elytral carina absent. Head with antennae on a short parallel-sided prolongation of head; posterior margin of antennal sockets in front of anterior eye margin (head held with labrum horizontal); eye size equivalent to male; clypeolabral suture not developed and junction of clypeus and labrum inflexible. No legs or parts thereof swollen and /or curved. LO in V6 only, lacking any elevations or ridges on V7; small depressed areas in midlateral area may represent postmortem torsion of D–V muscles.

**Larva** not associated.

**Etymology**. *Missimia* is considered a feminine noun and is latinised from the type locality Mt. Missim.

**Remarks.** *Missimia* is known only from the four specimens described here. It is distinguished from all other Luciolinae by the structure of the front portion of the head, which is well sclerotised and inflexible, the clypeus and labrum are fused and there is no obvious clypeolabral suture. In August 2007, J Lawrence confirmed his interpretation of the anterior plate of the head as the labrum. *Missimia* is superficially similar to *Pygoluciola,* and Ballantyne was first alerted to the distinctiveness of a single Aiyura female, which was tentatively assigned to *Pygoluciola* (Ballantyne, 1968). This female is included here. With so few specimens certain ‘variations’ that may be due to post-mortem changes have been difficult to assess and include the possibility of arching of V7 which occurred in one male after dissection (this is scored as non arched V7 as muscle impressions were not obvious posterior to the LO in V7). While interstitial lines were not as well developed as the sutural ridge in either of the males, they were so in the females. The wide difference in pronotal dimensions between the two males is due to a marked (horizontal) sinuousity of the lateral margins in the Missim male, which is mirrored in the Mt Shungol female pronotum. These specimens were included in Ballantyne & Lambkin (2000, 2001, 2006) as “Mt Missim”.

### ***Missimia flavida*** **sp. n.**

(Figs 21, 22, 27, 29, 30, 32–34, 246–254)

**Holotype.** Male. **PAPUA NEW GUINEA**: 7.15 S, 146.48 Morobe Pr., Mt Missim, 1810 m, xi.1981, J. Scott (BPBM).

Paratypes (3). **PAPUA NEW GUINEA**: E Highlands Pr: 6.00S, 147.00E, Wanatabe Valley, near Okapa, 5000 feet, taken in light trap, 5.ii.1965, M E Bacchus, male (BPBM). 6.30S, 145.9E, Aiyura, 5400 feet, 18.xii.1961, in house, J H Barrett, female (UQIC). 6.52S, 146.43E, Mt Shungol, 1650–2730 m, JS, female (JSC in QM).

**Male.** 12.2–13.1 mm long; 3.0 mm; W/L 0.2. Colour: dorsal surfaces dingy yellow–light brown; semitransparency of cuticle on dorsal surface allows white fat body to show through irregularly especially in the pronotum; remainder of body including head dark brown except for V6 and 7, which are white in the area of the LO and yellow in posterior area of V7; semitransparent yellow tergites 7 and 8. Pronotum 2.2–2.3 mm long, 2.2–3.0 mm wide; W/L 0.9–1.4. Elytron: 10–10.8 mm long; elytral interstitial lines variable, line 1 well–defined in Missim male and 2 and 3 fainter; lines 1 and 2 clearly defined in Okapa male. Head: GHW 2.0 mm; SIW 0.7–0.9 mm; SIW/GHW 0.35–0.45.

**Female**. Macropterous and assumed capable of flight. 12.9–13.3 mm long, parallelsided. Coloured as for male except for the white LO in ventrite 6, and light brown ventrites 7, 8. Pronotal outline as for male. Pronotum, head, and abdominal ventrites illustrated (Ballantyne 1968 Figs 130–132, 134). Ballantyne (1968) incorrectly indicated that the lateral depressions on V7 corresponded with the dorsal spiracles; they more probably represent sites of attachment of D–V muscles.

**Etymology.** The specific name (flavida, Latin, = pale) describes the pale dorsal colour.

### ***Photuroluciola* Pic**
(Figs 38–54)

*Photuroluciola* Pic, 1931:12.
*Luciola (Photuroluciola)* (Pic). McDermott, 1966:115. Fu & Ballantyne, 2008: 6.
**Type species.** *Photuroluciola deplanata* Pic (by monotypy).

**Diagnosis**. Known in collections from a single large, brightly coloured specimen with pinkish orange pronotum and black elytra; midlateral margins of pronotum elevated (margins appear sinuate from side); aedeagus with asymmetrical ML having an acute apex which is finely serrate along its dorsal edges; ML bearing infolding flaps behind its apex; left LL with preapical flap (right LL lacks this flap); LL just visible at sides of ML, both apices not visible in same plane, separated in apical 1/3; aedeagal sheath with sternite posterior to tergite articulations subparallel-sided in basal 1/3, then unevenly emarginated on both sides and narrowing to a slender obliquely truncate apex.

**Male.** Pronotum dorsal surface lacking irregularities in posterolateral areas; longitudinal grooves delimit edges in lateral areas; punctation dense. Anterior margin not explanate.

Pronotum (Figs 39, 40) wider across posterior area than rest; pronotal width less than humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent posteriorly; lateral margins in posterior half diverge further beyond line of anterior half, then converge such that posterolateral corners are broadly rounded and lateral margins appear sinuous from above; lacking indentation at mid-point; lateral margin elevated in median area (viewed from the side) appearing as a sinuousity in vertical plane; lacking indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners rounded, obtuse; posterolateral corners do not project as far as the median posterior margin and are not separated from it by a shallow emargination.

Hypomera closed. Median area of hypomeron elevated vertically; anterior area of hypomeron not flat to side of head, posterior half widely flat and closely adpressed; pronotal width/ GHW index 1.6.

Elytron (Figs 39, 40) punctation dense, not linear, not as large as pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extend almost to apex but not around it, and lack any further expansion of either in apical half; 3 interstitial lines, none exceed suture; elytral carina absent; viewed from below in horizontal specimen epipleuron at base covers humerus and viewed from above arises anterior to posterior margin of the MS; epipleuron developed as a lateral ridge along most of its length; sutural margins approximate along most of their length in closed elytra; lateral margins parallel-sided.

Head moderately depressed between eyes; moderately exposed in front of pronotum, not capable of complete retraction within prothoracic cavity; eyes moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum moderately separated; frons-vertex junction rounded, lacking median elevation; posterolateral eye excavation not strongly developed and not visible in resting head position; antennal sockets on head between eyes, not contiguous, separated by < ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when viewed with labrum horizontal; outer edges of transverse labrum reach beyond inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non–lunate, strongly flattened, shaped like a narrow triangle, 4 X as long as W, with inner edge entire not dentate or irregular. Antennae 11 segmented, length exceeds twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Figs 45–47) lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment; LO in V7 entire, reaching to sides, close to posterior margin, narrowly into MPP; neither anterior nor posterior margin of LO in V7 emarginate; posterior half of V7 not arched or swollen, muscle impressions not visible in this area; LO present in V6, occupying almost all the area. MPP present, symmetrical, apex rounded when viewed from beneath (is dorsally emarginated if viewed from behind, reflecting the dorsal groove of the MPP), entire, strongly laterally compressed, L >> W, not inclined dorsally nor engulfed by the apex of T8, lacking dorsal ridge and ventral median longitudinal trough; narrow dorsal median longitudinal groove along dorsal surface extending to posterior end. V7 lacking median carina, median longitudinal trough, anteromedian depression on face of LO, PLP, incurving lobes or pointed projections, median 'dimple', or reflexed lobes. T7 lacking prolonged posterolateral corners. T8 not strongly sclerotised, symmetrical, W=L, visible posterior area does not narrow abruptly, lacking prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally, nor engulfing the posterior margin of V7 nor the MPP, not extending conspicuously beyond posterior margin of V7; T8 ventral surface lacking flanges, lateral depressed troughs, median longitudinal trough, (except for oblique curved groove in posterolateral right and short straight groove in posteromedian right), asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 present, not as long as visible posterior portion, broad and slightly emarginated anteriorly, not laterally emarginated before origins, not expanded dorsoventrally, apices lacking bifurcation of inner margin and bases lacking ventrally directed pieces; lateral margins of T8 not enfolding V7 at sides.

Aedeagal sheath (Figs 38, 41–44) 3.4 X as long as wide; lacking paraprocts; asymmetrical only in posterior area of sternite; sternite evenly wide, approximately parallel-sided for 7/10 its length; sternite emarginated on both sides in posterior area; emargination of right side begins 1/3 of sternite length from posterior apex, is wider and deeper than left emargination which begins 1/5 of length from posterior apex, which is very narrow and obliquely truncate from right to left; anterior half of sternite broad, apically rounded; narrowed lateral arms of tergite visible at sides of tergite, join sternite at 4/10 of its length from anterior end; tergite not laterally subdivided; transverse line divides tergite into anterior and posterior portions; paired subtriangular pieces project along this line, lacking transverse band across anterior area of sheath tergite.

Aedeagus (Figs 48–55) L/W 5.6; LL lacking lateral appendages, apices may not both be visible from beneath at sides of ML depending on orientation; LL/ML narrow (1.9/1); LL of equal length, little shorter than ML, slightly separated along inner margins, converging at their apices; separation of LL begins at 11/16 their length from anterior margin (measured along median line dorsally); LL base width narrower than that of ML and not = LL apex width; apices of LL not expanded horizontally, strongly expanded vertically (LL appear very narrow when viewed from beneath); dorsal base of LL symmetrical, evenly excavated; LL lacking lateral hairy appendages or leaf–like lobes along their outer ventral margins, which are not produced preapically nor narrowly on their inner apical margin, not obliquely truncate along their preapical inner margins; left LL with rounded flap arising on its inner margin just behind flap on ML; ML asymmetrical, asymmetry due to curvature of ML; ML apex in shape of arrowhead, narrow and pointed when viewed from left, groove on ventral surface of ML follows curve of ML, begins in basal 1/3 to left side of ML, preapically enfolded on ventral side by ML flap and on left lateral, narrowly, by down turned margins of the ML which are finely rugulose along their margins; BP not very narrow, not strongly sclerotised, not hooded, not strongly emarginated along anterior margin.

**Female** and **Larva** unknown.

***Photuroluciola deplanata* Pic, 1931**
(Figs 38–55)

*Photuroluciola deplanata* Pic, 1931:12.
*Luciola* (*Photuroluciola*) *deplanata* (Pic). McDermott, 1966:115. Ballantyne, 2008:9. Fu & Ballantyne, 2008:1.

**Holotype**. Male. **MADAGASCAR**: Labelled (Fig. 56) 1. (printed) H. Taravellier Madagascar; 2. (Red printed) type; 3. (handwritten) Baie d'untoiyil; 4. (handwritten) nov. genre Photuroluciola; 5. (handwritten) Photuroluciola deplanata n. sp. (MNHN). Unique specimen.

**Male.** 14.7 mm long; 5.4 mm wide; almost 3 X as long as wide. Colour: Pronotum pinkish orange, semi-transparent and fat body is irregularly retracted beneath cuticle; MN orange; MS black; elytra dull black (this specimen has a superficial semitransparent layer on the elytra that is peeling in places and it may have been accidentally covered in another substance like glue); underside dull black except for creamy white LO segments; basal abdominal tergites dark brown, T 7 and 8 pale yellow, T8 semitransparent; dorsally reflexed edges of V2–5 brown, of V6 and 7 white. Pronotum: 3.5 mm wide across widest posterior portion (2.8 mm across anterior 1/3, 3.2 mm across middle), 2.7 mm long; W/L 1.3; 1/6 as long as whole body. Elytra 12 mm long. Head with GHW 2.7 mm; SIW 0.6 mm; SIW/GHW 0.2; frons not defined, area of frons-vertex junction rounded.

**Female and larva** unknown.

**Remarks**. The phylogenetic analysis reveals the distinctiveness of this single specimen, and this is emphasised by the form of its treatment here. Fu and Ballantyne (2008) included this species in a key to Luciolinae genera and figured some aspects of the aedeagus and sheath. The distinctive features of the aedeagus (especially the shape of the ML apex) suggest reproductive strategies different to those explored here in the Discussion.

***Pygatyphella* (Ballantyne)**
(Figs 23–26, 60–72, 255–487)

*Luciola (Pygatyphella*) Ballantyne, 1968:109.

**Type species**: *Atyphella obsoleta* Olivier

**Diagnosis**. With the exception of one species (*Pygat. wisselmerenia*) all species have the LO retracted into the anterior area of V7 and the posterior area arched and often swollen. Many species have a distinctive dorsal colouration that Ballantyne (1968) considered resembled bird droppings.

**Male.** Pronotum: dorsal surface lacking irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense. Anterior margin not explanate.

Pronotum wider across posterior area than rest; pronotal width greater than humeral width. Anterolateral corners rounded obtuse; lateral margins in anterior half divergent posteriorly; lateral margins in posterior half diverge then converge with rounded or angulate convergence (both types of convergence may be seen in one individual, and between individuals in same species) except in *Pygat. uberia* **sp. n.**, where lateral margins diverge along length; indentation at mid-point absent; lacking sinuousity in either horizontal or vertical plane; indentation in lateral margin near posterolateral corner present or absent (may differ from right to left sides of pronotum and between individuals in same species); irregularities at corner present or absent; posterolateral corners rounded or angulate; rounded corners obtuse, angulate corners approximately 90° or less (never very acute), and inclined obliquely to the median line; posterolateral corners project as far as, or beyond median posterior margin, separated from it by shallow emargination.

Hypomera closed. Median area of hypomeron not elevated vertically; anterior area of hypomeron not flat to side of head; posterior area widely and strongly flattened and strongly adpressed; median area of hypomeron shows marked transition between anterior and posterior areas in New Guinea species; pronotal width/ GHW index 1.6.

Elytron punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and suture extend beyond mid-point, do not extend as a ridge around apex and neither is expanded in apical half; 0 or 2 interstitial lines, if developed do not exceed suture; viewed from beneath with specimen horizontal epipleuron at elytral base narrow, covering humerus, and viewed from above arises anterior to posterior margin of the MS; epipleuron developed as lateral ridge along most of length; sutural margins approximate along most of length in closed elytra; lateral margins parallel-sided or convex.

Head moderately, often strongly depressed between eyes; moderately exposed in front of pronotum, or capable of complete retraction within the prothoracic cavity; eyes close to moderately separated beneath at level of posterior margin of mouthpart complex; eyes above labrum close except in *pulcherrima* where SIW/ GHW is 0.18; frons-vertex junction rounded, not well–defined; lacking median elevation; posterolateral eye excavation not strongly developed and not visible in resting head position; antennal sockets on head between eyes, contiguous or separated by less ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts functional; apical segment of labial palpi non–lunate, strongly flattened, in the shape of a wide triangle, with inner edge dentate, with 3 or more 'teeth'. Antennae 11 segmented; length>GHW to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel; FS always at least 2 X as long as wide.

Legs with inner tarsal claw not split; lacking MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen lacking cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment; LO in V7 entire, or bipartite; entire LO occupies most (in *marginata*), or half or less of V7, often restricted to anterior half of V7 or less, often medially emarginated across its posterior margin, sometimes deeply so; bipartite LO (in *uberia* **sp. n.** only) not restricted to anterolateral plaques; entire LO reaching to sides or not, not reaching to posterior margin; bipartite LO occupies > half V7; anterior margin of entire LO in V7 not emarginate; posterior half of V7 arched (except in *wisselmerenia* **sp. n.**), may be swollen, transverse muscle impressions usually visible in this area; LO in species with swollen posterior half of V7 emarginated posteriorly; posterolateral corners not produced, distinct or obliterated; if present rounded or angulate; LO present in V6, occupying almost all V6. MPP present, if symmetrical then apex rounded, pointed, squarely truncate, or bisinuate (in *okapa* **sp. n.**); if asymmetrical then obliquely truncate; not medially emarginated, not laterally compressed, short in *pulcherrima*, *tagensis;* usually L=W, L>W (in *uberia* **sp. n.**), not strongly inclined dorsally; not engulfed by the apex of T8 except in *undulata*; MPP with basal emarginations in *uberia* **sp. n.**; dorsal ridge of MPP often present, narrow to wide, to left of middle, or median in *karimui* sp. n, ridge lacking median elevations. V7 lacking median carina, median longitudinal trough, anteromedian depression on face of LO, PLP (except in *okapa* **sp. n.** where they are slightly produced, narrow and horizontal), incurving lobes or pointed projections, median 'dimple', or reflexed lobes; V7 dorsal surface with paired lobes in *peculiaris* only. T7 lacking prolonged posterolateral corners. T8 strongly sclerotised, not subparallel-sided, margins usually converge gently towards posterior end; symmetrical, W=L or L>W of visible posterior portion, which does not narrow abruptly; lacking prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally nor engulfing the posterior margin of V7 nor the MPP, except in *undulata*, where the posterior half of T8 is not strongly narrowed, with down turned portion a thickened wide shelf; T8 not extending conspicuously beyond posterior margin of V7 horizontally; T8 ventral surface lacking flanges, lateral depressed troughs; median longitudinal trough absent or present; if present margins fine, slightly thickened or well developed; median longitudinal trough if developed longitudinal except in *nabiria* **sp. n.**; trough very short in *japenensis* **sp. n.**; trough margins symmetrical except in *okapa* **sp. n.**; various asymmetrical projections in anterolateral and posterolateral left and right present in *uberia*; median posterior ridge present or not, usually curved, may be straight (*plagiata*); concealed anterolateral arms of T8 present, not laterally emarginated before their origins, narrow, either as long as visible posterior portion or narrow in *tomba* **sp. n.**, and expanded dorsoventrally except in *tomba* **sp. n.** and *wisselmerenia* **sp. n.**; apices lacking bifurcation of inner margin; bases with ventrally directed pieces present or absent.

Aedeagal sheath never > 4 times as long as wide; lacking paraprocts; asymmetrical in posterior area with sheath sternite either emarginated on right side from point of attachment of tergite, or subparallel-sided for a third its length past articulation with sheath tergite, and then emarginated on right side, or subparallel-sided along its length in *uberia* **sp. n.**; sternite not angulate on L or R sides; posterior margin entire, rounded, not emarginated on either side preapically except in *uberia* where it is unevenly emarginated preapically on the right side; anterior half of sternite broad, apically rounded; tergite lacking lateral arms that extend widely anteriorly at the sides of the sheath sternite; tergite not subdivided, lacking projecting pieces along posterior margin of tergite 9; anterior margin of tergite lacking transverse band (anterior margin sometimes more heavily sclerotised than.

Aedeagus L/W 3/1 or shorter; LL lack lateral appendages, visible from beneath at sides of ML except in *uberia* **sp. n.** where they may not both be visible in same plane, LL/ML wide to moderate; LL of equal length, slightly shorter than ML except in *uberia* **sp. n.** where ML much longer than LL; LL diverging along inner margins, and separated there by > half their length; LL base width not=LL apex width which is subequal to or narrower than that of ML; LL apices not expanded horizontally except in *eliptaminensis*; dorsal base of LL either symmetrical, or if asymmetrical, strongly produced to right; if symmetrical not excavated, median margin prolonged and broadly rounded; LL lacking lateral hairy appendages along their outer ventral margins, which may be produced preapically and also either narrowly or widely on their inner apical margin obliquely truncate along their preapical inner margins in *tagensis*, *huonensis* and lacking strongly developed tooth at anterior end of truncation; apices of LL out–turned in *peculiaris*; lacking projection on left LL only; inner margins lacking slender leaf-like projection; ML symmetrical, if asymmetrical then curved to left horizontally; paired lateral teeth may be present; lacking tooth to left side, not strongly arched, and apex not in shape of arrowhead, not bulbous, not inclined ventrally; BP not very narrow, not strongly sclerotised, not hooded, usually in two pieces and not strongly emarginated along anterior margin.

**Female.** Macropterous and either assumed capable of flight or observed in flight. Pronotum shaped as for male; lacking irregularities in posterolateral areas; punctation moderate to dense; pronotum > humeral width; indentation of lateral margin often present (may differ from one side of pronotum to the other in the one individual and between individuals in the one population), irregularities near posterolateral corner present or absent. Elytral punctation not as large as that of pronotum nor evenly spaced, punctation dense or sparse. Head not strongly reduced but can be retracted within prothoracic cavity, and antennae on head between eyes. Elytra with 0, 2, interstitial lines; elytral carina absent. No legs or parts thereof swollen and /or curved. LO in V6 only, lacking any elevations or depressions or ridges on V7 except for depressions in posterolateral areas in some species which probably reflect torsion of underlying D–V muscles.

**Larva** not associated.

**Remarks.** *Pygatyphella* (Ballantyne) exists in two clearly defined forms referred to in descriptions as *Pygatyphella* A or B:

*Pygatyphella* A: Dorsal colouration usually cryptic, very pale brown with dark markings on pronotum, MS, MN and elytral base and apex; pronotum often with angulate convergence along lateral margins, and small depression often present just anterior to posterolateral corner; lacking irregularities at the corners; posterolateral corners may project beyond median posterior margin; at least two interstitial lines usually well–defined; elytral margins convex or parallel-sided; posterior area of ventrite 7 may reach into LO (which is medially emarginated); apex of MPP rounded, pointed, or squarely or obliquely truncate; MPP lacking median dorsal ridge (except in *karimui* **sp. n.**), lacking curved, slightly off-centre posterior ridge on ventral surface of T8; dorsal surface of posterior area of MPP faced with cuticle that is not attached to the ventral surface of V7 and ends just behind the area of muscle attachment posterior to the LO; the anterior margins of this cuticle are reflexed in *Pygat. peculiaris*; median area of this facing cuticle lacking longitudinal split; T8 anterolateral prolongations lacking ventral projections at their base; aedeagal sheath not subparallel-sided in basal third; aedeagus L/W usually >3; LL/ML not wide; ML sometimes asymmetrical in a horizontal plane only, never with lateral teeth; anterior margin of LL often asymmetrically produced. Within *Pygatyphella* A, a group of species similar to *Pygat. obsoleta* in colour and terminal abdomen morphology is referred to in descriptions as the ‘‘obsoleta complex’’.

*Pygatyphella* B: Dorsal colouration with orange pronotum (sometimes with median dark mark), and dark brown elytra which may be pale margined except in *Pygat. russellia*, which is pale dorsally; pronotum never with angulate convergence along lateral margins, or small depression present just anterior to corner; with irregularities at corners; posterolateral corners always rounded obtuse, not projecting strongly if at all beyond median posterior margin; no interstitial lines well–defined; elytral margins convex-sided; posterior area of ventrite 7 never reaching into LO (LO not medially emarginated); apex of MPP rounded or squarely or obliquely truncate; MPP with dorsal longitudinal ridge; dorsal surface of the posterior area of the MPP faced with cuticle that is not attached to the ventral surface of V7 and ends just behind the area of muscle attachment posterior to the LO; the anterior margin of this cuticle is emarginate and the ridge that continues along the ventral surface of the MPP is a continuation of this emargination (e.g. Figs 342–349, especially Fig. 358); ventral surface of T8 with usually curved, slightly off–centre ridge close to posterior margin; T8 outlines in *Pygat. limbatipennis*, *limbatifusca* and *salomonis* characterised in Figs 438–442; T8 with pale partly membranous ventral projections from the bases of the anterolateral prolongations; aedeagal sheath sternite posterior to the lateral tergite articulations subparallel-sided in basal 1/3 to 1/2; aedeagus L/W<3; LL/ML wide; ML never asymmetrical, always with lateral teeth; anterior margin of LL never asymmetrically produced.

### List of species of *Pygatyphella*

* = *Pygatyphella* type B
\# = *obsoleta* complex
*eliptaminensis* (Ballantyne, 1968)
*huonensis* (Ballantyne, 1968)
*ignota* (Olivier, 1911)
*japenensis* **sp. n.**#
*karimui* **sp. n.**#
*kiunga* **sp. n.**#
*limbatipennis** (Pic, 1911)
*limbatifusca** **sp. n.**
*marginata* (Ballantyne, 1968)
*nabiria* **sp. n.**#
*obsoleta* (Olivier, 1909a)#
*okapa* **sp. n.**#
*plagiata* (Blanchard, 1853)*
*peculiaris* (Olivier, 1909a)
*pulcherrima* (Ballantyne, 1968)#
*russellia** **sp. n.**
*salomonis** (Olivier, 1911)

*tagensis* (Ballantyne, 1968)
*tomba* **sp. n.**
*uberia* **sp. n.**
*undulata* (Pic, 1929)
*wisselmerenia* **sp. n.**

**Key to species of *Pygatyphella* (Ballantyne) using males**

1. LO bipartite in V7; basal emarginations present at sides of MPP (Figs 468, 470, 471) ........... *uberia* **sp. n.**
   LO entire in V7; basal emarginations at sides of MPP absent........................................................... 2
2. Posterior margin of V7 neither arched nor swollen; LO occupies almost all of V7 and muscle impressions are not visible posterior to the LO (Fig. 487) ..........................................................*wisselmerenia* **sp. n.**
   Posterior margin of V7 arched, sometimes swollen (Figs 61, 61) with muscle impressions visible through cuticle posterior to LO ........................................................................................................... 3
3. MPP with dorsal ridge (Figs 306, 342–359); T8 (Figs 360, 361) with median posterior ridge on ventral surface; posterolateral corners of pronotum with irregularities (Fig. 341); lateral margins of pronotum lacking any indentations (*Pygatyphella* B Group)....................................................................... 4
   MPP lacking dorsal ridge except in *karimui* **sp. n.**; T8 lacking median posterior ridge on ventral surface; posterolateral corners of pronotum lacking irregularities; lateral margins of pronotum often with indentations near posterolateral corners on either or both sides.......................................................................... 8
4. Dorsal surface pale brownish yellow (Figs 405, 406) ........................................................*russellia* **sp. n.**
   Elytra always very dark brown, sometimes with paler margins (Figs 329–337, 340, 397, 417, 418–420) 5
5. Elytra dark brown, no paler margins ........................................................................................... 6
   Elytra always with paler margins (either lateral, apical or sutural or a combination of these) .................. 7
6. Pronotum orange with no dark markings (Figs 417, 418)............................................ *salomonis* (Olivier)
   Pronotum orange with darker median markings (Fig. 397) ....................................... *plagiata* (Blanchard)
7. Pronotum pale with no median darker markings......................................................... *limbatipennis* (Pic)
   Pronotum orange with median darker markings (Fig. 329, 338)...................................*limbatifusca* **sp. n.**
8. Posterior margin of LO shallowly to deeply emarginated (Figs 24, 61, 62) ............................................. 9
   Posterior margin of LO not shallowly to deeply emarginated................................................................ 13
9. MPP very short and wide, may be slightly reflexed dorsally and not visible from beneath (Figs 452–454) ............................................................................................................................................ 10
   MPP not very short and wide, always visible from beneath and not reflexed dorsally............................ 11
10. Posterior margin of T8 strongly downturned and engulfing the MPP down turned (Figs 452–454) .......... ..................................................................................................................... *undulata* (Pic)
    Posterior margin of tergite 8 not downturned and MPP not engulfed ....................... *tagensis* (Ballantyne)
11. Dorsal face of anterior area of MPP in V7 with paired lobes (Ballantyne, 1968 Figs 44, 45); MPP apically entire (Figs 315, 321) ................................................................................... *peculiaris* (Olivier)
    Dorsal face of anterior area of MPP in V7 lacking paired lobes; MPP may be medially emarginated .... 12
12. MPP narrow and posterior margin medially emarginate; LL of aedeagus not very narrow (Figs 24, 61, 62, 267)........................................................................................................... *huonensis* (Ballantyne)
    MPP broad and posterior margin apically entire and rounded; LL of aedeagus very narrow (Figs 320, 327, 328) ............................................................................................................. *kiunga* **sp. n.**
13. ML of aedeagus asymmetrical (curved to right horizontally)............................................................ 14
    ML of aedeagus symmetrical (does not curve to right in horizontal plane).......................................... 15
14. Apex of MPP squarely truncate; outer preapical margin of LL angulate (Figs 291, 292, 300, 301, 308) ... ...........................................................................................................................*nabiria* **sp. n.**

Apex of MPP rounded; outer preapical margin of LL rounded (Figs286–288, 296, 297, 307) ........................................................................................................................................ *japenensis* **sp. n.**

15. Dorsal surface of MPP with median ridge; posterolateral corners of pronotum may be < 90° (Figs 279, 304–306) ........................................................................................................ *karimui* **sp. n.**

Dorsal surface of MPP lacks median ridge ........................................................................................ 16

16 PLP very short and narrow; MPP trisinuate across its apex (Figs 309, 310) ............................ *okapa* **sp. n.**

PLP not developed; MPP not trisinuate across its apex ................................................................. 17

17. Interstitial lines not obviously developed; MPP symmetrical, apex rounded or pointed; posterolateral corners of pronotum rounded; outer and inner preapical areas of LL not produced (Figs 456–466)............................................................................................................................ *tomba* **sp. n.**

Interstitial lines developed (at least two); MPP symmetrical or not, apex rounded, pointed or truncate . 18

18. Aedeagus L/W <3/1; LL wide at their apices; outer preapical margin of LL produced and rounded; inner apical area produced and wide; apex of MPP narrowly rounded; LO very short occupying < 1/3 total area of V7; head concealed within prothoracic cavity in repose (Figs 264, 270, 271) ....................................................................................................................... *eliptaminensis* (Ballantyne)

Aedeagus L/W 3/1 or greater (complex is long and narrow); LL narrow at their apices; outer preapical margin of LL either produced and rounded, or not produced; inner apical area produced and narrow; apex of MPP rounded, pointed or truncate; LO longer occupying just less than half total area of V7 ............. 19

19. Dorsal surface with dark colour in median area of pronotum, markings on MS and MN, with usually wide triangular patch at base of elytra (sometimes restricted to a narrow band along base of suture) and patches of varying sizes near elytral apices ........................................................................................... 20

Dorsal surface either pale with no dark markings, or pronotum MS and MN marked as above with elytra pale brown with lateral margins narrowly paler ........................................................................... 21

20. Dorsal colouration yellow with black markings; pronotum with black marking extending from anterior to posterior margins widening posteriorly; all of MS and MN black; elytra with extensive basal dark marking; LO occupying > ½ visible area of V7; known from one specimen................*pulcherrima* (Ballantyne)

Dorsal colouration light dingy brown with darker brown markings; pronotum with median brown marking; MS and MN with median brown markings; LO occupying < ½ visible area of V7 (Figs 379–385, 387) ........................................................................................................................*obsoleta* (Olivier)

21. Dorsal surface pale with faint markings on pronotum, MS with median brown mark and faint markings at elytral apex; known from one specimen (Fig. 265) ........................................................... *ignota* (Olivier)

Dorsal surface with dark markings on pronotum, MS and MN; elytra pale brown with paler lateral margin ..............................................................................................................*marginata* (Ballantyne)

## ***Pygatyphella eliptaminensis*** **(Ballantyne, 1968)**

(Figs 64, 255, 264, 266, 270–273)

*Luciola (Pygatyphella) eliptaminensis* Ballantyne, 1968: 113.

**Holotype.** Male. **PAPUA NEW GUINEA**: West Sepik (Sandaun) Pr., 5.13S, 141.5E Eliptamin Valley, 1665–2530m, June 23–30, 1959, W. W. Brandt (BPBM).

**Material examined**. Holotype male, allotype female (same locality as holotype).

**Diagnosis.** A large species (12.4–15.4 mm long) (Figs 64, 255, 264), similar to *Pygat. peculiaris*, the males of which are < 10 mm long, distinguished by the absence of dorsal protuberances on V7, the distribution at high altitude, the shorter MPP of V7, the restricted LO occupying < half the area of V7 with posterior margin entire, and the scarce arching of V7 posterior to LO (Ballantyne, 1968, Figs 54, 55). Similar to *Pygat*.

*obsoleta* but larger, distinguished by the broad expansion of LL apices and the very short and broad production of the inner apical margin of the LL (Figs 270, 271).

**Male**. T8 with posterior (entire) area quite short (Fig. 273); aedeagal sheath (Fig. 272) with tergite narrow, anterior margin darker than rest, sternite narrowed in posterior half.

**Female**. Macropterous, 15.7 mm long, assumed capable of flight; characterised in Ballantyne (1968:114); V7 broadly and moderately deeply emarginated across posterior margin with posterolateral corners acutely angles (R corner rounded, L slightly angulate), and with oval depressions (corresponding to D-V muscles) within the posterolateral projections; V 8 median posterior margin narrowly and shallowly indented; lateral margins of T8 converge posteriorly with posterior margin truncate.

**Remarks.** Ballantyne (1968) described this species from two males and one female, highlighting its differences from *Atyphella peculiaris*. It is known only from these records.

***Pygatyphella huonensis*** **(Ballantyne, 1968)**
(Figs 23–26, 61, 62, 256, 267)

*Luciola (Pygatyphella) huonensis* Ballantyne, 1968:116. Lloyd 1973b:995 (light production); 1977:178–9 (light production). Ballantyne 1987a:179,182,183.
*Atyphella huonensis* (Ballantyne). Ballantyne and Lambkin, 2000:15; 2001:364, 2006: 30.

**Holotype.** Male. **PAPUA NEW GUINEA**: Morobe Pr., Huon Peninsula, Pindiu, 950–1200m, 7.iv.1963, JS (BPBM).

**Material examined**. **PAPUA NEW GUINEA**: Morobe Pr., 3.46S, 143.52E, 4mi n Wau elev c. 2800', nr Kunai Creek, Lae Rd, 16.xi.1969, J.E. Lloyd, 2 males (G609, 612 both with orange label)(JELC). Madang Pr., 5.55S, 146.4E, Finisterre Mts, Budemu, c. 4000 feet, 15–24.x.1964, stn No. 51, M. E. Bacchus, 7 males, 1 female (NHML). Morobe Pr., 6.6S, 147.85E, Finsch Haven Wareo, L. Wagner 16 males, 11 females (SAM); 6.45S, 147.51E, Huon Peninsula, Pindiu, 950–1200m, 17.iv.1963, JS paratype male (BPBM); Huon Pen, Bulang, 100 m, 29.1.1977, W. C. Gagné, 4 males (BPBM); 6.72S, 146.99E, Busu River E of Lae, 100m, 14.ix.1955, c, paratype male (BPBM). **INDONESIA IRIAN JAYA**: 1.45S, 136.15E Japen Island, SSE Sumberbaba, Dawni River, x.1962, N. Wilson 1 male (BPBM). Cyclops Mountains, 3400–4500 feet, iii.1936, L Cheesman, male, female (NHML).

**Code name**. *Luciola* 6 (Lloyd, 1973b)

**Diagnosis.** A moderate sized (8.5–12.0 mm long) species similar to, but distinguished from *peculiaris* and *eliptaminensis*, by the extent of the apical dark elytral marking (Figs 21–26, 256, 267), the apical excision of the MPP (Figs 21–26), the deep posterior emargination of the LO of V7 (Ballantyne, 1968, Figs 91, 92), the strong arching of V7 especially posterior to the LO (Figs 61, 62), and the lack of dorsal protuberances on V7. Macropterous, similarly coloured females are associated on the basis of label data.

**Female.** Macropterous. 10–10.6 mm long. Coloured as for male except creamy white LO restricted to V6 and abdominal ventrites and tergites 7, 8 brown-yellow, more heavily sclerotised than preceding segments. V7 with deep oval depressions in anterolateral areas (probably corresponding to positions of D–V muscles), and posterior margin widely and moderately deeply emarginate, posterolateral corners rounded; median posterior margin of V8 narrowly emarginate; T8 with lateral margins converging posteriorly, narrowing before posterior margin, which is not indented in median line.

**Remarks.** *Pygat. huonensis* was sympatric with *Pygat. peculiaris* "at the Namie–Bulolo site" (Lloyd, 1973b:995), where "they emitted series of single short flashes with a flash period of 1.5 sec", contrasting with the single flashes of. *peculiaris* with a flash period of 0.5 sec. Lloyd (1977:179) commented, "The fireflies of the *L. peculiaris* (sic) group (New Guinea) emit continuous trains of flashes…… The feeble nature of alternate flashes in *L. huonensis* suggests that these are being lost and that originally the timing was more like that of *L. peculiaris*."

Ballantyne (1968) described this species from 3 specimens from Pindiu and Busu River near Lae. Ballantyne (1987b Fig. 2 g–k) described and figured muscle attachments of the terminal abdomen, aedeagus within the aedeagal sheath, and (page 183) discussed their significance. The two males from Irian Jaya are tentative associations only.

### *Pygatyphella ignota* (Olivier, 1911)

(Figs 265, 268, 269, 274–277)

*Atyphella ignota* Olivier, 1911:174; 1913:417.
*Luciola (Luciola) ignota* (Olivier). McDermott, 1966:105.

**Holotype.** Male. **PAPUA NEW GUINEA**: Milne Bay Pr., 9.30S, 150.40E, Fergusson Is., ix, x, xi, xii, 1894, A. S. Meek (MNHN); labelled (Fig. 277) 1. (Printed) Fergusson I., ix.x.xi.xii.94 (printed number 5 overwritten with large 4) (A. S. Meek). 2. (Handwritten on red paper) *ignota* Ern Oliv.

**Diagnosis.** Medium sized (9.4 mm long); dorsal colouration of elytra dingy pale brown; most similar to *Pygat. obsoleta*, distinguished by the dorsal colouration, the scarce production of the preapical outer margin of the LL, the squarely truncate MPP apex, and the apparent lack of a median longitudinal trough on the ventral surface of T8.

**Male redescription**. 9.4 mm long; 4.0 mm wide; W/L 2.3. Colour (Figs 265, 268): Pronotum dingy pale yellow with small paired median light brown patches, semitransparent in areas where fat body retracted; MN pale cream, pale brown markings cover most of median area of each plate; MS greyish cream with an extensive anteromedian brown area not extending to lateral or posterior margins; elytra very pale light brown with lateral margins dingier cream; inner margins of epipleura finely dark brown; dorsal surface of elytral apex with narrow pale brown band extending across outer edge of epipleuron just anterior to elytral apex; under surface of elytral apex dark brown; head, antennae, palpi dark brown except for dingy cream inner margin of apical segments of maxillary palpi. Pronotum: 2.2 mm long, 3.6 mm wide; W/L 1.6; both lateral margins with angled convergence and small indentation before angulate posterolateral corners, corners approximately 90° and oblique to median line. Elytron (Fig 265): 7.2 mm long; parallel-sided; inner two interstitial lines well–defined. Head: retracted within prothoracic cavity at rest and not visible from above; GHW 2.0 mm; SIW 0.25 mm; SIW/GHW 0.1. R labial palp apex with 6 slender teeth along inner margin, L palp with 2 broad basal and 2 slender apical. Abdomen, ventrites (Figs 268, 269): LO entire in V6, V7 reaching sides but not posterior margin of V7, median posterior margin not emarginate, occupying > ½ area of V7. MPP as long as wide, posterior margin squarely truncate (very slightly emarginate in dried pinned specimen, entire after immersion in hot water to soften); lacking dorsal ridge. Tergites (Fig. 274): T8 visible (coloured) posterior portion considerably wider than long; anterolateral prolongations very elongate, narrow, expanded vertically, lacking flanges; ventral surface of T8 lacking posteromedian ridge. Aedeagal sheath: emargination on right side begins at tergite articulations. Aedeagus (Figs 275, 276): L/W 3.5/1; LL/ML 2.8; LL divergent along their length dorsally, and slightly shorter than ML; preapical outer margin of LL barely produced; preapical inner margin of LL produced, short and narrow; base of LL asymmetrically produced to the left; ML symmetrical, lacking lateral teeth.

**Female, Larva.** Not associated.

**Remarks.** While superficially similar to *Pygat. obsoleta*, *Pygat. ignota* is not simply a paler variety of that species, and the aedeagal complex resembles that of *Pygat. wisselmerenia* **sp. n.** rather than that of *Pygat. obsoleta*. The dorsal elytral colouration is distinctive in lacking the dark markings along the suture characteristic of pale *obsoleta*. Although Olivier (1913) recorded this species from some mainland localities, it is possible that these are records of *obsoleta* (I am unable to relocate these specimens).

***Pygatyphella japenensis* sp. n.**
(Figs 278, 286–288, 296, 297, 307, 311)

**Holotype.** Male. **INDONESIA IRIAN JAYA**: 1.45S, 136.15E, Japen Island, SSE Sumberbaba, Dawai River, x.1962, N. Wilson, (BPBM).

**Paratypes (5)**. Same data as holotype, 2 males, 3 females.

**Diagnosis**. One of the '*obsoleta* complex'; distinguished by the 90° angle of the posterolateral corners of the pronotum, the rounded apex of the MPP, the very short median trough on the ventral surface of T8, the asymmetrical ML which curves to the left horizontally, and the very short inner apical projections of the LL.

**Male**. 6.8–7.0 mm long; 2.8–3.0 mm wide; W/L 0.4. Colour (Fig 278): Pronotum whitish yellow, semi-transparent with underlying white fat body, narrow median hour-glass brown area does not reach to anterior margin and is wider across posterior area; MN pale yellowish, with median brown area; MS with median brown area that narrows anteriorly and just abuts the median anterior margin in 2/3, or covers almost all of MS in 1/3, other margins pale; elytra very pale brown, semitransparent, anterior brown marking either extending or not extending to suture or edge of MS in anterior 1/6 in 2/3, not reaching lateral margin, extending posteriorly along suture for 1/3 elytral length, and then narrowly along the suture just past half elytral length; extreme base of suture just behind MS very narrowly marked in brown, next 1/6 of suture pale in 2/3, or all of suture to past half length of elytron brown; apices of interstitial lines 1 and 2 narrowly brown marked (marking not extending to posterior margin); elytral lateral margins with brown marking just anterior to apex; head, antennae and palpi very dark brown; ventral aspect of thorax dingy yellow except for brown metasternum; legs yellow with brown tarsi; V3 pale at edges, brown across median half; V4 mostly brown, paler at edges; V5 very dark brown; basal ventrites dingy brown; LO yellow, posterior area of V7 semitransparent, pale yellow; T 7 and 8 yellow. Pronotum: 1.5 mm long; 2.5–2.6 mm wide; W/L 1.6; lateral margins with angulate convergence (on both sides of pronotum) in 2/3, one male with rounded and angulate convergence on either side; Posterolateral corners angulate, approximately 90°. Elytron: parallel-sided; 5.3–5.5 mm long; with 2 well–defined interstitial lines with line 2 is slightly larger than line 1 in 2/3. Head: can be partly retracted into prothoracic cavity and thus may only be narrowly visible from above; GHW 1.5–1.7 mm; SIW 0.15mm; SIW/GHW 0.05–0.1; ASD<ASW (sockets are very close, almost but not quite contiguous). Abdomen, ventrites (Fig. 307): LO entire in V7, reaching sides but not posterior margin; posterolateral 'corners' angulate; LO occupies less than half the area of V7. MPP well–defined, apex rounded. Tergites: T8 (Fig. 311) about as long as wide (visible entire posterior portion), with median posterior margin slightly produced and narrowly rounded; ventral darkened portion short; with very short median longitudinal trough; anterolateral prolongations elongate, expanded in vertical plane, lacking ventrally directed flanges. Aedeagal sheath: sternite emarginated on its left side from the tergite articulation. Aedeagus (Figs 286–288, 296, 297): L/W>3; LL/ML moderate; LL narrowly divergent along their length dorsally, slightly shorter than ML; outer preapical margin of LL produced and rounded, inner apical margin produced, short and narrow; base of LL asymmetrically produced to left; ML lacking teeth at about level of ejaculatory orifice, asymmetrical, curved to the left horizontally.

**Female**. Colour: As for male with these exceptions: pronotum yellowish brown, semitransparent with underlying cream fat body, narrow median hour-glass brown area does not reach to anterior margin and is narrower across posterior area in 1/3 and wider in 1/3; pronotum dingy pale brown with median markings scarcely discernable in 1/3; MS with narrow median brown area in 1/3, MS with broad dark brown area that almost covers all the area in 2/3, other margins pale; 1/3 with suture irregularly pale along 2/3 of its length within the otherwise brown basal area; bases of interstitial lines 1, 2 narrowly pale in 2/3. V4, 5 dark brown, V6 creamy white, V7, 8 yellowish semi-transparent; all of posterior margin of V7 shallowly emarginated with lateral areas showing depressed areas which probably represent torsion of D–V muscles in 1/3; lateral margins of T8 converge smoothly posteriorly and median posterior margin of both V8 and T8 are narrowly emarginated.

**Larva**. Not associated.

**Etymology**. The specific name is genitive case, (meaning 'of japen') latinised from the type locality.

***Pygatyphella karimui* sp. n.**

(Figs 279–281, 284, 289, 290, 298, 299, 304–306)

**Holotype.** Male. **PAPUA NEW GUINEA**: Chimbu Pr., 6.30S, 144.50E, Karimui 1080 m, 14.vii.1963, JS (BPBM).

**Paratypes** (6). Same data as holotype, 4 males, 2 females (BPBM).

**Diagnosis.** One of the *obsoleta* 'complex' distinguished by the strongly arched and swollen V7, the broad apically truncate MPP, and the very narrow apices of the LL of the aedeagus.

**Male.** 8.4–9.6 mm long; 2.8–3.3 mm wide; W/L 0.3. Colour (Fig. 279): Dorsal surface light brown, mostly semitransparent with fat body showing through the cuticle, and brown markings in median area of pronotum (small, paired, and faint), a narrow median dark band on the MS which reaches anterior margin, narrowly dark along the basal ¼ of suture from posterior margin of MS, small brown area at base of elytra between bases of interstitial lines 1 and 2, and two small preapical brown spots, one at posterior end of interstitial line 1 and the other at outer margin; head antennae and palpi very dark; ventral aspect of thorax yellowish except for brown metasternum; legs yellow with brown tarsi; basal ventrites yellowish, V5 dark brown with anterolateral pale patches; LO yellowish, posterior area of V7 yellowish with underlying muscle impressions clearly visible; basal tergites brown, T7 and 8 yellow. Pronotum (Fig. 284): 1.6–1.8 mm long; 2.9–3.3 mm wide; W/L 1.8; lateral margins with rounded (3/5) or angulate (1/5) convergence, and indentations in lateral margins in 5/5; posterolateral corners angulate, < 90° and inclined obliquely to the median line. Elytron (Fig. 279): parallel-sided; 6.8–7.8 mm long; with 2 well–defined interstitial lines. Head: can be partially retracted into prothoracic cavity, narrowly visible from above in resting position; GHW 1.9–2.0 mm; SIW 0.15mm; SIW/GHW 0.08; ASD<ASW (sockets very close). Abdomen, ventrites (Figs 304–306): LO retracted into anterior 1/3 of V7 where it may not reach sides, not reaching posterior margin, posterior margin either entire or slightly and narrowly produced in 1/5; V7 arched and swollen; posterolateral corners rounded angulate; muscle impressions extend almost to tip of MPP. MPP moderately broad, apex squarely truncate; dorsal surface with a wide median ridge (Fig. 306, arrowed). Tergites: T8 (Fig. 306) very well sclerotised, about as long as wide, thickened lateral margins converge gently posteriorly; anterolateral prolongations elongate, narrow, expanded vertically, more widely so in median area; ventral surface with a slightly developed long median trough with fine lateral margins. Aedeagus (Figs 289, 290, 298, 299): L/W>3/1; LL/ML moderate; lateral margins of LL converge posteriorly and LL narrow at apices; LL not divergent along dorsal length except near apices, slightly shorter than ML; outer preapical margin of LL slightly produced and rounded, inner apical margin produced, short and narrow; base of LL asymmetrically produced to left; ML lacking teeth at about level of ejaculatory orifice, symmetrical, not curved left horizontally; dorsolateral margins of ML behind apex slightly produced and pointed (may be visible from beneath as tooth like projections (Figs 289, 290, 298, 299).

**Female**. 8.8–9.6 mm long. Coloured as for male (Figs 280, 281) with these exceptions: pronotum lacking any median darker markings (irregularities in colour attributed to underlying muscles), MN very pale in ½, MS with wider median dark band in 1/2, very pale brown along the basal ¼ of suture from posterior margin of MS, small brown area at base of elytra between bases of interstitial lines 1 and 2 in 1/2; V6 with yellowish LO, V7, 8 brownish yellow, semitransparent; posterior margin of V7 broadly emarginated, posterolateral corners rounded, anterolateral areas slightly depressed; median posterior margin of V8 narrowly emarginate, with a shallow slightly depressed groove along its length in 1/2; lateral margins of T8 converge posteriorly, posterior margin straight.

**Larva.** Not associated.

**Etymology**. The specific name, the type locality, is considered as a noun in apposition.

***Pygatyphella kiunga*** **sp. n.**
(Figs 317, 319–320, 327–328)

**Holotype.** Male. **PAPUA NEW GUINEA**: Western Pr., Fly River, Kiunga, 35 m, viii.1969, JS, (BPBM).

**Paratypes** (4). Same data as holotype, males (BPBM).

**Diagnosis**. Similar to *Pygat. peculiaris*, differing in the wider apex of the MPP, lacking the dorsal projections of V7, and with very narrow apices of the LL.

**Male**. 9.5–10.8 mm long; 4.0–4.5 mm wide; W/L 0.4. Colour (Figs 317, 319): Pronotum yellow, semitransparent in 4/5, dingy pale brown in 1/5, fat body retracted in posterolateral areas, either with faint traces of paired median brown areas in 4/5, or with wider and more obvious brown areas in 1/5 (colour may be a reflection of underlying muscles); anterolateral corners narrowly brown on ventral surface (visible from above depending on orientation); MN yellow with median brown areas, reaching inner margins in 1/5; MS yellow with median dark marking, broad anteriorly (occupying about half width anterior area) in 3/5; elytra pale yellowish, semitransparent, with extensive brown markings at base and apex; basal dark area not extending to anterior margin and irregularly emarginated along lateral margin near MS, not covering humerus; inner margin of basal dark area extending along suture for approximately half its length, outer margin of basal dark area extending for about half this length posteriorly and then running obliquely and slightly irregularly across to suture; apical dark marking an elongate somewhat irregular oval, reaching suture and lateral margins narrowly along its posterolateral edges; head very dark reddish brown, antennae and palpi slightly lighter, inner margins of apical segments of both maxillary and labial palpi paler brown; under surface of thorax yellowish (metasternum appears light brown); legs 1 yellowish with anteroventral face of femora, ventral surface of tibiae and ventral surface of tarsi brown; legs 2 and 3 yellowish (a median orange line along the anterior face of the femora is probably due to the underlying muscle); basal ventrites light brownish yellow; LO creamy white, posterior area of V7 yellowish, semitransparent (muscle impressions visible); tergites brown, terminal two tergites orange yellow, heavily sclerotised. Pronotum (Fig. 317): 2.0–2.3 mm long; 3.5–4.0 mm wide; W/L 1.7; lateral margins divergent posteriorly with angled convergence on both sides in 5/6, and angled convergence on one side and rounded on the other in 1/6; posterolateral corners approximately 90°, angulate, inclined obliquely to median line; slight kink in lateral margins on both sides in 5/6. Elytron: parallel-sided; 7.5–8.5 mm long; with 2 well–defined interstitial lines. Head: can be retracted almost completely within prothoracic cavity and may not be visible from above; GHW 1.9–2.0 mm; SIW 0.2 mm; SIW/GHW 0.1; ASD<ASW (sockets very close but not contiguous). Abdomen, ventrites (Fig. 320): LO in V7 reaches to sides, not posterior margin, shallowly medially emarginated across posterior margin; posterior area of V7 arched and swollen; posterolateral areas of V7 rounded, corners not obvious. MPP as long as wide, dorsal surface lacking ridge; posterior margin rounded (slightly medially emarginated in 1/5). Tergites: T8 with slightly developed and laterally margined median longitudinal groove on ventral surface; anterolateral prolongations elongate, narrow, expanded vertically and lacking projections at their bases. Aedeagal sheath: emargination of right side of sternite begins at point of attachment of tergal arms laterally. Aedeagus (Figs 327, 328): L/W>3/1; LL/ML moderate; LL divergent along their length dorsally, just shorter than ML at very narrow apices; LL apices narrower than ML apex, lacking outer preapical expansion and inner apical prolongation; preapical inner margin of LL with very small tooth; base of LL asymmetrically produced (to the left); ML lacking lateral teeth.

**Female, Larva.** Not associated.

**Etymology**. The specific name, the type locality, is considered as a noun in apposition.

***Pygatyphella limbatifusca*** **sp. n.**
(Figs 329, 338, 341, 362, 363, 370, 371)

**Holotype.** Male. **SOLOMON ISLANDS:** Makira Pr., San Cristobal: 10.35S, 161.30E, Manipwena, Magoha River, 13.viii.1960, COB (BPBM).

**Paratypes** (26). Collector is COB. **SOLOMON ISLANDS:** Makira Pr., San Cristobal: 10.35S, 161.30E, Manipwena, Magoha River, 13.viii.1960, 6 males, 3 females; Kira Kira light trap, 15.viii.1960, male; Napagiwae, 20.viii.1960, 5 males; Wugiroga, 10.viii.1960, male; Bweinaniawarikiapu, 11–12.viii.1960, 7 males, 4 females (BPBM).

**Diagnosis**. Part of the *Pygatyphella* B complex; very similar to *Pygat. limbatipennis*, which is not known from San Cristobal, distinguished by the median pronotal markings, the paler brown elytra, the slightly paler and much wider lateral elytral margins, and the restricted occurrence on San Cristobal.

**Male.** 8.1–9.8 mm long; 3.4–3.9 mm wide; W/L 0.4. Colour (Fig. 329, 338): Pronotum orange yellow, semitransparent with underlying fat body visible, and 2 small median dark brown areas; elytra mid-brown, lateral margins widely pale yellow and semitransparent, pale margins extending from outer edge of humerus to apical area of suture; MS and MN pale yellow; head, antennae and palpi very dark brown; venter of thorax pale orange yellow except for very dark brown tarsi and apical ¾ of tibiae; basal ventrites yellowish, V3 with dark markings in one Bweinaniawarikiapu male and two Napagiwae; V4 extensively in representatives from all locations, V4 lightly marked in Bweinaniawarikiapu (3) and Manipwena (2); V5 always very dark brown, V7 yellowish and semitransparent behind LO; basal tergites yellowish, T 4–6 marked irregularly in light brown; T 7 and 8 orange yellow and semitransparent. Pronotum (Fig. 338): 1.7–2.3 mm long; 3.0–3.7 mm wide; W/L 1.6–1.7; lateral margins with rounded convergence in posterior areas; lacking indentation near posterolateral corners; with slight irregularities along rounded posterolateral corners, which project at least as far as median posterior margin. Elytron: convex-sided; 6.0–7.5 mm long; interstitial lines not well–defined. Head: large, moderately exposed, not able to be completely retracted into prothoracic cavity; GHW 1.9–2.4 mm; SIW 0.2–0.3 mm; SIW/GHW 0.1; ASD<ASW, sockets very close but not contiguous; frons not defined. Abdomen, ventrites: LO in V7 occupying half or less than half the area, not reaching sides, posterior margin not emarginated; muscle impressions clearly visible through cuticle in arched, not swollen, posterior half; posterolateral corners of V7 angulate. MPP symmetrical or asymmetrical, squarely or obliquely truncate (slightly obliquely truncate in Wugiroga 1, Bweinaniwarikiapu 1, Manipwena 3, and Napagiwae 1; obliquely truncate in remainder, very strongly in Bweinaniwarikiapu 1 and Kira Kira 1); with a broad dorsal ridge developed slightly to the left of centre. Tergites: T8 outline pattern 4 (Fig. 440); as wide as long, with low rounded curved elevation in posterior area to one side of mid-line; lateral margins converge posteriorly and median posterior margin (viewed from above) narrowly rounded; anterolateral prolongations of T8 elongate, narrow, and expanded vertically; ventrally directed pieces at bases of prolongations of T8 present. Aedeagal sheath (Figs 362, 363) subparallel-sided for 1/3–1/2 of its length past articulation with sheath tergite, then right side emarginate; anterior margin of tergite not emarginated; tergite with slight projection to R (as in Figs 360, 361). Aedeagus (Figs 370, 371): L/W <3; LL/ML wide; LL diverge along most of their length dorsally, slightly shorter than ML, apices rounded and subequal in width to ML; ML bearing narrow pointed lateral teeth, apex rounded truncate; base of LL not asymmetrically produced, slightly irregularly rounded.

**Female.** 9.0–9.6 mm long. Coloured as for male with these exceptions: V6 with yellowish LO which is retracted narrowly across the posterior margin which is semitransparent with whitish fat body visible in irregular clumps; V7, 8 semitransparent with underlying fat body confusing the basic colour, V7 with diffuse brown markings in median and anterolateral areas in all but one Bweinaniwarikiapu female. V7 lacking anterolateral depressions; with median posterior margin shallowly emarginate, and posterolateral areas broadly rounded; V8 median posterior margin narrowly emarginate; T8 with lateral margins converging posteriorly and posterior margin rounded.

**Larva.** Unknown.

**Etymology.** The specific name is a noun formed by combining part of the name of the species it most resembles (*limbatipennis*) and 'fusca' (dark) to highlight the dark markings on the pronotum. For a discussion on the possible variability in colour and morphology in specimens of this species, *Pygat. limbatipennis* and *Pygat. salomonis* see below and Tables 8, 9.

**TABLE 8.** Morphological features of Males of *Pygat. limbatipennis* at different localities in the Solomon Islands (Items in bold indicate both *Pygat. limbatipennis* and *Pygat. salomonis* taken at this locality). Abdominal colour 1=at least half of V3 dark, V4 and V5 dark marked; 2=V4, V5 dark marked; 3=V5 only. MPP shape R=rounded; T=truncate; SOT=slightly obliquely truncate; OT=strongly obliquely truncate. Tergite 8 shape see Figs 438–440 for scoring patterns.

| No. | Abd col. | MPP shape | T8 shape | length in mm | Elytral margins narrow | Locality |
|---|---|---|---|---|---|---|
| | | | | | | Bougainville |
| 2 | 3 | SOT, OT | 1 | 11 | Y(1) | Kukugai |
| 2 | 2 | SOT | 1 | 8.2–8.7 | | Mutahi |
| | | | | | | Choiseul |
| 3 | 2 | SOT, OT | 1, 4(1) | 8.5–9.5 | | **Kitipi River** |
| 1 | 2 | OT | 1 | 9.5–10.3 | Y (1) | **Malangona** |
| | | | | | | Western province |
| 24 | 2 | SOT | 1 | 9–10 | | Kolombangara |
| 4 | 2 | SOT, OT | 1 | 8.5–9.7 | | Pepele |
| 4 | 1,2 | SOT | 1 | 8.4–9.3 | | Iriri |
| | | | | | | Santa Isabel |
| 1 | 2 | SOT | 1 | 9.2 | | Kolotuve |
| 1 | 2 | SOT | 1 | 9.0 | Y | Tatamba |
| 3 | 2 | OT | 1 | 9–10.0 | Y | Rasa |
| | | | | | | Guadalcanal |
| 4 | 2 | SOT | 1 | 9.1–9.6 | | **Kolosulu** |
| 12 | 2–3 | R, SOT, OT | 1 | 8.5–11.0 | Y (1) | Lame |
| 7 | 2 | SOT | 1,4(1) | 7.2–8.2 | | **Honiara** |
| 5 | 2 | SOT | 1, 4 | 8.7–11.0 | | **Betikama River** |
| 2 | 2 | SOT | 1 | 9.3 | | **Paripao** |
| 1 | 2 | SOT | 1 | 8.5 | | **Sahuluatea** |
| 6 | 2 | SOT OT, E(1) | 1 | 8.3–9.4 | | Tetere |
| 1 | 2 | SOT | 1 | 8.0 | | Tambalia |
| 1 | 2 | SOT | 1 | 10.3 | | Mt Galliego |
| 1 | 2 | R | 4 | 7.5 | | Poha R. |
| 1 | 2 | SOT | 1 | 9.2 | Y | Lunga Bridge |
| 11 | 2 | SOT | 4 | 10.0 | | Mt Austen |
| 1 | 2 | SOT | 1 | 7.0 | | Kukunm |
| | | | | | | Florida Group |
| 23 | 2 | OT, SOT | 1,4 | 9.4–10.2 | Y | **Haleta** |
| 8 | 2 | SOT, OT | 1 | 8–10.5 | Y | Gairava |
| | | | | | | **Malaita** |
| 1 | 3 | OT | 3 | 11.3 | Y | Auki |
| 10 | 2 | SOT (6), OT (4) | 4 | 8.5–10.2 | Y | Takopekope |

**TABLE 9.** Morphological features of Males of *Pygat. salomonis* at different localities in the Solomon Islands (Items in bold indicate both *Pygat. limbatipennis* and *Pygat. salomonis* taken at this locality). Abdominal colour 1=at least half of V3 dark, V4 and V5 dark marked; 2=V4, V5 dark marked; 3=V5 only. MPP shape R=rounded; T=truncate; SOT=slightly obliquely truncate; OT=strongly obliquely truncate. Tergite 8 shape see Figs 438–440 for scoring patterns.

| No. | Abd col. | MPP shape | T8 shape | Length in mm | Elytral margin lighter brown | Locality |
|---|---|---|---|---|---|---|
| | | | | | | Bougainville |
| 4 | 3 | OT | 1 | 9.5–11.0 | Y(1) | Togerao |
| 1 | 3 | T | ? | 11.2 | | Kokure |
| | | | | | | Choiseul |
| 1 | 3 | SOT | 1 | 6.5 | | **Kitipi River** |
| 1 | 2 | SOT | 1 | 6.6 | | **Malangona** |
| | | | | | | New Georgia group |
| 6 | 2 | SOT, T | 1 | 7.5–8.5 | | Gizo |
| | | | | | | Vella Lavella |
| 1 | 2 | T | 1 | 8.2 | | Mt Arewanna |
| 2 | 2, 3 | SOT | 1 | 8.0 | | Gingola |
| 5 | 1, 2 | R, SOT | 1 | 7.6–8.1 | | Kow |
| 3 | 1, 2 | SOT, OT | 1 | 7–8.2 | | Kundurum |
| 16 | 2 | T, SOT | 1, 4 | 7.9–9.5 | | Pusisoma |
| 12 | 2 | SOT, T | 1, 4 | 7.9–9.4 | | Ulo Crater |
| | | | | | | Santa Isabel |
| 1 | 3 | E | 1 | 8.2 | | Buala |
| 1 | 1 | OT | 1 | 10.5 | | Moloa |
| | | | | | | Guadalcanal |
| 6 | 2 | E(1),SOT, | 1 | 6.5–7.0 | | **Kolosulu** |
| 34 | 1–3 | SOT, T | 2 | 6.8–7.7 | Y (1) | **Lame** |
| 1 | 2 | SOT | 1 | 7.5–7.9 | | **Honiara** |
| 1 | 2 | SOT | 1 | 7.0 | | **Betikama River** |
| 4 | 2 | SOT,T | 2 | 6.9–7.4 | | **Paripao** |
| 5 | 2 | SOT,T, E | 1,4 | 6.3–7.2 | | **Sahuluatea** |
| 3 | 2 | SOT | 1,4 | 6.8–8.2 | | **Tambalia** |
| | | | | | | Florida Group |
| 3 | 2 | SOT | 1 | 6.7–8.4 | | **Haleta** |
| 1 | 1 | R/T | 3 | 7.5 | | **Malaita (Auki)** |
| 3 | 1,3 | R/T | 3 | 7.3–7.8 | | Malaita (Dala) |

***Pygatyphella limbatipennis* (Pic, 1911)**
(Figs 330–337, 339, 340, 342–361, 364–369, 372–376)

*Atyphella salomonis* var *limbatipennis* Pic, 1911:165.
*Luciola* (*Luciola*) *salomonis* var. *limbatipennis* (Pic). McDermott, 1966:112.

**Holotype**. Male. **SOLOMON ISLANDS:** labelled 1. printed label 'Type'; 2. printed 'Solomon Is R A Lever'; 3. Lunga; 4. handwritten '*Atyphella salomonis* var *limbatipennis* Pic; 5. handwriting unclear could be Gauda (? = Guadalcanal) 7 Dec (NHML).

**Other specimens examined**. **PAPUA NEW GUINEA**: Bougainville, 6.0S, 155.0E, Kukugai village 150m, xii.1960 WB 2 males; 5.6S, 154.9 E Mutahi 700m 18 km SE Tinputz 1–7.iii.1968 Tawi 2 males (BPBM). **SOLOMON ISLANDS**: Western Pr., 7.10S, 156.95E, Choiseul, Kitipi River, 80m, 17.iii.1964 PS 3 males, female; Malangona River 10–30m, 2–7.iii.1964 PS 4 females (BPBM); Malangona 25.viii.1963 P

Greenslade male, female (NHML). Western Pr., 7.95S, 157.05E, Kolombangara 9–11.vi.1922 E Armytage female, 2 males (NHML); Pepele 30m, 7–9.ii.1964 PS, 4 males malaise trap; Iriri 2 m 3.vii.1964 JS 2 males (BPBM). Isabel Pr., 8.00S, 159.10E Santa Isabel, Kolotuve 15–16.vi.1960 COB male, 2 females; SE Tatamba 14.ix.1964 RS male; Haguelu 10 km SW Tatamba 400 – 650m 1–3.x.1964 native collector male (BPBM). Rasa 12.ii.1964 P Greenslade 2 males 2 females (NHML); Rasa 25.v.1963 P Greenslade male (NHML). Guadalcanal Pr.,9.28 S, 159.52E, Guadalcanal, 10 mi NW Honiara, at Mavo Bridge, 25–26.xi.1969, J E Lloyd, 11 males (G649–652, 654, 655, 657–658, 660–662 of which 660, 662 have flashes recorded) (JELC). 9.35S, 160.12E, Betikama River, ix.1960, WB, 5 males, female (BPBM); Honiara 0–200m, xii.1976 NK 2 males (NHML), i–ii.1985 5 males NK (BPBM); Kolosulu, native garden, 20.v.1960, COB 4 males 4 females; Lame near Mt Tatuve 300m, 18.v.1960 COB, 12 males 2 females; Lunga River (bridge) 4.ix.1960 COB male; Mt Austen 50m, palms, 11.x.1981 JG male (BPBM); Mt Galliego, Royal society BSIP 1965, lower camp site, male (NHML); Paripao, 21.v.1960 COB 2 males; Poha River 5 m, 2.vii.1956 JG male; Sahuluatea 200 – 400m, i.1973 NK male; Tambalia, 30 KM W Honiara, 22.v.1964 RS male; Tetere, 17.6 km E Roroni-Tathimani, 12.v.1960 COB 6 males (BPBM); Kukun 3.x.1963 P Greenslade male (NHML). Central Pr., Florida Group, Gairava, 14.ix.1960 COB 8 males, 3 females (BPBM); 9.08S, 160.25E, Nggela Is, Haleta 0–100m, 2–17.x.1964 RS 2 males (1 male sago stumps), 3 females (1 female malaise trap) (BPBM); 0–250m, Takopekope, 12.ix.1960, COB 10 males, female (BPBM). Malaita Pr., 9.00 S, 161.00E, 14.iv.1954 E Brown male (NHML).

**Diagnosis.** One of the *Pygatyphella* B complex; dorsal colouration orange pronotum with dark brown elytra which are pale margined along their lateral margins; most similar to *Pygat. limbatifusca* sp.n., distinguished by the absence of small paired dark markings on the pronotum, the very dark brown elytra and the narrower lateral pale band. Distinguished from other similarly coloured species by features listed on page 69 and from *Pygat. salomonis* in Tables 8, 9.

**Male.** 7.2–11.3 mm long; 3.0–4.2 mm wide; W/L 0.4. Colour (Figs 330–337, 339, 340): Pronotum orange yellow, semitransparent with underlying fat body visible; elytra very dark brown, lateral margins pale yellow, semitransparent, pale margins extending from outer edge of humerus narrowly around apex, not to suture; apical ¼ lateral margin brown in single Malaita male; margins either wider than underlying epipleuron, or as narrow as epipleuron (Figs 421,422; Table 8); 10 Takopekope males with lateral elytral margins narrowly paler brown enhanced by microscope illumination, 1 male with paler elytral margin visible macroscopically; Haleta male with paler brown elytral margins enhanced by microscope illumination, second male with narrow very dingy orange elytral margins; MS and MN pale yellow, MS appearing dusky brown if semitransparent; head, antennae and palpi very dark brown; venter of thorax pale orange yellow except for very dark brown tarsi; abdomen (Figs 342, 345, 346, 350, 353, 354, 359) (Table 8) with basal ventrites yellowish, ventrite colour patterns in Table 8 (either V3, 4 and 5 dark, or V3 pale, V4 and 5 dark; or only V5 dark); V5 always very dark brown, V7 yellowish and semitransparent behind LO; basal tergites yellowish, T4–6 marked irregularly in light brown; T7 and 8 orange yellow and semitransparent. Pronotum: 1.6–2.4 mm long; 2.5–4.0 mm wide; W/L 1.5–1.6; lateral margins with rounded convergence in posterior areas; lacking indentation near posterolateral corners; with slight irregularities along rounded posterolateral corners, which project at least as far as median posterior margin. Elytron: convex-sided; 5.6–8.1 mm long; interstitial lines not well–defined. Head: large, moderately exposed, not able to be completely retracted into prothoracic cavity; GHW 1.7–2.3 mm; SIW 0.15–0.2 mm; SIW/GHW 0.1; ASD<ASW, sockets very close but not contiguous; frons not defined. Abdomen, ventrites: LO in V7 occupies half or less V7, does not reaching sides, posterior margin of LO not emarginated; muscle impressions clearly visible through cuticle in posterior half which is arched but not swollen; posterolateral corners of V7 angulate. MPP (Figs 342–359) with broad dorsal ridge slightly to left of centre; MPP either symmetrical with apex rounded or truncate, or asymmetrical, with apex squarely or obliquely truncate (see Tables 8, 9). Tergites (Figs 360, 361): T8 (Table 8; conforms to patterns 1 or 4 except 3 in Malaita male) as wide as long, with low rounded curved elevation in posterior area to one side of mid-line; lat-

eral margins converge posteriorly and median posterior margin (from above) usually narrowly rounded; anterolateral prolongations of T8 (Figs 360, 361, 377) elongate, narrow, expanded vertically; ventrally directed pieces on bases of prolongations of T8 present. Aedeagal sheath (Figs 360, 361) subparallel-sided for 1/3–1/2 of its length past articulation with sheath tergite, then right side emarginate; anterior margin of tergite not emarginated; tergite with slight projection to R. Aedeagus (Figs 364–369, 372–376): L/W <3; LL/ML wide; LL diverging along most of length dorsally, slightly shorter than ML, LL apices rounded subequal in width to ML; ML bearing paired narrow pointed lateral teeth, apex of ML rounded truncate; base of LL not asymmetrically produced, slightly irregularly rounded.

**Female.** 8.5–10.2 mm long. Coloured as for male with these exceptions: lateral pale margin not extending around apex in 3 Gairava females; 2 Haleta females with narrow dusky orange lateral margins, 1 Haleta female with wide bright orange lateral margin; V6 with yellowish LO; V7, 8 semitransparent yellow. V7 lacking anterolateral depressions; with median posterior margin shallowly emarginate, and posterolateral areas broadly rounded; V8 median posterior margin narrowly emarginate; T8 with lateral margins converging posteriorly and posterior margin rounded.

**Larva.** Unknown.

**Remarks.** LB has been guided by geographical locations in the placement of many of these specimens in addition to differences in colour and morphology. Pronotal colour may be difficult to interpret as areas of retraction of underlying muscles may appear as coloured patches (see Discussion). Microscopic illumination can make determination of the extent of paler lateral margins more difficult, (particularly so in the Takopekope and Haleta specimens)). Both these populations are tentative assignments only. *Pygat. limbatipennis* and *Pygat. salomonis* were taken together at several locations, and Tables 8, 9 give comparisons between them. Comparisons between different populations were limited by paucity of specimens from some areas, and discussion following *Pygat. salomonis* suggests that further studies are necessary.

### *Pygatyphella marginata* (Ballantyne, 1968)

*Luciola* (*Pygatyphella*) *marginata* Ballantyne, 1968:116.

**Holotype.** Male. **PAPUA NEW GUINEA**: Northern Pr., 8.77S, 148.24E, Popondetta, 28.ii.1966 (QM).

**Diagnosis.** A moderate sized (8.5–10 mm long) species with pale brown, pale margined elytra; distinguished from most pale coloured *Pygatyphella* by the absence of distinct elytral markings at base and apex.

**Remarks.** Ballantyne (1968) described this species from 3 specimens.

### *Pygatyphella nabiria* sp. n.
(Figs 282, 291, 292, 300, 301, 308, 312, 313)

**Holotype.** Male. **INDONESIA IRIAN JAYA**: 3.22S, 135.28E, Nabire 5–50m, 25.viii–2.ix.1962, JS (BPBM).

**Paratypes** (2). Same data as for holotype (males) (BPBM).

**Diagnosis.** One of the '*obsoleta*' complex distinguished by the light brown dorsal colouration of the elytra which may lack darker markings, the very narrow posterior margin of T8 which has rounded and slightly projecting corners; short narrow prolongation of the inner apical margins of the LL, and the asymmetrical ML which bends left in a horizontal plane.

**Male**. 6.4–6.7 mm long; 2.5–2.7 mm wide; W/L 0.4. Colour (Fig 282): Pronotum pale brown, posteromedian area marked in brown (extends to posterior margin); pronotum semitransparent and underlying pale fat body makes pronotum appear slightly paler than elytra, MN pale brown with median brown areas reaching inner and anterior margins; with posterior and lateral margins narrowly yellow; MS light brown with narrow median dark marking; elytra pale brown, semitransparent, lacking darker markings except for pale brown areas in posterior lateral areas, with fat body irregularly distributed in small clumps; head very dark reddish brown, antennae and palpi slightly lighter, inner margins of apical segments of both maxillary and labial palpi paler brown; under surface of thorax yellowish (metasternum appears light brown); legs yellowish with dark brown tarsi; basal ventrites light brownish yellow, V3 and 4 with median brown area that occupies about half the area, V5 very dark brown with paler anterolateral corners; LO creamy white, posterior area of V7 yellowish, semitransparent (muscle impressions visible); tergites brown, terminal two tergites semitransparent, yellow, heavily sclerotised. Pronotum: 1.3–1.4 mm long; 2.4 mm wide; W/L 1.8; lateral margins divergent posteriorly with angled convergence on both sides in 2/3, and rounded convergence in 1/3; posterolateral corners approximately 90° and angulate, inclined obliquely to the median line; slight kink in lateral margins on both sides in 1/3 and on left side only in 2/3. Elytron: parallel-sided; 5.1–5.3 mm long; with 2 well–defined interstitial lines. Head: can be retracted partially within prothoracic cavity and may not be visible from above; GHW 1.5 mm; SIW 0.15 mm; SIW/GHW 0.1; ASD<ASW (sockets very close, not contiguous). Abdomen, ventrites (Fig. 308): LO in V7 reaches sides but not posterior margin and is shallowly bisinuate across its posterior margin; posterior area of V7 arched but not swollen; posterolateral areas of V7 rounded, corners not obvious. MPP as long as wide, dorsal surface lacking ridge; posterior margin squarely truncate. Tergites (Figs 312, 313): T8 longer than wide, lateral margins converge strongly posteriorly, much narrower across posterior margin, depending on orientation appears slightly medially emarginated; posterolateral corners rounded, projecting slightly; median longitudinal area flat with ridge like lateral margins, raised above slightly sloping sides; anterolateral prolongations elongate, narrow, expanded vertically and bases lacking projecting pieces. Aedeagal sheath: emargination of right side of sternite begins at point of attachment of tergal arms laterally. Aedeagus (Figs 291, 292, 300, 301): L/W>3/1; LL/ML moderate; LL not strongly divergent along their length dorsally, and a little shorter than ML at their apices; outer preapical area of LL produced angulate; inner apical area of LL prolonged, short, narrow; base of LL asymmetrically produced to left; ML lacking lateral teeth.

**Female, Larva.** Not associated.

**Etymology.** The specific name, the type locality, is considered as a noun in apposition.

### *Pygatyphella obsoleta* (Olivier, 1911)

(Figs 257, 258, 377–396)

*Atyphella obsoleta* Olivier, 1911:174. Ballantyne & Lambkin, 2000:15.

*Atyphella obsoleta* var. *immaculata* Olivier, 1911:174.

*Luciola (Luciola) obsoleta* (Olivier). McDermott, 1966:110. Haneda, 1966: Fig.3. Gressitt and Hornabrook, 1977: Fig. 15 (***Nec*** plate 6f)**.**

*Luciola (Pygatyphella) obsoleta* (Olivier). Ballantyne, 1968:110; 1987b: 175–180, 183–185. Lloyd, 1972:155; 1973b:268; 1977:164; 1978:241; 1979:25; 1979b:6; 1981:95.

**Holotype.** Male. **PAPUA NEW GUINEA**: labelled 1. (printed) ♂; 2. (printed) Nieuw Guinea expedition; hand written Dignel; 3. pink label handwritten in ink ‘obsoleta Ern Oliv.’ (MNHN).

**Diagnosis.** A small to moderate sized species (6–10 mm long) distinguished from other *Pygatyphella* by a series of features including the slight production of the middle of the posterior margin of the LO, the arched but not swollen posterior area of V7, the asymmetrical base of LL which is produced to the right, the apex of the MPP which in typical specimens is angulate and pointed, and the most prevalent dorsal colouration which has a wide triangular dark marking at the base of the elytra.

**Male**. Overview: Typical *obsoleta* (Figs 377–379) have extensive dark markings on pronotum, median dark spots on both MN and MS, and extensive dark triangular marks at elytral base with two or three small spots towards elytral apex; lateral margins of pronotum variously rounded or angulate, sometimes differing from left to right side in one individual, kinks either absent, or developed on one or both sides, in both rounded or angulate lateral margins; head (Figs 393, 394) can be retracted within prothoracic cavity thus often not visible from above; antennal sockets very close not contiguous; LO (Figs 387 –389) retracted to anterior portion of V7 with median posterior margin slightly produced; area posterior to LO arched not swollen; posterolateral corners of V7 angulate; T8 (Figs 390–392) with very long anterolateral prolongations expanding vertically; ventral surface of T8 (Figs 391, 392) with well–defined and well margined median longitudinal groove, posterior margin of which may appear ridge like in pinned specimens if MPP abuts against it; inner left side of anterior margin of median groove often appearing slightly elevated with respect to right side (appears thus viewed from side in pinned specimens only); MPP usually angulate-pointed; LL (Figs 395, 396) have rounded projection in their lateral preapical area, with inner apical area short; base of LL (dorsal aspect) asymmetrically produced to left.

Wide colour variations were noted (Ballantyne, 1968), and Lloyd (1972) surmised on the probable existence of more than one species. Ballantyne (1993) addressed the variability of morphology in differing populations and this is extended below.

*Group 1*, typical *obsoleta*. Conforms to description above except for slight variations listed below.

Collectors for Wau 1961–1965 JS, JHS and MS variously.

**PAPUA NEW GUINEA**: Wau Morobe Pr., 7.20S, 146.42E, 1.x.1961–15.xii.1961: male female (16–1700m), 3 males (1300m), 22 males 9 females (1200 m), female (1150m), 8 males, 3 females, (1050m), 1–4.x.1962, 3 males (1200m); 25.i.1963, male (1090m); 21.iv.1963, male (1200m) (BPBM); Hospital Creek, 10.v.1965, male (1250m)(BPBM); 1 mi N Wau 2800 feet, near Kunai Creek, Lae Road, 15.x.1969, J E Lloyd, 5 males, female (G260–263, G263 is tube of ethanol with 2 males 1 female (JEL); Bulolo River 850–900m, male (4.ii.1966), female 24.viii.1965, (BPBM).

Extensive colouration (as for Figs 377–379) on pronotum, basal area of elytron with wide triangular brown marking; pronotum angulate convergence both sides 7/41; rounded convergence 34/41; left margin only angulate 3/41, right margin only angulate 4/41; kink in lateral margin on both sides in 5/41; on left side only in 8/41, on right side only in 3/41; MPP pointed in 40/41 (Figs 387, 388), rounded in 1/41.

**PAPUA NEW GUINEA**: Morobe Pr., 7.18S, 146.64E, Bulolo, 6.xi.1969 JS, 1 male (700m); 18.v.1959, JS 1 male (700m); 21.viii.1956, E J Ford jnr, 1 female (1170m); Bulolo River, 8.v.1969, JS, 680m, 4 males 2 females, 2.ii.1969, JS male (BPBM).

Colouration as above (Fig. 377); pronotum angulate on one side only in 4/6; kink in lateral margin on both sides in 2/6, on left side only in 2/6, on right side only in 1/6, no kink either side in 1/6; MPP pointed.

**PAPUA NEW GUINEA**: Morobe Pr., 6.30S, 147.34E, Huon Peninsula, Pindiu, 3 males 20 –22.iv.1963 JS (one recorded at 750–850m) (BPBM).

Colouration as above (Fig. 379); pronotum not angulate on either side; no lateral kinks in 2/3, kink on R side only in 1/3. MPP pointed.

**PAPUA NEW GUINEA**: Morobe Pr., 6.43S, 146.59E, Lae: vii–viii.1944, F E Skinner, 7 males; 18–24.i.1962, JS 2 males (malaise trap); 10.xii.1964, M E Bacchus, 6 males (stn 116); 26.vii.1955, JLG, male (BPBM); Lae at Markham River Bridge, 14.x.1969, J E Lloyd 5 males 2 females (G233–34 females, 238–239 males, G240 3 males JEL); Botanic Gardens J B Buck, ‘7 PNG VI/1’ 7 males (ANIC).

Colouration (Figs 258, 380). Pronotum with dark median markings in 5 males, markings reduced to faintly defined areas in remainder; elytron with apical spots small or faintly defined; dark markings restricted to a narrow band along basal 1/3 of suture in most males; 1 male has the extensive elytral colour of the group above, 2 males have dark marking extending from the dark suture to interstitial line 1 or 2; pronotum either angulate on both sides, right or left side only or not angulate on either side; MPP pointed.

**PAPUA NEW GUINEA**: Morobe Pr., 7.52S, 147.13E, Garaina: 13–18.i.1968, JS 4 males 1 female (800m), 1 male (700–750m); 11–14.vii.1969 1 male 1 female JLG; 20.xi–17.xii.1969 W Hutton, 1 male; no date (900–1800m), 1 male 800m JS (BPBM).

Colouration (Fig. 381). Pronotum with faint traces of median brown markings; elytra with reduced markings along suture as for Lae group above; left side of pronotum angulate in 2/9, right side angulate in 8/9, not converging posteriorly in 1/9; kink present on left side in 4 (with rounded convergence), kink present on right side in 3 (with rounded convergence). MPP pointed in 5/9, rounded, broadly in 2/9, narrowly rounded in 1/9.

*Group 2. Madang–Sek Harbor group.* Has extensive colouration of Group 1 Wau group; MPP very slightly medially emarginated and the median posterior margin of T8 is narrowly rounded.

**PAPUA NEW GUINEA**: Madang Pr., 6.07S, 147.57E, Madang: 8.iv.1965 Y Haneda 6 males (ANIC); 29–30.v.1968, J Buck, 26 males (in two tubes of ethanol) (ANIC). Sek Harbor, 10 mi N. Madang, 1969, J.E. Lloyd, 3 males, 23.ix (G45–47); 5 males, 2–5.x (G115–118, 120 all Behavior Voucher specimens (BHVS); G116 has abdomen missing); male, 4 females, 3.x (G157, 155, 156, 152, 151 BHVS); female, 5.x (G149 BHVS); male, 12.x (G230); male, 22.x (G384); male, 29.x (G105, BHVS); male, 30.x (G106, BHVS). (JELC).

Colouration extensive, pronotum with wide median marking, elytron with triangular brown basal area like Group 1; pronotal margins rounded in all pinned specimens, angulate on left side only in 5/26 tubed specimens; kink in L only, R only and both sides of 3 pinned specimens; in tubed specimens kink on both sides in 3/26, on right side only in 4/26, no kink on either side in remainder of tubed specimens. MPP always slightly emarginated in pinned specimens; slightly emarginated in 7/26 tubed specimens and not emarginated in 11 (Not all have abdomens).

*Group 3, E Highlands group*.

**PAPUA NEW GUINEA**: Eastern Highlands Pr., 6.30S, 145.90E, Aiyura, 5400 ft, J H Barrett, 32 males 4 females (ANIC). 6.02S, 145.22E, 10.2 mi east Goroka, J E Lloyd, 2 males (G385, 387) (JELC).

Colouration (Fig. 383). With extensive dorsal dark markings as for Wau group, pronotal markings faint in 24/32 males while occupying the same area as those with dark marked pronotum; MS MN and markings at elytral base as for Wau group; pronotal lateral margins with angulate convergence on both sides in 5/32, angulate on L side only in 3/32, angulate on R side only in 6/32, remainder rounded; kink absent in 24/32, on R side only in 7/32, on L side only in 4/32 (kink coincides with rounded convergence on both sides in 2/32, kink on R side only coincides with angulate convergence in 3/32 and rounded in 3/32, and kink on L side only coincides with L side only angulate margin). V7 with posterolateral 'corners' rounded in 16/32, angulate in 6/32; length from posterior margin of LO to tip of MPP 2/3 total length of V7; posterior margin of MPP pointed (2/32), truncate (1/32), rounded in rest.

**Remarks.** Lloyd (1972:163) described the complex mating behaviour, which "suggests the possibility that *L. obsoleta* is actually a complex of cryptic species". These observations did not include a record of a synchronous display. He described the "sedentariness" of the males and the "intricate and expensive mating system" the significance of which "is that it reduces mating mistakes... since it maximizes opportunities for identification". None of Lloyd's (1972) observed mountings led to copulation; many coupled pairs (which apparently remained coupled throughout the next day) were subsequently found. Lloyd (1979a:330) gave details of 57 further "nuptial chases"; only 4 males mounted a female; none copulated. "My original interpretation of this elaborate pair-forming behavior was that a number of sympatric, sibling species, which morphological evidence suggests occur, make it necessary for reproductive isolation". Lloyd (1981:95) considered "in the seemingly variable emissions of males there is individuality that females remember and use to certify….. that the successful chaser is the one she has observed and evaluated".

Ballantyne (1993) investigated the potential variability in this species on a smaller number of specimens and localities than is done here, and suggested the same morphological groupings. Lloyd (pers. comm., 1989), after having seen Ballantyne's (1993) results, was not sure that a strong distinction could be made between these morphological groups.

Because of the variability in the female morphology encountered here, females are tentatively assigned and no further description presented. Ballantyne (1968:111) did not encounter the same variability and characterised females.

***Pygatyphella okapa*** **sp. n.**
(Figs 283, 285, 293–295, 302, 303, 309, 310, 314)

**Holotype.** Male. **PAPUA NEW GUINEA**: E Highlands Pr., 6.0 S, 147.0 E, Okapa, c 5000 ft, 20.xii.1964, R Hornabrook (BPBM).

**Paratypes** (4). Female labelled as for holotype (BPBM). Eastern Highlands Pr., 6.08S, 145.39E, 10.2 mi E Goroka, 22.x.1969, J Lloyd, males (G384, 385, 387) (JEL).

**Diagnosis.** One of the '*obsoleta* complex', distinguished by the trisinuate tip of the MPP, and the slightly projecting and angulate posterolateral corners of V7.

**Male.** 7.7–9.9 mm long; 2.8–3.6 mm wide; W/L 0.3–0.4. Colour (Figs 283, 285): Pronotum pale brown, either with well–defined dark posteromedian brown area (Goroka), or with posteromedian area very slightly darker than rest of pronotum (Okapa); pronotum appearing paler than elytra because of semitransparency and underlying pale fat body, MN pale brown with median brown areas attaining anterior margin, not reaching inner margin; MS light brown with wide median dark marking; elytra pale brown, semitransparent, with broad triangular basal marking and two small spots preapically; fat body irregularly distributed in small clumps; head very dark reddish brown, antennae and palpi slightly lighter; under surface of thorax brownish with metasternum and metepisternal plates very dark brown, metepipleural plates pale; legs largely brown (fore and middle coxae pale, hind coxae brown), with paler apices of femora and base of tibiae (giving appearance of pale 'knees'); apical 2/3 tibiae and tarsi very dark brown; ventrites 2–5 dark brown (basal ventrites irregularly lighter brown laterally; LO creamy white, posterior area of V7 yellowish, semitransparent (muscle impressions visible); tergites light brown, terminal two tergites semitransparent, yellow, heavily sclerotised. Pronotum (Fig. 285): 1.4–1.9 mm long; 2.7–3.2 mm wide; W/L 1.7–1.9; lateral margins divergent posteriorly with angled convergence on both sides in 2/3 (Okapa 1, Goroka 1), rounded convergence in 1/3 (Goroka); posterolateral corners narrowly angulate, inclined obliquely to median line; slight kink in lateral margins on both sides in 2/3 (Okapa 1, Goroka 1), absent from either side in one Goroka male. Elytron: parallel-sided; 6.3–8.0 mm long; with 2 well–defined interstitial lines. Head: can be partially retracted within prothoracic cavity but remains moderately exposed from above; GHW 1.5–2.0 mm; SIW 0.15–0.2 mm; SIW/GHW 0.1; ASD<ASW (sockets very close but not contiguous). Abdomen, ventrites (Figs 309, 310): LO in V7 reaching sides, not posterior margin and projecting posteriorly slightly in the middle of its posterior margin; posterior area of V7 arched not swollen; posterolateral areas of V7 narrowly rounded projecting slightly posteriorly (scored as PLP present). MPP as long as wide, dorsal surface lacking ridge; posterior margin trisinuate. Tergites (Figs 313, 314): T8 width subequal to length, lateral margins converge gently posteriorly; median trough present on ventral surface of T8, slightly asymmetrically margined, margin more strongly thickened in anterolateral left; anterolateral prolongations elongate, narrow, expanded vertically and lacking flanges. Aedeagal sheath: emargination of right side of sternite begins at point of attachment of tergal arms laterally. Aedeagus (Figs 293–295, 302, 303): L/W>3/1; LL/ML moderate; LL moderately divergent along their length dorsally, little shorter than ML at apices; outer preapical area of LL produced angulate; inner apical area of LL prolonged, elongate narrow; base of LL asymmetrically produced (to left); ML lacking lateral teeth.

**Female**. Associated by similarity of label data only. Coloured as for male with these exceptions: pronotum lacking defined brown markings (median area appears diffusely slightly darker); median dark marking on

MS narrow and extends to mid-point only; fat body in elytra not obvious; V6 with creamy white LO; V7, 8 pale yellow and semitransparent; posterior margin of V7 widely emarginated with small narrow emarginations just inside lateral margin on each side across posterior margin; posterior margin of V8 narrowly emarginated; lateral margins of T8 converge posteriorly, posterior margin straight.

**Larva.** Not associated.

**Etymology**. The specific name, the type locality, is considered as a noun in apposition.

**Remarks.** Interpretation of the posterolateral 'corners' of ventrite 7 as slightly and narrowly prolonged was made when the shape was retained after soaking the abdomen in water.

***Pygatyphella peculiaris* (Olivier, 1909)**
(Figs 259, 315, 316, 318, 321–326)

*Luciola peculiaris* Olivier, 1909a:317
*Atyphella peculiaris* (Olivier). Olivier, 1911:174; 1913:417.
*Luciola (Luciola) peculiaris* Olivier. McDermott, 1966:111. **Synonymy**. Lloyd, 1973b:992 (light production); 1977:178, 179 (light production).
*Luciola (Pygatyphella) peculiaris* Olivier. Ballantyne, 1968:112; Ballantyne,1987a:179.

**Holotype**. Male. **PAPUA NEW GUINEA** (MCSN).

**Material examined. PAPUA NEW GUINEA**: Morobe Pr., 3.46S, 143.52E, 4mi n Wau elev. c. 2800' nr Kunai Creek, Lae Rd. 1969, J.E. Lloyd, 5 males, 17.x, (G316, 319, 321, 324, 331); 2 males, 18.x (G351, 354); 2 males, 12.xi (G566 orange label, G565); 5 males, 13.xi (G583, 584, 587, 589, 596); male, 14.xi (G604); female, 16.x, (G616) (JELC). Northern Pr., 9.02S, 148.2E, Mt Lamington, NE Papua, 1300–1500 feet, C T McNamara, 13 males, 4 females (one male at light) (SAM). Northern Pr., 8.52S, 147.73E, Kokoda, Papua, 1200 feet, 14.vii.1933, at light, L. Cheeseman, 6 males, 4 females (NHML).

**Code name.** *Luciola* 5 (Lloyd 1973b)

**Diagnosis.** A moderate sized species (9.3–9.8 mm long) distinguished from all other *Pygatyphella* by the possession of paired dorsal protuberances of V7 in the male; similar to *Pygat. eliptaminensis* and distinguished by its smaller size, and colour of PN and elytra.

**Male**. Additional features. Aedeagal sheath (Figs 325, 326) with posterior half of sternite relatively narrow; tergite short with anterior margin darker than rest. T8 (Fig. 322) lacking median longitudinal groove.

**Remarks.** *Pygat. peculiaris* was sympatric at Kunai Creek with *Pygat. huonensis*. Lloyd (1973b) described the single flash pattern of the males, which flew singly, with a flash period of 0.5 sec, contrasting with a flash period of 1.5 sec for *huonensis*. The projections on the dorsal surface of V7 are apparently reflexed parts of the anterior margins of the dorsal cuticle, which 'faces' the MPP, and are visible in almost all the males examined. They may be a consequence of drying and appear to have no obvious function.

***Pygatyphella plagiata* (Blanchard, 1853)**
(Figs 397–404)

*Luciola plagiata* Blanchard, 1853:75, Fig. 15, plate v. Lacordaire, 1857:337. Olivier, 1902:85.
*Luciola caledonica* Bourgeois, 1884:285. Olivier, 1902:75. Heller, in Sarasin and Roux, 1916:243. Fauvel, 1904:139. New synonymy.
*Luciola (Luciola) caledonica* Bourgeois. McDermott, 1966:100. New synonymy.
*Luciola* (*Luciola*) *plagiata* Blanchard. McDermott, 1966: 111. New synonymy.

**Types.** *Luciola caledonica* Bourgeois. New Caledonia, Iles des Pins, not found MNHN 2002 by LB.

*Luciola plagiata* Blanchard. Solomon Islands (Ile St. George). Location of type unknown.

**Specimens examined.** Solomon Islands, 8.00 S, 159.10 E: Tatamba, 0 – 50m, 2 – 15.ix.1964, RS 3 males; Tirotongna on Freycinetia, JLG, 17.x.1981, 1 male; Pirega, 22.vi.1960, COB 1 male. Florida Group, Takopekope, 12.ix.1960, COB 2 males (BPBM).

**Diagnosis.** Moderate sized (6.0 – 7.4 mm long); pronotum red yellow with an anterior median dark mark; elytra black; venter of body yellow; median posterior projection of ventrite 7 with rounded apex; T8 with ventrally directed flanges on long and vertically expanded anterior prolongations; MPP with dorsal ridge; T8 with short posteromedian ridge; ML of aedeagus with lateral teeth; aedeagal sheath with basal 1/3 of posterior area subparallel-sided.

**Male**. 6.0–7.4 mm long; 2.6 – 3.3 mm wide; W/L 0.4. Colour (Figs 397, 398): PN orange, anteromedian 'hourglass' shaped dark mark almost reaching anterior but not posterior margin; MN light orange, MS light brown; elytra dark brown; head antennae and palpi dark; ventral surface of thorax and base of all legs dingy yellow, all tarsi dark brown, apical half all tibiae dark brown; all tergites pale yellow and semitransparent; ventral abdomen yellow except for brown posterior half V4, dark brown V5, pale LO in 6, 7. Pronotum (Fig. 397): 1.3 – 1.7 mm long; 2.1 – 2.7 mm wide; W/L 1.6; lateral margins with rounded convergence, lacking indentations; posterolateral corners broadly rounded, with irregularities. Elytron: 4.7 – 5.7 mm long; interstitial lines not as well–defined as sutural ridge except Takopekope male with 3 lines. Head: not able to be retracted completely into prothoracic cavity; GHW 1.5–1.8mm; SIW 0.15mm; SIW/GHW 0.1; ASD<ASW (sockets very close but not contiguous). Abdomen, ventrites (Figs 401–404): posterior margin of LO in V7 entire, not emarginated, LO not reaching sides or posterior margin, occupying half or less of V7. MPP about as long as wide, conspicuous, apex truncate or rounded; MPP with broad dorsal slightly off–centre ridge. Tergites: T8 (Fig. 404) wider than long (visible entire posterior portion), median posterior margin slightly produced, narrowly rounded; conforms most closely to pattern 3; ventral surface of posterior median area with short, slightly elevated straight ridge; anterolateral prolongations elongate, expanded in vertical plane, and with ventrally directed projecting pieces at their bases (Not visible in Fig. 404). Aedeagal sheath: sternite subparallel-sided for about 1/3 of its length from tergite articulation before emargination on left side. Aedeagus (Figs 399, 400): L/W<3; LL/ML moderate; LL divergent along length dorsally, slightly shorter than ML; apices of LL rounded, not out–turned width narrower than that of ML; base of LL produced and rounded; ML with paired wide rounded lateral teeth at level of ejaculatory orifice.

**Female, Larva.** Not associated.

**Remarks**. In the absence of types or reliably identified specimens it is reasonable to identify these specimens as *plagiata*. Two species of *Luciola* with dark marked pronota were recorded from the general study area, *caledonica* from New Caledonia and *plagiata* from the Solomons Ile St George (presumed to be St Jorge Island off the SW coast of Santa Isabel). Blanchard's (1853) specimens approach these specimens in size, colouration and their type locality. Bourgeois (1884) described a convex shape and size, which approaches species like *salomonis;* however his description of the colour and morphology of the abdomen strongly suggests a female, and on that basis the synonymy is suggested (females are often larger than the males).

Only two species from the Solomon Islands studied here have dark markings on the pronotum (the other *Pygat. limbatifusca* has two small dark spots on the pronotum, and pale margined elytra). Ballantyne and Buck (1979) suggested an overall similarity between *aphrogeneia*, *caledonica*, and *carolinae*, which are all distinguished here (*aphrogeneia* retained in *Atyphella* and *carolinae* assigned to *Magnalata*).

Two distinctively coloured species are recorded from New Caledonia, viz. *Bourgeoisia antipodum* (Bourgeois) which is entirely black dorsally, and *Luciola caledonica* (Bourgeois). Heller (1916) recorded *caledonica* from Ile Art, Ile Nou and Ile des Pins. He recorded only species from New Caledonia with no reference to sex of specimens. Fauvel (1904) recorded a description of luminosity on Ile d'Art on trees and bushes by 'Lucioles' (he considered it could have been *L. caledonica*, but it could just as easily have been *Bourgeoisia antipodum*). LB found no specimens of *caledonica* in the Bourgeois collection in Paris in 2002 and specimens from New Caledonia treated here as "New Caledonia 2" have strong eye emarginations in the male. Recent collections on New Caledonia by the QM team included only specimens which were entirely dark dorsally.

***Pygatyphella pulcherrima* (Ballantyne, 1968)**
(Fig. 260)

*Luciola (Pygatyphella) pulcherrima* Ballantyne, 1968, p. 114.

**Holotype.** Male. **PAPUA NEW GUINEA**: Southern Highlands Pr., 6.33S, 143.30E, Tage, Lake Kutubu (QM).

Diagnosis. This species was described for a single specimen, distinguished from all other *Pygatyphella* by its striking yellow dorsal colouration with black markings. The aedeagus is of the same pattern as seen in the '*obsoleta* complex'.

***Pygatyphella russellia* sp. n.**
(Figs 405–416)

**Holotype.** Male. **SOLOMON ISLANDS**: Central Pr., Russell Island: Pavuvul Is, Pepesala, 0–100 m, 19.vii.1964, RS (BPBM).

Paratype (1). **SOLOMON ISLANDS**: Central Pr., Russell Island, R Lever (NHML); carries identification label as possible new species (Fig. 411).

**Diagnosis.** The only species in the *Pygatyphella* Group B complex with pale dorsal colouration.

**Male.** 8.8–9.2 mm long; 3.8–4.0 mm wide; W/L 0.4. Colour (Figs 405–407): Pronotum very pale light brownish yellow, semitransparent with underlying fat body visible, 2 barely defined small median brown areas; elytra yellowish brown, semitransparent, basal 1/3 very slightly darker than rest; head, antennae and palpi very dark brown; venter of thorax pale yellowish brown except for brown tarsi; V1, 2 yellowish, V3 with small midlateral brown markings, V4 mostly dark brown with lateral areas narrowly pale; V5 very dark brown with 4 very small yellow spots along anterior margin; LO in V6, 7 creamy white, posterior area of V7 yellowish; basal tergites yellowish, T4–6 marked irregularly in light brown, extent of markings increases from 4–6; T7 and 8 orange yellow and semitransparent. Pronotum (Fig. 407): 2.0–2.2 mm long; 3.4–3.5 mm wide; W/L 1.6; lateral margins with rounded convergence in posterior areas; lacking indentation near posterolateral corners; with slight irregularities along posterolateral corners, corners rounded and projecting beyond median posterior margin. Elytron: parallel-sided; 7.0 mm long; interstitial lines not well–defined. Head: moderately exposed, not able to be completely retracted into prothoracic cavity; GHW 2.0–2.3 mm; SIW 0.2 mm; SIW/GHW 0.1; ASD<ASW, sockets very close not contiguous; frons not defined. Abdomen, ventrites (Figs 408–410): V6 very short (probably post–mortem effect as it seems to be retracted anteriorly beneath V5); LO in V7 occupying less than half V7, not reaching sides, posterior margin not emarginated; muscle impressions clearly visible through cuticle in posterior half which is arched not swollen; posterolateral corners of V7 angulate. MPP symmetrical, elongate, subparallel-sided, posterior margin very slightly obliquely truncate (scored as rounded), with broad dorsal ridge slightly to left of centre. Tergites: T8 (Fig. 410) as wide as long, with low rounded barely curved elevation in posterior area to one side of mid-line; lateral margins converge posteriorly and median posterior margin (from above) narrowly rounded; anterolateral prolongations of T8 elongate, narrow, anterior ends narrowly rounded, expanded vertically; ventrally directed pieces on prolongations of T8 appear to be present at base of prolongation. Aedeagal sheath (Figs 414, 415) subparallel-sided for half its length past articulation with sheath tergite, with right side emarginate; left lateral margin of anterior arms of

tergite slightly produced; anterior margin of tergite not emarginate. Aedeagus (Figs 412, 413, 416): L/W 2.25; LL/ML wide; LL diverge along most of length dorsally, are slightly shorter than ML, with apices rounded and subequal in width to ML; ML bearing narrow pointed lateral teeth, apex rounded truncate; base of LL not asymmetrically produced, slightly irregularly rounded.

**Female, Larva.** Unknown.

**Etymology.** The specific name is a noun in apposition formed from the type locality. Olivier recognised the distinctiveness of the NHML specimen (Fig. 411).

***Pygatyphella salomonis* Olivier, 1911**
(Figs 417–439)

*Atyphella salomonis* Olivier, 1911:172.
*Nec Atyphella salomonis* var. *limbatipennis* Pic, 1911:165.
*Nec Luciola (Luciola) salomonis* var. *limbatipennis* Pic. McDermott, 1966:112.

**Holotype.** Male. **SOLOMON ISLANDS**. (NHML).

**Other specimens examined. PAPUA NEW GUINEA**: Bougainville, 1931, J Waterhouse, 5 males, 2 females (BPBM); 5.91S, 154.98E, Togerao 15–21.iv.1968, Tawi, 5 males, 2 females (BPBM); 6.40S, 155.7E, Kokure, 9–16.vi.1958, EF, male 2 females (BPBM). **SOLOMON ISLANDS**: Western Pr., Choiseul 7.10S, 156.95E, Kitipi River, 80m, 14.iii. RS male (BPBM); Malangona 2.iii.1964 PS male (BPBM). 8.07S, 156.75E, Gizo 2–60m, 18.xi.1963 JG 2 males, female (BPBM); 0–140m xii.1980 NK female; Gizo Island 30m, MV light, 4.viii.1964, JS, male (BPBM); 1–100m, 11.vii.1959, JG, 2 males (one male at light); 0–100m, iii.1985, NK, female; 50–120m, 16–26.iv.1964 malaise trap, JS male (BPBM). Western Province, Vella Lavella 7.75S, 156.65E: Mt Arewana 100–400, 16.ix.1963, JG, male, female (BPBM); Gingola 10m, ix.1964, JG, PS, 2 males, 2 females (BPBM); Kow, 30m, 25–28.xi.1963, PS, 5 males, 2 females (BPBM); Kundurumbangara 60–80m, 15.xi.1963 JG, PS, 3 males, female (BPBM); Pusisoma, 14–29.xi.1963, PS, 16 males, female (BPBM); Ulo Crater, 10m, 7–17.xii.1963, JG, PS, 12 males, 7 females (3 males, 1 female in malaise trap) (BPBM). Isabel Pr., Santa Isabel: 8.00S, 159.10E, Buala, 18.viii.1964 RS, male light trap (BPBM); Molao 30.vi.1960 COB, male (BPBM). Guadalcanal Pr., Guadalcanal, 8.0S, 159E, Kolosulu, 20.v.1960 COB, 6 males 3 females (BPBM); 9.61S, 160.28E, Lame near Mt Tatuve, 300m, 18.v.1960, COB, 4 males 2 females (BPBM); 9.32S, 160.12E, 10mi nw Honiara, at Mavo bridge 25–26.xi.1969 J.E.Lloyd, 11 males (G649–652, 654, 55, 657–658,660–662, of which 660 and 662 have flashes recorded). (JELC); 13 kms SE Honiara 50–500m, 1.xi.1970, NK, male (BPBM); Betikama River, ix.1960, WB, male (BPBM); 9.53S, 160.36E Paripao, 21.v.1960, COB 4 males, female (BPBM); Sahuluatea 200–400m, i.1973 NK, 5 males (BPBM); Tambalia 30 – 35 km E Honiara, 22–25.v.1964 JS, RS, 3 males (one male sweeping) (BPBM). Malaita Pr., Malaita 9.00S, 161.00E: Auki, 2–20m, Calamus, 2.x.1957 JG, male; Dala 7–30.vi.1964, RS, JS 3 males, female (male in malaise trap) (BPBM). 9.08S, 160.25E, Nggela Is, Haleta 200–250m, 11.viii–10.x.1964, RS, 2 males, female (BPBM).

Code name. *Luciola* 1 (Lloyd, 1973b)

**Diagnosis.** Distinguished from other similarly coloured species by the retracted LO in V7, the arched posterior area of V7. Distinguished from *Pygat. limbatipennis* by the pale lateral elytral margins, and narrower and apically pointed teeth on the ML in the latter (see Tables 8, 9 for comparisons).

**Male.** The major island populations of this species are distinguished in Table 9. 6.5–11.2 mm long. Colour (Figs 417–420; Table 9): PN orange-yellow, semitransparent (irregular retraction of fat body material beneath cuticle leaves various patches which may appear pale brown); MN usually paler yellow than PN, often with aggregation of fat body beneath cuticle; MS orange, retraction of material beneath cuticle may appear slightly darker colour depending on direction of illumination (especially in Gizo males); elytra very dark brown–black; epipleuron of Bougainville males brownish–orange often with narrow aggregation of fat body; under microscope illumination from above lateral margins of elytra appear slightly semitransparent but are not paler; head antennae and palpi very dark brown; most of ventral surface yellow (semitransparent in area of metasternum and also basal abdomen), legs yellow with brown tibiae and tarsi of legs 1 only, and brown tarsi only of legs 2, 3, or all legs coloured as for legs 1; V2 and 3 yellow; V3 narrowly (some Vella Lavella) or widely (Malaita) dark brown; V4 dark brown, yellow margined laterally, sometimes with median pale yellow area, except in Gizo males where all of V4 is dark brown,; V5 entirely dark brown; V6, 7 creamy yellow in area of LO, posterior area of V7 yellowish, semitransparent and well sclerotised; basal abdominal tergites brown, T 7, 8 uniformly dingy yellow, semitransparent. Pronotum: Bougainville 2.0–2.4 mm long; 3.0–3.9 mm wide; W/L 1.5–1.6. Vella Lavella 1.5–2.0 mm long; 2.7–3.3 mm wide; W/L 1.6–1.8. Gizo 1.6–2.1 mm long; 2.8–3.4 mm wide; W/L 1.6–1.7. Guadalcanal 1.4–1.7 mm long; 2.4–3.0 mm wide; W/L 1.7. Elytron: Bougainville 7.2–8.8 mm long; Vella Lavella 5.5–6.5 mm long; Gizo 6.0–6.5 mm long; Guadalcanal 5.0–6.3 mm long; convex-sided, with 3 barely elevated interstitial lines. Head: can be partially retracted within prothoracic cavity thus often not visible from above; Bougainville: 1.9–2.5 mm; SIW 0.15–0.2 mm; SIW/GHW 0.1; Vella Lavella GHW 1.8–2.0 mm; SIW 0.15–0.2 mm; SIW/GHW 0.1; Gizo 1.8–2.0 mm; SIW 0.2mm; SIW/GHW 0.1; Guadalcanal 1.5–1.9 mm; SIW 0.15–0.2 mm; SIW/GHW 0.1; antennal sockets very close not contiguous; ASD <ASW. Abdomen, ventrites (Figs 421–427): LO occupying all of V6; LO in V7 occupying less than half area of V7, not reaching sides, posterior margin not emarginated; muscle impressions clearly visible through cuticle in posterior half which is arched not swollen; posterolateral corners of V7 angulate. MPP (Figs 422–428) symmetrical or not, elongate, lateral margins converge slightly posteriorly, posterior margin rounded, squarely or obliquely truncate, or medianly emarginate (see Table 9); with a dorsal ridge developed to the left of centre. Tergites (Figs 421, 422–427, 436–440): T8 conforms to patterns 1–4 (Table, 9) and occasionally as wide as long, with a curved elevation in posterior area to one side of mid-line; lateral margins converge posteriorly and median posterior margin (from above) elongate and narrowly to moderately broadly rounded, except very short in Malaita males; anterolateral prolongations of T8 elongate, narrow (from below), and expanded vertically; ventrally directed pieces on prolongations of T8 present arising from ventral surface of prolongations. Aedeagal sheath like that of *Pygat limbatipennis*. Sternite subparallel-sided for 1/3–½ of its length past articulation with sheath tergite, with right side emarginate; left lateral margin of anterior arms of tergite slightly produced; anterior margin of tergite not emarginate. Aedeagus (Figs 428–435): L/W<3; LL/ML wide; LL diverging along most of length dorsally, slightly shorter than ML, LL apices rounded and subequal in width to ML; ML bearing broad rounded lateral teeth, apex of ML rounded truncate; base of LL not asymmetrically produced, slightly irregularly rounded.

**Female.** 4.7 (Kukugai)–7.5 (Bougainville) mm long. Coloured as for male with these exceptions: basal abdominal ventrites yellow, V5 dark brown, LO creamy yellow in V6; V7, 8 orange yellow, semitransparent and well sclerotised. Pronotum of similar outline to that of male. Head of winged female form. Posterior margin of V7 shallowly emarginated with posterolateral corners widely rounded; median posterior margins of V8 not emarginated; lateral margins of V8 converge evenly posteriorly, posterior margin truncate.

**Remarks.** Olivier (1911) described the uniformly black elytra and obsolete interstitial lines of *Atyphella salomonis*. Pic's (1911) variety *limbatipennis* differed only in the yellow elytral margin.

A description of the light production of this species follows the description of *M. limbata*. Assignment of any specimens other than those with associated flashing data is tentative only. Island populations differ from each other and within the differing localities on each island, especially in the shape of the MPP and the length of the median posterior area of T8 (see Tables 8, 9). This species was taken with *Pygat. limbatipennis* at six locations on Guadalcanal, and two on Choiseul. Interpretation of colour patterns in some specimens assigned here to *Pygat. limbatipennis* (q.v.) has been difficult as microscopic illumination confused the issue and it is possible that subsequent studies may find intergrades between the two species.

***Pygatyphella tagensis* (Ballantyne, 1968)**
(Figs 261, 262, 445, 446, 449)

*Luciola (Pygatyphella) tagensis* Ballantyne, 1968:117.

**Holotype.** Male. **PAPUA NEW GUINEA**, Southern Highlands Pr., 6.33S, 143.30E, Tage, Lake Kutubu, 2700 feet, 15.x.1960, flying after dark, J. H. Barrett (QM).

**Diagnosis.** Most similar to *Pygat. undulata*, with which it shares a bluntly rounded V7 with a broad short MPP; MPP not enveloped by the apex of T8 which is not down turned; distinguished by its smaller size (8–10 mm vs 13–14 mm), and variable brown markings on the pronotum (*undulata* has an unmarked pale pronotum).

***Pygatyphella tomba* sp. n.**
(Figs 456–466)

**Holotype.** Male. **PAPUA NEW GUINEA**: Western Highlands Pr., 5.49S, 144.1E Tomba, slopes of Mt Hagen, 2450m, 23–25.v.1963, JS (BPBM).

Paratypes (10). Same data as for holotype, 9 males. **PAPUA NEW GUINEA**: Southern Highlands Pr., 6.4S, 143.4E, Dimifa, SE Mt Giluwe, 2200m, 11.x.1958, JLG, male (BPBM).

**Diagnosis.** Elytra pale brown, semitransparent, with wide inner margin along suture darker brown; interstitial lines not well developed; MPP symmetrical, quite broad, with apex rounded or slightly pointed; posterolateral pronotal corners rounded; outer and inner preapical areas of LL not produced.

**Male.** 8.6–9.8 mm long; 3.2–4.0 mm wide; W/L 0.4. Colour (Figs 456–461): Pronotum (Fig. 462) pale yellowish brown, very semitransparent in lateral areas, with median area widely marked in dark brown (extending almost to posterior margin and narrowly retracted from anterior margin), with irregular darker brown areas in 6/11; lateral margins of median dark area converging slightly posteriorly and edged with thin line of fat body corresponding to the area on the hypomeron where the lateral flattened area slopes vertically; MN whitish yellow (underlying fat body contributes to apparent colour), with sparse and very pale brown median areas in 6/11, brown area expanding almost to posterior margin and slightly darker brown in 4/11; MS light brown with narrow to wide median dark marking; elytra pale brown, very semitransparent especially at edges where colour not confused by underlying hind wing and body outline, with an extensive (semitransparent) darker brown area extending from and adjacent to MS laterally to humerus and anteriorly to elytral base, and posteriorly along suture almost to apex (Figs 458–461); apical area extending across to outer margin near apex in 4/11 (Fig. 459), or separated from an outer brown area in 7/11 (Fig 461); basal brown area restricted to basal half of elytra in 1/11 (Fig 460) with brown apical area continuous obliquely from suture to lateral margin; head very dark reddish brown, antennae and palpi slightly lighter; under surface of thorax light brown; metasternum darker brown, metapleural plates yellow (underlying dried muscles may show through cuticle and appear darker brown); legs with bases light brown, all tibiae and tarsi dark brown; basal ventrites very dark brown, LO in V6, V7 creamy white, remainder of V7 yellowish, whitish yellow if an underlying cluster of fat body; basal tergites dark brown, T7, 8 and 9 light brown semitransparent. Pronotum (Fig. 462): 1.6–1.7 mm long; 2.8–3.0 mm wide; W/L 1.7; lateral margins strongly divergent posteriorly with angled convergence on both sides in 3/11, one side angled one side rounded in 1/11, and rounded convergence in remainder; indentation of lateral margin apparent on left side only of 1/11 (scored as absent); posterolateral corners approximately 90° and angulate, inclined obliquely to median line; anterior area of hypomeron flattened and curved, not differentiated from widely flattened posterior area. Elytron: parallel-sided; 7.2–8.2 mm long; no interstitial lines well–defined. Head: can be retracted partially within prothoracic cavity; GHW 1.6–1.7 mm; SIW

0.25 mm; SIW/GHW 0.15; ASD<ASW (sockets close not contiguous). Abdomen, ventrites (Figs 463, 464): LO in V7 not reaching sides or posterior margin, entire across posterior margin; posterior area of V7 is scored as (very gently) arched but does not have obvious underlying muscle impressions (fat body covers much of the posterior area of V7); posterolateral areas of V7 rounded or pointed (pointed MPP and rounded T8 in 6/11; pointed MPP and angulate posterior margin of T8 in 2/11, rounded MPP and rounded margin of T8 in 3/11). Tergites: T8 longer than wide, lateral margins rounded or converging slightly posteriorly, and posterior margin rounded in 9/11, with angulate posterolateral 'corners' and a short, pointed median posterior margin in 2/11; ventral surface with a shallow median longitudinal trough which is finely margined; anterolateral prolongations shorter than posterior (entire) area T8, narrow, not obviously expanded, lacking ventrally directed pieces. Aedeagal sheath: emargination of right side of sternite begins at point of attachment of tergal arms laterally. Aedeagus (Figs 465, 466): L/W>3/1; LL/ML moderate; LL divergent along their length dorsally, a little shorter than ML, LL apices subequal in width to ML; outer preapical area of LL not produced, inner apical area of LL not prolonged; base of LL asymmetrically produced (to left); ML lacking lateral teeth. MPP as long as wide, dorsal surface lacking ridge.

**Female, Larva.** Not associated.

**Etymology.** The specific name, the type locality, is considered as a noun in apposition.

***Pygatyphella uberia*** **sp. n.**
(Figs 467–478)

**Holotype.** Male. **PAPUA NEW GUINEA**: Morobe Pr., 3.46S, 143.52E, Wau, elevation ca 2800feet, X–XI.1968, J E Lloyd (G593 ANIC).

**Paratypes** (20). **PAPUA NEW GUINEA:** Morobe Pr., 3.46S, 143.52E, Wau, same data as holotype, 3 males (G595ANIC; G320, 323 JELC); 1050m, 4–11.xi.1961, JS, 3 males, female (BPBM). Chimbu Pr., Uberie, 26.ix.1966, R Carver, R Mackay, 6 males (ANIC). Hudewa, L Wagner, 6 males 2 females (SAMA).

**Code name**. *Luciola* 12 (Lloyd, 1973b)

**Diagnosis**. The only species of *Pygatyphella* with bipartite LO in V7.

**Male.** 7.8–7.9 mm long; 3.0 mm wide; W/L 0.4. Colour (Figs 467–469): Pronotum pale yellowish, semitransparent, with paired median darker markings appearing heart shaped; clumps of fat body clearly visible through cuticle confusing colour; MN yellowish, pale brown markings covering most of inner area of each plate adjacent to MS and fat body evident especially around margins; MS light brown, quite transparent, devoid of fat body; elytra pale light brown, semitransparent, fat body in interstitial lines and around most punctures, lateral margin irregularly dark brown and some fainter traces of brown spots over inner paler area in Hudewa and Uberie males, lateral margin pale in three Wau males with faint traces of apical brown areas; head, antennae, palpi dark brown; most of ventral surface of thorax yellowish (except for brown metasternum) and all tarsi brown; basal abdominal ventrites very pale yellowish with fat body clearly visible beneath transparent cuticle; LO creamy yellow, posterior area of V7 behind LO yellowish; . Pronotum: 1.3–1.4 mm long, 2.5 mm wide; W/L 1.9; lateral margins straight, divergent slightly posteriorly, lacking small indentation before rounded/ angulate posterolateral corners, which are < 90° and inclining obliquely to median line; width across posterior margin of pronotum subequal to, or slightly wider than (Hudewa males) that across elytral humeri. Elytron: 6.3–6.5 mm long; parallel-sided; inner two interstitial lines well–defined. Head: barely retracted within prothoracic cavity at rest and visible from above; GHW 2.0 mm; SIW 0.15 mm; SIW/GHW 0.1; ASD much less than ASW; antennal sockets very close not contiguous. Abdomen, ventrites (Figs 468, 470, 471): LO entire in V6, bipartite in 7 reaching sides not posterior margin, occupies > ½ area of V7, with LO halves closely approaching in median line. Ventrite 7 with rounded emarginations (Figs 470, 471) to either side of MPP base; MPP longer than wide, lateral margins converging slightly posteriorly, posterior margin rounded; lacking dorsal ridge. Tergites (Figs 472, 473): T8 visible posterior portion about as wide as long;

posterolateral areas of T8 angulate, posterior margin between these 'corners' produced, lateral margins converging with posterior margin broadly truncate or rounded; anterolateral prolongations very elongate, narrow, expanded vertically, lacking projections at their bases; ventral surface of T8 (Figs 472, 473) lacking posteromedian ridge; with projections in anterolateral left (small flange), posterolateral left (1–3 lines, strongly curved in Hudewa male, 1–3 lines in Uberie males, 1 line in Uberie and Sisiak male), anterolateral right (scarcely developed in Sisiak and Hudewa male), 1–2 oblique in posterolateral right. Aedeagal sheath (Figs 478–480): emargination on right side begins at tergite articulations; further narrow emargination on right side just before apex. Aedeagus (Figs 474, 475): L/W 4; LL/ML moderate; LL narrow, divergent along length dorsally, considerably shorter than ML; LL very narrow at apices; ML asymmetrical curving to left in horizontal plane.

**Female**. Associated by similarity of label data and dorsal colour pattern to that of Hudewa and Uberie males. 7.5–7.7 mm long. Coloured as for male with these exceptions: Wau female has pale coloured elytra with very faint traces of the lateral dark markings seen in the other females; LO creamy yellow in V6; V7, 8 orange yellow, semitransparent and well sclerotised. Pronotum of similar outline to that of male, median anterior margin not produced. Head of winged female form. Posterior margin of V7 widely emarginated with posterolateral corners rounded; median posterior margins of V8 and T8 narrowly emarginated; lateral margins of V8 converge evenly posteriorly, posterior margin rounded.

**Remarks.** The differences in colour of the elytral margins between the Wau males and the Hudewa and Uberie populations may not be significant as the single Wau female has the lateral elytral margins with paler outlines of the more pronounced colour in the coloured males. Lloyd (1973b:995) characterised the twinkling pattern of light production, a "rapid twinkle-like burst of 2 [or more, up to 7, Lloyd pers. comm.] short modulations of increasing intensity". The dappled dorsal colouration may well resemble bird droppings or light dappling and function as protection in the day time. Only Lloyd's specimens are characterised by patterns of light production.

### ***Pygatyphella undulata*** **(Pic, 1929)**
(Figs 263, 441–444, 447, 448, 450–455)

*Atyphella undulata* Pic, 1929:12.
*Luciola (Luciola) undulata* (Pic). McDermott, 1966:114.
*Luciola (Pygatyphella) undulata* (Pic). Ballantyne, 1968:115.

**Holotype.** Female. **PAPUA NEW GUINEA:** in collection of Dr W. Wittmer, Switzerland.

**Other material examined.** All specimens in BPBM unless indicated otherwise. **IRIAN JAYA**: 4.10S, 138.95E, Nabire: 5–50m, 25.viii–2.ix.1962, 2 males, J. S.; S. Geelvink Bay 13 males, female (10–15m, 1–5.ix.1962, J. S., 3 males; 10–30 m, 1–4.ix.1962, male; 5–50m, 25.viii–2.ix.1962, 7 males, J. S.; 10–40 m, 5.x.1962, jungle, light trap, male, H. Holtman; 7.x.1962, female, jungle, N. Wilson. Cyclops Mts: 2.34S, 140.31E, Ifar, 450–500m, 8.ix.1962, male; 300–500m, 26.vi.a1962, male, J. S.; Sabron, 930 feet, vi.1936, 1 male, L. Cheesman (NHML)

**Diagnosis.** A large (13–14 mm long) species with uniformly bright yellow pronotum and dingy yellow elytra with very dark brown apical and basal markings; V7 large, swollen and apically truncate, apex largely enveloped by the down turned apex of T8; most similar to *Pygat. tagensis*, in which T8 apex does not engulf the apex of V7, distinguished by its larger size and the uniform colour of the pronotum.

**Female.** 14.5 mm long. Coloured as for male except pronotum is paler yellow, the creamy white LO restricted to V6 and V7, 8 and T7, 8 are orange yellow, and more heavily sclerotised than preceding segments. Ballantyne (1968:116) characterised the holotype female.

**Remarks.** Ballantyne (1968) felt the distinctive colouration allowed reliable association of sexes, and assigned 11 males.

***Pygatyphella wisselmerenia*** **sp. n.**
(Figs 479–487)

**Holotype.** Male. **IRIAN JAYA**: 3.55S, 136.21E Moanemani, Kamo Valley, 1500m, 15.viii.1962, JS (BPBM).

Paratypes (22). Same data as holotype, 14 males, 2 females. **IRIAN JAYA**: 3.55S, 136.21E Wisselmeren: Itouda, Kamo valley, 1500–1700 m, 18.viii.1962, JS, male; 13.viii.1955, JLG, male. Enarotadi, 1500m, 14.viii.1962, JS, 3 males. Urapura–Itouda, Kamo Valley, 12.viii.1955, JLG, male (BPBM).

**Diagnosis.** Similar to the '*obsoleta*' complex in its dorsal colouration, distinguished from all other *Pygatyphella* by the extensive LO in V7 which reaches to sides and almost to the posterior margin, and the lack of any arching of the area posterior to the LO.

**Male**. 8.2–10.2 mm long; 3.4–4.0 mm wide; W/L 0.4. Colour (Fig. 479, 480): Pronotum pale yellowish, posteromedian area with subtriangular brown area (extending to posterior margin) in one Itouda male, entirely pale in one Itouda male, and with median brown area restricted and somewhat irregular in remainder; semitransparent, underlying pale fat body makes pronotum appear slightly paler than elytra, MN pale with faint traces of median brown areas not reaching inner and anterior margins in 4/11 (Moanami); MN entirely pale (Itouda male); MN with median brown areas dark brown in 5/11 (Itouda and Moanami); MS light brown with narrow median dark marking in all but 2 Itouda males where median marking is 1/2 width of MS and ¾ its length; elytra pale brown, semitransparent, with fat body fairly regularly distributed in small clumps; subtriangular basal dark area is darker along extreme base of suture, not approaching outer margins of MS, reaching to anterior margin of elytron, not covering outer anterior edge of humerus, and is paler brown in outer half; head very dark reddish brown, antennae and palpi slightly lighter, under surface of thorax light brown except for very dark brown metasternum and apparently pale metepipleural plates (underlying fat body confuses interpretation); legs pale with dark brown tibiae and tarsi; basal ventrites very dark brown; LO creamy white, occupying almost all of V7 with narrow posterior margin semitransparent (muscle impressions not visible here); basal tergites light brown with paired darker spots in lateral areas, T7 pale brown semitransparent, T8 yellowish semitransparent. Pronotum: 1.7–2.0 mm long; 3.0–3.5 mm wide; W/L 1.7; lateral margins divergent posteriorly with rounded convergence on both sides in all but one male where R side is angulate; posterolateral corners approximately 90° and angulate, inclined obliquely to median line; slight kink in lateral margins on both sides. Elytron: parallel-sided; 6.5–8.2 mm long; with 2 well–defined interstitial lines. Head: can be retracted partially within prothoracic cavity, usually visible from above; GHW 1.8–2.1 mm; SIW 0.25 mm; SIW/GHW 0.1; ASD<ASW (sockets very close not contiguous). Abdomen, ventrites (Fig. 487): LO in V7 reaching to sides and almost posterior margin, not emarginated across posterior margin; posterior area of V7 very narrow, not arched or swollen; posterolateral areas of V7 rounded, corners not obvious. MPP short, dorsal surface lacking ridge; posterior margin rounded. Tergites: T8 longer than wide, not strongly sclerotised, posterior margin rounded; ventral surface lacking median longitudinal groove; anterolateral prolongations elongate (shorter than posterior entire portion), narrow, not obviously expanded vertically and lacking projections from their bases. Aedeagal sheath (Figs 483, 484): emargination of right side of sternite begins at point of attachment of tergal arms laterally; anterior margin of tergite darker than rest, all of tergite component quite short. Aedeagus (Figs 485, 486): L/W>3/1; LL/ML moderate; LL divergent along length dorsally, a little shorter than ML at apices; outer preapical area of LL slightly produced and rounded; inner apical area of LL prolonged, short and narrow; preapical inner margin of LL with very small tooth; base of LL not asymmetrically produced; ML lacking lateral teeth.

**Female**. 9.5–10.0 mm long. Coloured (Fig 481, 482) as for male with these exceptions: pronotum pale with no dark markings in one, with very faint brown markings in second female; MS with short narrow median dark line half as long as MS and not extending to posterior margin; elytra almost entirely pale in one, second female with irregular and very pale markings at elytral base along inner two interstitial lines and a single brown preapical spot near elytra apex; second female has extensive basal colour of male but considerably paler brown; V7,8 light brown semitransparent; V7 with posterior median emargination and posterolateral corners broadly rounded; posterior margin of V8 with narrow medial emargination; lateral margins of T8 converge posteriorly with a small emargination in each side just before the straight posterior margin.

**Larva.** Not associated.

**Etymology**. The specific name, the type locality, is considered as a noun in apposition. This species exhibits the characteristic dorsal colouration of the '*obsoleta* complex' and the distinctive aedeagal modifications but ventrite 7 is neither arched nor swollen and the LO occupies most of this ventrite.

## Species Incertae

### *Luciola (Luciola) antica* (Boisduval, 1835)

*Lampyris antica* Boisduval, 1835:128.
*Luciola antica* (Boisduval). Olivier, 1902: 99.
*Luciola (Luciola) antica* (Boisduval). McDermott, 1966:99.

**Type.** "South Seas" location of type unknown.

**Remarks.** Boisduval described a specimen, which he did not sex, with a yellow pronotum having an anterior dark spot, the underside 'lutea' and the abdomen black ringed.

### *Luciola marginipennis* (Boisduval, 1835)

*Lampyris marginipennis* Boisduval, 1835:126
*Luciola Marginipennis* Laporte, 1833:151. Nomen nudum.
*Colophotia marginipennis* Dejean, 1837:103. Nomen nudum**.** Germar, 1848:184. (Incorrect record from Adelaide).
*Luciola marginipennis* Guérin-Méneville. Motschulsky, 1854: 53. Lacordaire, 1857:338. Olivier, 1902: 83. Lea, 1909: 46, 106. McDermott, 1966: 109. *Luciola marginipennis* Boisduval. Olivier, 1913: 417. Incorrect attribution of author to Guérin-Méneville.

**Type.** Ile Waigiou (may be Waigeo off NW tip of Irian Jaya 130E, 0S). Location of holotype unknown.

**Remarks.** Ballantyne believes Olivier (1913) incorrectly synonymised *L. limbata* and *L. rubiginosa* with *L. marginipennis*. Both Blanchard's (1853) *Luciola limbata* and *Luciola rubiginosa* Olivier (1883) from the Solomons were described with the MS black, consistent with the specimens described here as *M. limbata*, while Guérin-Méneville's (1838) *L. marginipennis* was described with a red MS.

This species is not reliably identified in collections due in part to confusion over the actual publication date of Guérin-Méneville's (1838), and also the lack of type material. Cowan (1970) and Bocák (1998) resolved the issue of the publication date and their opinions are followed here.

Guérin-Méneville (1838) has been considered the author of *marginipennis* in all references to the species since Motschulsky (1854). Although Boisduval (1835) attributed *Lampyris marginipennis* to Guérin-Méneville, Boisduval's description of the species is the first published use of the name to be associated with a description, although it is impossible to determine the sex. His specimens were taken in 'Ile Waigiou', which is probably Waigeo (130E, 0S) off the NW tip of Irian Jaya. Guérin-Méneville's (1838) work has consistently been quoted in the literature as 1830 and both Laporte (1833) and Boisduval (1835) had apparently seen Guérin-Méneville's work long before it was published (Ballantyne, 1988). Guérin-Méneville's description of the antepenultimate abdominal segment yellow and the penultimate emarginated indicates he based *Lampyris marginipennis* on a female. However the specimen was 7 mm long and taken in Papua at 'Offak' (Lea 1909 thought this could have been Mt Arfak). While this study has not revealed any species with orange pronotum, dark brown elytra with lateral pale margins from the island of New Guinea, several *Luciola* and *Pteroptyx* species with colouration of orange pronotum and dark elytra are known (these also conform to the smaller size described) (Ballantyne 1987a; work in progress). Dejean's (1837) record is a catalogue name only, and Germar's (1848) record of the species from Adelaide is erroneous. [No species of firefly have been recorded in Australia south of Sydney (Ballantyne & Lambkin 2000)].

## Incorrect record of genus from New Guinea

### *Pygoluciola* Wittmer, 1939

*Pygoluciola* Wittmer, 1939:21. Ballantyne & Lambkin, 2006: 21. Ballantyne 2008:1. Fu & Ballantyne (2008):1.
*Luciola* subgenus *Pygoluciola* (Wittmer). McDermott, 1966: 115; Ballantyne, 1968: 119; Ballantyne & McLean, 1970: 233; Ballantyne & Lambkin, 2000: 82; 2001: 361; 2006: 21.

**Type species**. *Pygoluciola stylifer* Wittmer, 1939, by monotypy (RMNH).

Specimens of *Luciola obsoleta* Olivier were incorrectly identified by Haneda (1966) as *Pygoluciola* sp. (Ballantyne 1987b). This genus has not been recorded from New Guinea; Ballantyne (1968) described a single unusual New Guinean female, which she tentatively assigned to *Pygoluciola*. This female is assigned here to *Missimia* **gen. n.**

*Pygoluciola* was described for a single species, *stylifer,* possessing unusual modifications to abdominal ventrite 7 and T8 (Wittmer, 1939). McDermott (1966) regarded *Pygoluciola* as a subgenus of *Luciola*. Ballantyne (1968) redescribed the subgenus, keyed and described four species (two of them new), and assigned *Luciola hamulata* Olivier to *Pygoluciola*. Ballantyne and McLean (1970) figured aspects of the morphology. Ballantyne (1987b) described certain presumed sexual characters of certain species of *Pygoluciola* (eg curved legs, and terminal abdomen structure) and suggested uses in a reproductive context. Ballantyne and Lambkin (2001) described a new species and (2006) reassigned *Pygoluciola* to generic status based on representatives from Borneo only. Ballantyne (2008) described a new species from the Philippines, and Fu and Ballantyne (2008) a new species from mainland China, and an extended generic description.

## Discussion

Overview

Problems with homology and assignment of polarity to characters are explored. These include the nature of the labrum and interpretation of the bipartite light organ. The identification of flightless females as wingless either by neoteny or somatic mutation is challenged. Abdominal segmentation, use of the terms ventrite and sternite, and the numbering of actual versus apparent sternites are overviewed. Difficulties in character interpretation in soft bodied insects, relating to their method of preservation, are expanded from a previous treatment (Ballantyne, 2008). Additional problems of interpretation encountered here have solutions suggested. Functional morphology is explored with respect to the terminal abdomen modifications. Colour patterns especially patterns of crypsis are discussed.

Taxonomic outcomes

In this taxonomic review of the Luciolinae concentrating on the *Atyphella* ‘complex,’four new genera are established and the existing genus (*Atyphella*) redefined. Eight Luciolinae genera are discussed and two subgenera of *Luciola* are assigned to generic status (Tables 4, 5). Species unassigned in previous analyses (‘Sisiak’ and ‘Missim’) are assigned (‘Sisiak’ to *Pygatyphella*, and ‘Missim’ to a new genus *Missimia*).

In previous analyses (Ballantyne & Lambkin 2000, 2001, 2006) a narrower focus precluded addressing the wider Luciolinae complex. In this study the status of several genera not within the *Atyphella* ‘complex’ is elucidated while the direction of future studies is clarified especially for *Luciola*.

Species of *Luciola* sensu latu fall into five clades (Table 4, Figs 1–3). Species of New Guinean and Australian *Luciola*, unresolved in this analysis, are the basis of ongoing research (Ballantyne & Lambkin in prep.), together with the Luciolinae fauna of New Caledonia and the genus *Bourgeoisia*. Along with species of *Pteroptyx* already addressed (Ballantyne, 1987a) this will complete the taxonomic work arising from the Alpha Helix expedition of 1970.

Two distinct groups within the genus *Pteroptyx* are confirmed. A new genus appears necessary for the bent winged fireflies of New Guinea and northern Australia (Ballantyne & Lambkin in prep). *Pyrophanes* is defined for the four species included in McDermott (1966), while *Colophotia* includes the type and two other species, all of which have many morphological features in common (median carina on ventrite 7, bipartite light organ, very elongate aedeagal sheath, aedeagus with very short lateral lobes, and very long and horizontally expanded posterolateral prolongations of T8).

Directions in *Luciola*

This analysis indicates directions for future subdivisions within *Luciola* s. str. However the extent of the species complex (Fig. 2 node 46) that includes the type species of *Luciola* s. str. will only be resolved when it is possible to determine the variability within European populations of *italica* (the type species). In this study several populations of New Caledonian fireflies, which fit an existing definition of *Bourgeoisia*, are distinguished by the extent of the eye emargination. The treatment of *Lampyroidea* in this study was hampered, as only one specimen of the type species, *syriaca*, was available.

These subdivisions of species presently described as *Luciola* can be distinguished:

1. *Luciola* clade (node 46 Fig. 2) includes the type species *L. italica*, species of *Bourgeoisia* and one species of *Lampyroidea*; *L. kagiana* Matsumura, *L. curtithorax* Pic may belong here. Male: aedeagal sheath appears symmetrical; apices of LL visible from beneath, as wide as at base and separate along most of dorsal length, inner ventral margins bear elongate symmetrical apically acute lobes (some aedeagal pattern assessment based on Jeng *et al*. 2003b; Jeng unpublished observations). *L. italica*: pronotal width less than humeral width. Female: *kagiana* and *curtithorax* macropterous and can fly (Jeng pers. comm.).
2. *L. anceyi* Olivier, *L. cerata* Olivier, *L. terminalis* Olivier, *L. chinensis* (L.) and *L. praeusta* Kiesenwetter are not accommodated in any *Luciola* clade nor the key to genera here. Male: aedeagal sheath symmetrical, apices of LL visible from beneath, narrower than at their base; LL fused dorsally; cylindrical hairy apically rounded lobes originate behind the inner (ventral) margins of the LL. Humerus not visible from below and pronotum narrower than humeral width. Female: macropterous. Larva: *L. anceyi* have lateral spiny and hairy projections (Chen, 2003 page 173, 176); *L.cerata*, *L. terminalis* and *L. praeusta* larvae appear similar to those of *P. qingyu* (Fu & Ballantyne, 2008; Chen, 2003 page 166, 174, 176). Jeng *et al*. (2003b) considered *L. terminalis* and *L. praeusta* both belong to a *Luciola chinensis* 'complex' (all of which have yellow dorsal colouration with elytral apices black).
3. *Luciola leii* Fu *et* Ballantyne, *Luciola ficta* Olivier (node 2 Fig. 2) key close to *Atyphella* (but not to *Luciola* s. str.). Male: aedeagal sheath asymmetrical; sheath sternite strongly bent to right; LL visible from beneath, lacking any lobes along their inner ventral margins, apices narrower than at their bases, hooked, widely splayed and separate along most of dorsal length. Humerus narrowly visible and pronotal width less than that across elytral humeri. Female: macropterous. Larva: aquatic with gills (Fu & Ballantyne 2006:345).
4. *L. cruciata Motsch. L. owadai* Sâto et Kimura (node 1 Fig. 2), and possibly *L. hydrophila* Jeng *et al*. Suzuki (1997) indicated a close relationship between *L. cruciata*, *L. owadai* and *L. lateralis* Motsch. while Branham and Wenzel (2001, 2003) did not. Male: aedeagal sheath asymmetrical in posterior half of sheath sternite; being emarginate on right side, LL lack inner lobes, are widely expanded at apices in horizontal plane; elytral epipleuron not well developed at base, not covering humerus from below; pronotal width

subequal to or less than humeral width (in these latter respects this group differs markedly from *Atyphella* Olliff). Female: macropterous. Larva: aquatic with gills, similar to 3 above.

5. *Luciola substriata* Gorham (node 4 Fig. 2), also *L. cingulata* Olivier, *L. seriata* Olivier, *L. brahmina* Bourgeois, *L. aquatilis* Thancharoen. Male: aedeagal sheath may be asymmetrical along posterior margin of sternite, subparallel-sided for most of posterior half; LL apices visible from beneath, wide, well–separated dorsally; LL lack lobes on their inner margins; humerus not visible ventrally and pronotal width less than that across elytral humeri. All species have serial punctures on the elytra, the light organ in V7 slightly emarginate in median anterior margin, and (Ballantyne obs.) sclerites that occur in the intersegmental membrane and surround the aedeagal sheath (Jeng *et al.*, 2003a, Fig. 14). Known females macropterous. Larva: *L. substriata* metapneustic in later stages.
6. Certain Australian and New Guinean species of *Luciola* (nodes 31, 34, 36 Fig. 2), distinguished in the key to genera, show a close relationship with New Guinean *Pteroptyx*, and will be investigated further. *L. trilucida* Jeng *et al*. may belong here.

Comparison with other analyses

Ballantyne and Lambkin's (2000, 2001, 2006) analyses of the Luciolinae established a monophyletic group. Monophyly of a more restricted sample of the Luciolinae, based on eight species, six of which we include here, was established in Branham and Wenzel (2001, 2003). Based on 10 species within the Japanese fauna, Suzuki (1997), using molecular studies, distinguished a Luciolinae clade, which included *Pristolycus sagulatus* Gorham. His results, like ours, distinguished *Hotaria* and *Curtos*. Bocáková *et al.* (2007) in their molecular studies arrived at a similar definition of the Lampyridae that included a Luciolinae clade of two Luciolinae species and a *Bourgeoisia*, with *Curtos* appearing as a sister clade to the Luciolinae. Ballantyne examined Bocáková's *Bourgeoisia* specimens and determined they are not species of *Bourgeoisia*, but was unable to determine the actual species identity. Bocáková *et al.* (2007) established a connection between the soft bodied condition and neoteny within the Lampyridae, but not within the Luciolinae. Bocáková's work, which omitted *Atyphella* spp., did not include any examples of wingless or flightless females, and is otherwise similar to our results with the omission of *Atyphella*.

Problems with homology and polarity

We believe using representatives of all genera and subgenera listed by McDermott (1966) in phylogenetic analyses, allows quantitative determination of placement of taxa. The *Atyphella* complex is quantitatively compared to our existing definition of the Luciolinae and all genera and subgenera within it. Jeng (pers. comm.) considers our choice of the highly specialised *Photuris trivittata* Lloyd *et* Ballantyne as an out-group may interfere with the assignment of polarity of many characters. Our aim here was not to challenge any definition of other subdivisions, but as the Luciolinae appears to be a monophyletic group, our single out-group is clearly distinct. However, the interpretation of polarity of certain characters still raised difficulties. These include interpretation of neoteny in flightless females, nature of the labrum, abdominal segmentation and reduction of the light organ, which are explored below.

Interpretation of female aptery

Flightless females, regardless of length of elytra (full, brachelytral) are characterised by a hind wing length below some unknown threshold value. We score any reduction in length of fore or hind wings as a secondary loss, by out-group comparison (as in Ballantyne & Lambkin 2000, 2001, 2006).

Various authors have used the terms larviform, brachelytral or brachypterous in reference to lampyrid females inconsistently. While Branham and Wenzel (2003:7) consider that 'adult female Lampyridae can possess anything from only a few to an entire suite of larval characters', they also noted that various brachypterous, apterous, or physogastric females have been identified as 'larviform' while not actually displaying larval characters. Branham (pers. comm. and verbatim quote) indicated that in his view, certain specific morphological characters that are found in all firefly larvae can be carried over to the imaginal state. These characters apparently first arose in larvae and appear in adults (in various combinations) only due to arrested development (i.e. larval characteristics that are retained in the adult), and include a tarsungulus instead of paired claws, stemmata rather than compound eyes, and larval antennae (rather than an adult antenna with greater than 7 antennomeres) (end verbatim quote). Cicero (pers. comm.) defines characters as ‘more larval’ or ‘more imaginal’ in terms of where they appear in the holometabolous life cycle (see below). Branham (pers. comm.) defines ‘larval’ characters in terms of structure, function and similarity of position. In particular it appears that either wingless or brachelytral females, which often have large pale fleshy abdomens when gravid, were interpreted originally as 'larviform'. McDermott (1964) keyed two tribes within the Lampyrinae using 'females larviform' without defining the term. Elsewhere he listed 15 genera with larviform females, and referred to *Atyphella scintillans* Olliff (p. 44), which has both shortened fore and hind wings, as both larviform and brachelytral. This interpretation is expanded in both Cicero (1988) and Bocáková *et al.* (2007) who describe any females with fore wing loss as neotenic.

From the huge complex of lampyrid species with females that do not have the textbook characters of the males, Cicero (1988) (verbatim quote) attempted to simplify the problem by segregating into groups those with character dimorphisms that maintain ontogenetic register across the range of the specimens he used (end of verbatim quote). He attributed any wing loss within this range of specimens as neoteny, and listed a series of neotenic females spanning the gradient from brachelytral forms with slightly differentiated thoracic nota, to wingless forms with thoracic and abdominal terga which are serially undifferentiated. Of his series, levels 1–3 have short wings in combination with correspondingly immature pterothoracic sclerite development, which in Cicero’s view indicated that the whole body is operated on, not just the wings. According to Cicero, if the female of one species has wings that are a quarter the length of the male's, while another has wings that are half the length of the male's, then both bodies were arrested during the active elaboration of that character. Other characters undergoing active elaboration at this time in ontogeny will also appear ‘more larval’ in the first and ‘more imaginal’ in the second too. Characters that have finished elaboration before this point appear equally elaborated in both. However, Branham (pers. comm.) indicated that Cicero does not consider character change in terms of a phylogenetic analysis (the phylogeny dictating the order of character state changes). Cicero’s register, and the evoked conclusion that the entire body is being endocrinologically operated on, is currently unrefuted (Cicero, pers. comm.).

Reduction in wing length of either fore or hind wings in *Atyphella* females is interpreted here as a secondary (partial) reduction in wing length (none is apterous). Cicero (pers. comm.) considers hind-wing-less luciolines to be outside the sphere he postulated, on advice from Ballantyne that they do not have other characters that are clearly in the same cross section of the developmental continuum that he examined. *Atyphella atra* has apparently fully developed fore wings and no hind wings. *Atyphella flammans* females have elytra that cover the abdomen, and shortened hind wings. The mesoscutellum and mesonotal plates appear to correspond in degree of development with the male (examination by Ballantyne), the head is of the wingless female (adult) form, and the elytral epipleuron is continuous as a ridge around the elytral apex as in the male (indicating no apparent reduction in fore wing development). The brachelytral species *A. scintillans*, however, may be found to belong within this sphere, if an ontophylogenetic character analysis is eventually performed (Cicero pers. comm.).

Branham (pers. comm. and verbatim quote) considers both brachyptery and aptery to be both derived and convergent within Lampyridae. Both are scattered throughout the family as well as within various genera (end of verbatim quote). Branham feels that the only way ‘aptery’ in *Atyphella* could be considered ancestral is if it appears in the most ancestral *Atyphella* species. In such a case it would be an ancestral condition only within the scope of that genus but still a derived condition within the family (Branham pers. comm.; Branham & Wenzel 2003).

Bocáková *et al.* (2007) follow Cicero's interpretation and their Figure 2 (Page 479) contains four examples of flightless females (two with shortened elytra), which appear to approach the situation we see here in *Atyphella*. Bocàkovà *et al.* interpreted neotenic females from literature examples, did not examine any *Atyphella* species and thus did not interpret the Luciolinae as exhibiting neoteny (Bocáková pers comm.).

The interpretation of the length of elytra in females is difficult. Some females may appear to have full length elytra but still have shortened hind wings (ranging from just shorter than the elytra to about half the length). Character 270 state 0 incorporates both fully developed and slightly shortened elytra. There are not many females in collections, and pinned females often have dehydrated and shrunken abdomens. They may be physogastric but the interpretation is clearly subjective as it depends on whether the abdominal apex is visible beyond the elytral apices.

It may, however, be possible to deduce a capacity to fly where the elytra, and possibly the hind wings, are only a little shortened. Character 113 distinguishes the difference between heads of winged and wingless females, and the particular situations in winged females of *Missimia* and *Photinus* where the antennal sockets are on an anterior prolongation of the head. Lateral margins of this prolongation are subparallel-sided in *Missimia* and *Photinus* females (which are flighted), and the margins converge anteriorly on the head in wingless or flightless females. Fourteen firefly species have females with elytra scored here as fully or partially developed, but hind wings reduced or absent. Of the five species with apparently well developed fore wings covering the abdomen, three (*A. palauensis, A olivieri*, and *A. flammans*) have slightly shortened hind wings, while *A lychnus* and *A. atra* have hind wings vestigial or absent. In *L. italica* the fore wings are slightly shortened, while two species are more obviously physogastric (*Luciola parvula*, and *Bourgeoisia hypocrita*, where at least four abdominal segments are visible). *A. similis, A. scintillans, A. inconspicua, A. conspicua, A. lewisi* and *Lamp. syriaca* are brachelytral, all either lacking, or with vestigial, hind wings and clearly incapable of flight. Of these 14 species only two do not have the wingless female type of head as described above and in character 276, state 2. *A. olivieri* and *L italica* have slightly shortened hind wings and may be able to undertake some mode of flight even if only for short distances.

Bocàkovà *et al.* (2007) considered that female aptery could affect fecundity with 'trade offs between production of a flight apparatus and egg production'. The issue is probably more complicated than this. Cicero (pers. comm.) considers there are no studies that watch the female emerge from pupation to see if the abdomen is already distended because of supernumeration, or if it is of normal girth and stretches to the greatly enlarged shape as eggs mature. The latter may be possible because the adult post teneral cuticle is untanned and very flexible. Does the female come out of pupation fully laden with eggs that are later fertilized, and thus is the large abdomen a consequence of gravidity? Two females of *Atyphella flammans* (QM) (Figs 130, 131), which were accidentally bred from larvae, were pinned soon after emergence and have a wide but flat abdomen, and while eggs are not visible under the cuticle, fat body is. The large larvae were kept in a moist container after collection but not fed, and the subsequent emergence of the females was unexpected (G. Monteith pers. comm.). The nature of the abdomen may not reflect the usual condition on emergence.

Hayashi and Suzuki (2003) found that where species did not produce prespermatophores the females had marked degeneration of all wings (and usually very large bodies), suggesting that these females had a larger nutrient reserve than the males and did not receive much nutrient from spermatophores.

The issue of appropriate interpretation of flightless females in the genus *Atyphella* is presently unresolved. Cicero, together with Ballantyne, is investigating it further.

*Labrum.* McDermott (1964:11) distinguished the Photurinae and the Lampyrinae by the nature of the clypeus and labrum. Lawrence’s interpretations differ. McDermott designated the membranous area visible in front of the labrum as the labrum itself (it is the epipharynx). Lawrence (pers. comm. and based on two specimens sent by Ballantyne) interprets the anterior strongly sclerotised plate on the head of *Photuris trivittata* as the labrum, the extent of the clypeus is reduced, “it seems as if there is a clypeolabral suture, at least slightly impressed, which is curved and lines the base of the labrum entirely. The frontoclypeal suture is an internal ridge, which coincides with the clypeolabral suture mesally, but not laterally" (Lawrence verbatim quote). The anterior membranous area is the epipharynx and not the membranous labrum. The Luciolinae examined for this analysis have no frontoclypeal suture or ridge, no external clypeus, a well–defined labrum, and the anterior membranous projection is the epipharynx (wider interpretation by Ballantyne).

*Abdominal segmentation and terminology.* Determination of the ancestral state with respect to abdominal segmentation is a work in progress. We are indebted to John Lawrence and Ming-Luen Jeng for their input into this discussion. Elateroidea for the most part have a concealed sternite 2 which Lawrence considers ancestral for the Elateroidea. Consequently where sternite 2 is exposed in the Elateroidea, it is derived. Elateroidea also have a hidden 8$^{th}$ sternite (the 8$^{th}$ segment is withdrawn within the abdomen), except in the Cantharoidea, which have an 8-sternite abdomen, with the second sternite visible and the 8$^{th}$ exposed. In the Luciolinae sternite 2 is visible, the light organ occupies sternites 6 and 7, tergite 8 is visible, but sternite 8 is membranous and withdrawn within the abdomen (apparently a uniquely Luciolinae feature). Lawrence asks if the Luciolinae situation is derived from a well developed sternite 8, but was it originally visible or concealed? Jeng questions whether the presence of sternite 2 is derived in the Luciolinae. He thinks that the expression of the responsible gene has been turned on and off at various times but the gene has not been lost. We score our out-group (8 sternite abdomen) as ancestral and the reduction to the 6-sternite abdomen (actual sternites 2–7) in the Luciolinae as derived. This is a feature of all Luciolinae thus far examined. This method of determination concurs with our intention to compare the Luciolinae species of the *Atyphella* complex with other genera and species of the Luciolinae, thus using many out-groups.

Branham and Archangelsky (2000) preferred use of the term ventrite to refer to the ventral plate of the abdominal segments. They considered the median area was the sternite, with the lateral area comprising part of the pleurite which is dorsally reflexed and may contain the spiracles. Branham and Archangelsky also numbered the ventrites according to their visible, not actual number. Thus ventrite 1 (the first visible abdominal sternite in the Luciolinae) is the ventral plate of the actual second abdominal segment.

Lawrence (pers. comm.) revaluated the terminology at Ballantyne's request and uses the term ventrite equivalent to visible sternite, but does not consider lateral sclerites to be pleurites. In Ballantyne and Menayah (2002), larval plates are interpreted according to Lawrence. The lateral spiracle bearing plates in the thorax are laterotergites (the true pleural elements being two small sclerites attached to the coxa), and in the abdomen the pleural region is the membranous connection between the spiracle bearing laterotergites and the sternites. In most Lampyridae adults the spiracles have moved onto the sternites, which in the Luciolinae are reflexed dorsally.

Here we continue to use the term ventrite and refer to visible abdominal sternites as V2, 3 etc using actual segment numbers. Interpretation of abdominal segmentation has been in the past inconsistent but most recent firefly publications now address the numbering of segmentation (if not the actual name) in a consistent way. While the Luciolinae have lost both sternites 1 and 8, there is no loss of tergites. Numbering the sternites/ventrites to refer to actual segments (which can be confirmed by reference to the tergites and their spiracles, there being no reduction at the anterior end of the abdomen in tergite number) is in wide use (McDermott & Buck, 1959; Green, 1956; Ballantyne, 2001, 2008; Ballantyne & Lambkin 2001, 2006; Ballantyne & Menayah, 2002; Lloyd & Ballantyne 2003; Fu & Ballantyne, 2006, 2008, Thancharoen *et al.* 2007). Thus in any one segment tergite and ventrite/sternite correspond in numbering.

*Light organs.* Determination of ancestral and derived states of light organ morphology is difficult. Ballantyne's (1987b) functional interpretations for many of the terminal abdomen modifications in males (which included reduction in area of the light organ) related to the need for areas of muscle attachment, given that sternite 8 is internal and membranous in the Luciolinae, and this interpretation is followed here. Light organs are for the most part entire and occupy most of ventrite 6 and ventrite 7 in both out-group and most of the Luciolinae. Ballantyne and Lambkin (2000, 2001, 2006) and herein interpret any reduction in light organ area, whether reduction in size of the entire organ, or the bipartite condition, as derived (e.g. characters 103, 104, 111, 113,114) and score the full light organ as ancestral. Because reduction in light organ area occurs in both the Photurinae and many Luciolinae, Jeng (pers. comm.) questions which state of lantern morphology is ancestral and which derived. As the bipartite light organ exists in more than one form, our rationale for its scoring is addressed. Three types of bipartite light organ development occur:

1. Many *Pteroptyx*, all *Pyrophanes* and some *Colophotia* spp: The median area of ventrite 7 has muscle attachments that diminish the light organ area. In *Pteroptyx valida* Olivier the arching of the abdomen is dependant on longitudinal muscles which insert in this area, pull on the median posterior projection of ventrite 7 and contribute to the copulation clamp (Wing *et al.* 1983; Ballantyne 1987a, b). *Pt. tener* Olivier (which has a bipartite light organ) was shown by Case (1984) to bend its abdomen into the face of the female and thus blind her to the advances of other males. In many *Pteroptyx* posterior emargination of certain more basal abdominal ventrites occurs with the bipartite light organ. These emarginations represent positions of attachment of longitudinal muscles in more anterior segments (Ballantyne 1987b).

2. In *A. ellioti* and *A. kirakira* two separate distinct patches of light organ are closely adpressed to the lateral areas of ventrite 7 while the intervening area is filled with fat body. Lack of information on light production makes interpretation of the extent of the functional area difficult, and this is reflected in how this organ is scored. The attachment of the light organ may merely be a post–mortem artefact.

3. In *A. scabra* the light organ patches in both ventrites 6 and 7 are small and clearly separated, with no intervening fat body, and in *B. hypocrita* this pattern occurs only in ventrite 6, there being no apparent light organ in 7. Here the light organs may be undergoing reduction rather than having their area diminished because of the development of muscle attachments.

Problems with interpretation of characters in soft bodied insects

Ballantyne (2008) highlighted problems that can occur with interpretation of characters and states in soft bodied material which is usually subject to distortion. More solutions to these problems are developed here and explained in the elaboration to the list of characters. In some cases the problem is further exacerbated by the numbers of specimens available, as a single uniquely representative holotype does not present the same problems in interpretation as a range of specimens. Characters previously thought not to be variable have been found to be so. The type of *Atyphella messoria* has faintly defined interstitial lines while a second specimen standing alongside the type, from the same locality, has well–defined lines, and the species is thus scored polymorphic for this character. Polymorphic states in our analysis are almost always a consequence of this variability. These include some pronotal characters, as dehydration may cause the pronotal edges to droop. Dehydration does not however, fully explain the variability of the pronotal margins seen in many species of *Pygatyphella*, especially *Pygat. obsoleta*. The outline of tergite 8 in males of *Pygat. limbatipennis* and *salomonis* is more difficult to interpret in dried pinned specimens and while use of this character is made in the descriptions the feature was not used in the analysis (see Tables 8, 9).

An additional and unexpected problem occurred with interpretation of whether margins of elytra in certain *Pygat. limbatipennis* and *salomonis* are pale. Correct interpretation was exacerbated by the microscopic illumination, which can make the lateral margins appear paler, and a small group of specimens in both species are tentative associations only and not included in the analysis.

The inappropriate use of the character of head coverage by the pronotum within the Luciolinae was expanded in Ballantyne (2008) and it appears that the character is of limited use, if any, in the Luciolinae. Here a combined use is made of visibility of the resting head from above, with an indication that if the maximum head width is narrower than the width across the edges of the prothoracic cavity the head can be partially retracted. However there are still situations where the male head can be partially retracted within the prothoracic cavity and yet is large enough to be visible from above, often because the anterior margin of the pronotum is not expanded.

Arching of the strongly sclerotised posterior area of abdominal ventrite 7 in species of *Pygatyphella* is related, at least in part, to the presence of muscles which meet in the median line posterior to the transverse light organ, or also within the posterior medial emargination of the light organ. They contract in a fan like shape to a narrow area where they attach to the underside of the edges of tergite 7. Both ventrite 7 and tergites 7 and 8 are heavily sclerotised in such species and do not lose their shape when pinned and dry. Where abdomens are scored here as 'arched and swollen' the strongly developed area is not further enhanced by muscle contraction and maintains its shape when dry.

In species where the light organ area in ventrite 7 is reduced it may be difficult to determine whether the posterior area of ventrite 7 is arched. In *Pygoluciola*, *Luciola nigra* Olivier and *L. flavicollis* Macleay the light organ in ventrite 7 is retracted from the sides and the posterior margin, and there may be a small area posterior to the light organ and in front of the median posterior projection. This area has not been observed to contain muscle attachments as in *Pygatyphella* species. The main dorso-ventral muscle attachment in *Pygoluciola* species (Ballantyne & Lambkin 2001, 2006) is from the dorsal surface of the anterolateral areas of ventrite 7 to the under surface of the lateral areas of tergite 7, where corresponding depressions in the cuticle may be evident from above. In certain *Pygoluciola* this muscle arrangement allows ventrite 7 and tergite 8 to 'splay' open at their posterior ends (Ballantyne & Lambkin 2006 Fig. 26), unlike most *Pygatyphella* spp. where muscle contraction causes the tips of ventrite 7 and tergite 8 to be closely adpressed. Dorso-ventral muscle attachment in *L nigra* and *L. flavicollis* has not been closely investigated but muscle impressions are not visible in the posterior area of ventrite 7.

*Problems of 'wet' preservation*. Preservation of specimens in ethanol preserves flexibility and permits ease of dissection, but may destroy colour and can make interpretation of certain features difficult (see review in Ballantyne, 2008). In particular interpreting the nature of the ventral surface of tergite 8 (particularly the presence of a longitudinal median groove, or posterior median curved ridge) is more difficult when the specimen is 'wet' preserved, or when it has been soaked to soften it prior to dissection. The posterior median curved ridge on tergite 8 may not be visible and its elevation may be diminished, but the character itself is not merely an artefact of drying. The close proximity of the tergite 8 ridge and a slightly off–centre dorsal ridge on the median posterior projection of ventrite 7 suggest that there is some relationship between the two.

## Functional morphology

### Terminal abdomen morphology and function

Luciolinae males possess an array of terminal abdomen modifications that have led to speculation about their function (Ballantyne 1987a). However only one modification has been explained – the copulation clamp (Wing *et al*., 1983). Known only in *Pteroptyx valida* Olivier, it involves longitudinal abdominal muscles that attach between light organ halves, contracting against the median posterior projection (MPP) of ventrite 7 and flexing it dorsally against a deflexed elytral apex. The female abdomen is wedged between both these structures during copulation.

In other genera where there is erosion of the light organ area of ventrite 7, coupled with development of the MPP, the problem is to explain the function. Ballantyne (1987b) related function partly to the need for the abdomen to flex and the musculature involved. All fireflies are probably able to flex their abdomens to some extent (even to introduce the aedeagus requires some flexion). Flexion is primarily a result of longitudinal muscles, and the end point of the muscle attachment will be in ventrite 7. Are the terminal modifications of ventrite 7 reflecting merely a need to stabilise this segment? The strength of the long muscle pull must finally be against a fairly inflexible structure like the MPP (Ballantyne, 1987b). Ballantyne suggested that many of the modifications could be seen as mechanical only, contributing extra surface area for muscle attachment in an abdomen where sternite 8 is missing, and area for muscle attachment diminished. Thus modifications like those seen in the terminal abdomen of *Pygatyphella* spp. may not be directly related to the copulatory process itself. Reduction in light organ area (including the emargination of the posterior area) provides a surface for longitudinal and dorso-ventral muscle attachment, and the development of the MPP in such cases could be a strengthening rod against which these muscles pull. Such muscle pull causes the tip of the MPP to be strongly pressed against the preapical area of tergite 8, either engaging in a median longitudinal groove on its ventral surface (in many of the '*Pygatyphella* A' complex), or with a median ridge on the dorsal surface of the MPP engaging against a ridge on the ventral surface of tergite 8 (in the '*Pygatyphella* B' complex).

In dried pinned males the close approximation of the strongly bent tergite 8 and ventrite 7 may not necessarily mirror the situation with live specimens. Ballantyne and Lambkin (2006) described a male of *Pygoluciola wittmeri* (Ballantyne) with terminalia widely splayed open after killing by immersion in ethanol. Dorso-ventral muscle attachments between ventrite 7 and tergite 7 arise at the anterolateral areas of ventrite 7 where the light organ is absent, and attach to the lateral areas of the ventral surface of tergite 7. The attachment areas are visible externally from above at the sides of tergite 7 as strong depressions in the cuticle, and visible from below through the cuticle of ventrite 7.

What then of species such as the Australian *Atyphella* where the light organ in ventrite 7 occupies most of the area and the MPP is a short, rounded, and weakly chitinised structure? Some Australian *Atyphella* are associated with flightless females so perhaps the energetics of mating is not required here.

There is currently little information about production of spermatophores and internal female structures, like bursa plates, which might aid interpretations. Do bursa plates hold a spermatophore in place and prevent its dislodgement? Are bursa plates always associated with species that produce spermatophores? South *et al.* (2008) recent investigations may indicate that bursa plates are responsible for holding the spermatophore in place near the spermatheca rather than preventing its dislodgement, and that the length of coupled time may relate to the need for full extrusion of the spermatophore so that it reaches well into the bursa.

*Colour patterns*. Within *Pygatyphella* the most common colour pattern resembles bird droppings and probably conceals the resting firefly from detection. This pattern could also confuse the body outline to a predator. Observation under microscope illumination of this particular pattern enhances the distribution of the fat body, the semitransparency of the elytra and the outline of the body beneath, but whether this is a pattern visible to predators is difficult to assess. Does the existence in collections of large numbers of specimens with this pattern attest to its success?

Patterns of mimicry almost always involve orange pronota and very dark elytra, which may be pale margined (sometimes around all margins). While there are few examples on the island of New Guinea within species treated here of the orange pronotum and black elytral pattern (*Lloydiella* spp. and *A. guerini* being the exceptions), many of the *Luciola* and almost all of the *Pteroptyx* species have this pattern (Ballantyne 1987a; 1993). Most *Pygatyphella*, *Convexa* and *Magnalata* species of the Solomon Islands have one of two colour patterns–orange pronotum and black elytra in *Pygat. salomonis*, or dark elytra with paler margins in *Convexa wolfi,* several *Pygatyphella* and *M. limbata*. Again microscopic examination clouds the issue – the ventral surface of the epipleuron in some *Pygat. salomonis* specimens may be paler than the dorsal surface and the lateral margin thus appears slightly paler to the microscopist, but how does it appear to a predator?

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## Appendix 1. List of characters and states

Characters and states are numbered to reflect their number in Ballantyne and Lambkin (2006) e.g. 11(8)=character 11 here was character 8 there. To accommodate the much greater range of variability encountered in this work, new characters are necessary, and modifications are made to many others (218 extra characters occur here). The listing below indicates the extent of these changes e.g. Pronotum (10, 30) indicates that in this category Ballantyne and Lambkin (2006) had 10 pronotal characters and that is expanded to 30 here. New and modified characters are as follows:

Male characters: Pronotum: (10, 30) new 1–5, 9–13, 15–16, 19, 21, 24–25, 28–30; modified 6–8, 14, 17–18, 20, 22–23, 26–27. Elytron: (8, 20) new 32–35, 37, 40–42, 45–49; modified 31, 36. Head antennae and mouthparts: (23, 35) new 62, 65, 70, 74–75, 82; modified 52, 54, 56–57, 60–61, 63–64, 66, 68–69, 71–73, 77. Legs (8, 11) new 88, 91, 92. Abdomen–ventrites: (21, 56) new 98–105,107–108, 110, 112–113, 117, 121–122, 124, 125, 127, 129, 131–136, 138–139, 141, 143, 152; modified 109, 114–116, 118–120, 126, 128, 130, 145–148. Abdomen–tergites: (6, 34) new 153, 155–161, 163–165, 168–169, 171–174, 176, 179–185; modified 154, 177, 178. Aedeagal sheath: (8, 25) new 187, 189–191, 193–200, 202–204, 206, 208–211; modified 188, 201, 205, 207. Aedeagus (12, 50) new 215–220, 222, 224–225, 227–228, 230, 233, 235–238, 241, 243, 245–261; modified 226.

Female characters: (11, 29) new 262–268, 277–280, 286–290; modified 269, 271–271, 275–276, 282–283.

Larval characters: (8, 31) new 292, 295–297, 300–305, 307, 310–321. Colour patterns (6, 22) new 323, 325–335, modified 322, 324, 329–333, 341, 343.

Morphological terminology in Ballantyne and Lambkin (2000), and characters in Ballantyne and Lambkin (2006) are considerably expanded to accommodate the variability encountered in this study. Most are explained beneath their listing. Other important issues are more fully elaborated here:

1. Effect of dehydration: The dehydration of soft bodied specimens affects interpretation of certain characters; these may be scored either as ? or as polymorphic and this problem is covered in the Discussion (see also 13 below).This is further complicated by the small range of specimens in certain species.
2. Measurements referred to as 'moderately' or 'slightly' in taxonomic descriptions are given numerical values here.
3. Male head: eye emargination is reinterpreted (Fig. 59). A strong eye emargination is visible when the head is in resting condition; *Luciola* (*Lampyroidea*) *syriaca* is scored 0 for this character here.
4. Male head: antennal socket measurements. Distance between antennal sockets (ASD), and width of an antennal socket (ASW) are now measured along the same horizontal line (ASW is not now necessarily a representation of actual maximum width of socket as previously). This line may differ from the line along which smallest interocular width, SIW, is measured, as if eyes are very close SIW may be taken on a line above that for ASW and ASD. The proximity of antennal sockets (ASD) now distinguishes between contiguous sockets and those having some separation between the inner socket margins.
5. Labrum reinterpretation (Figs 27, 28, 30, 31, 559, 560): John Lawrence re-examined the nature of the labrum in male female and female specimens of *Colophotia praeusta* Eschscholtz, *Luciola* near *aquatilis* Thancharoen, *Photuris trivittata* Lloyd & Ballantyne, a male of *Atyphella similis* Ballantyne, and a female of *Missimia flavida* **sp. n.** In *Photuris trivittata* Lloyd & Ballantyne the labrum is the most anterior inflexible head plate, a surface clypeolabral suture may be missing, a distinct ridge beneath (visible as a dark line from above) is the frontoclypeal ridge. In *Luciola, Atyphella* and *Colophotia* there is a distinct strongly curved clypeolabral suture and no trace of a frontoclypeal ridge or suture. In all these species the membranous projection in front of the labrum is the epipharynx, and in *C. praeusta* there is no distinct line between the anterior end of the labrum and the beginning of the epipharynx. Lawrence's interpretations were based on a very restricted number of specimens and Ballantyne made the wider interpretations within the Luciolinae addressed here. These specimens will be lodged as taxonomic vouchers in ANIC.
6. Female head. Characters 275, 276 (state 2 in each) address wingless or flightless females, which have the eyes reduced relative to the situation in the male, and female heads are categorised as either 'winged female' or wingless female' forms. 'Winged female' head has eyes somewhat reduced but either no anterior prolongation of the head between the eyes (antennal sockets between the eyes on the head), or a parallel-sided anterior prolongation carries the antennal sockets. 'Wingless female' head is very small, eyes are much reduced, and the antennal sockets are on an anterior prolongation of the head the lateral margins of which converge anteriorly.
7. Female brachelytry (Figs 130–136). We continue to interpret brachelytry in females as derived, and the discussion covers various other possible interpretations.
8. Male lateral pronotal margins which conform to characters 8–0, 9–0 and 11–0 are described in abbreviated fashion as "divergent with rounded convergence"; those conforming to 8–0, 9–0 and 11–1 as "divergent with angulate convergence".
9. Colour. Width of pale lateral elytral margins. Under the microscope using incident illumination on the dorsal surface the extent of the underlying epipleuron may be visible and the width of the coloured lateral band can be compared to the width of the epipleuron; a 'wide' paler band of colour is wider than the width of the epipleuron, a narrow band is as wide as or narrower than the epipleuron.
10. Degree of development of interstitial lines. Lines are compared in width and height to the sutural ridge, and are well–defined when both those parameters equal or exceed that of the suture. Lines are numbered 1 (nearest suture) to 4 (nearest lateral margin).
11. Abdomen, revised terminology. We follow Branham and Archangelsky (2000) using 'ventrite' to refer to visible ventral segments of the abdomen (ventrite=visible sternite). We number the ventral abdominal segments by their actual not visible number i.e. ventrite 7 = the ventral plate of actual abdominal segment 7, while being the visible 6$^{th}$ sternite (see Discussion).
12. Abdomen, ventrite 7: Interpretation of the posterolateral corners of ventrite 7 as produced is exacerbated occasionally by dehydration, and overcome by soaking the dissected abdomen in hot water. Posterolateral corners were interpreted present if still produced after soaking e.g. *Atyphella scabra* and *Luciola owadai* are scored lacking, while *Missimia flavida* sp. n and *Pygatyphella okapa* **sp. n.** score positive.
13. Abdomen, tergite 8 shape. In the *Pygatyphella salomonis* and *limbatipennis* complex, categorisation of various shapes of tergite 8 (Figs 436–440) was made from hydrated specimens, the patterns then applied to dried pinned specimens and these shapes were not scored in the phylogenetic analysis. See also 1 above.
14. Aedeagal sheath: The significance of the 'aedeagal sheath' (abdominal segments 9 and 10 which are retracted within the abdomen) was not realised until 1987 and certain specimens dissected before then may not have this feature described. Collectors often partially extracted the aedeagus so it protrudes beyond the abdomen, but this process can sometimes destroy the integrity of the sheath.

## Male characters (1–261)

*Pronotum* (1–30)

**Dorsal surface and dimensions**

1. Irregularities in posterolateral areas (Figs 488, 491)

| | |
|---|---|
| absent | 0 |
| present | 1 |

2. From above lateral margins of pronotum delimited from median area by longitudinal groove (Fig. 40)

| | |
|---|---|
| absent | 0 |
| present | 1 |

The groove coincides at its anterior end with the lateral edges of the prothoracic cavity, and may be a consequence of the elevation seen in the lateral margins in the only species (and unique specimen) of *Photuroluciola deplanata* to possess it.

3. Density of punctation in lateral areas of disk

| | |
|---|---|
| moderate to dense, closely spaced | 0 |
| small sparse, widely separated (Fig. 490) | 1 |

4. Pronotal dimensions

A= width across anterior 1/3; B= width across middle; C= width across posterior

| | |
|---|---|
| A subequal to C | 0 |
| B>A or C | 1 |
| C>A or B | 2 |
| B subequal to C | 3 |
| C< A or B | 4 |

5. Width across posterior portion of pronotum/width across elytral humeri (elytra closed, specimen horizontal)

| | |
|---|---|
| less than (Fig. 75) | 0 |
| subequal to (Fig. 76) | 1 |
| greater than (Fig. 73) | 2 |

**Margins**

6(10). Explanation of anterior margin of pronotum (Lloyd & Ballantyne 2003 Figs 5, 19, 23) (Fig. 494, 495)

| | |
|---|---|
| narrowly explanate | 0 |
| not explanate | 1 |

States changed; outgroup becomes state 0

7(3). Shape of anterolateral corners of pronotum

| | |
|---|---|
| obliterated (Fig. 494) | 0 |
| rounded, (Fig. 489, 490, 492) | 1 |
| angulate (Ballantyne & Lambkin 2006 Figs 1, 3–5) (Figs 540, 543, 34) | 2 |

States 1 and 2 are combined, state 3 becomes state 2.

8(2) Inclination of lateral pronotal margins, anterior half

| | |
|---|---|
| divergent posteriorly (Figs 488–491, 494, 497, 498, 499, 500, 504, 506) | 0 |
| subparallel (Figs 493, 502) | 1 |
| converging posteriorly (Fig. 492) | 2 |

Character 2 split to reflect divergence or convergence of lateral margins in both anterior and posterior halves; this character addresses subparallel and convergent margins; 4 becomes 1, 5 becomes 2. Margins which are termed subparallel here along their length either have the anterolateral and posterolateral corners essentially in a line parallel to the longitudinal axis of the body or the posterolateral corners deviate very slightly to the side.

9. Nature of posterior half of lateral pronotal margins that diverge in the anterior half

| | |
|---|---|
| convergent | 0 |
| subparallel | 1 |
| divergent with posterior convergence (Fig 490) | 2 |
| divergent along length (Figs 488, 491) | 3 |

10. Nature of divergence in posterior half

| | |
|---|---|
| in line with anterior half (Figs 488, 491) | 0 |
| divergent beyond line of anterior half (Fig. 40) | 1 |

11. Nature of posterior convergence of lateral margins that diverge in anterior half or more
rounded (Fig. 63, 490) 0
angulate (Fig. 64) 1

Male lateral pronotal margins which conform to characters 8–0, 9–0 and 11–0 are described in abbreviated fashion as "divergent with rounded convergence"; those conforming to 8–0, 9–0 and 11–1 as "divergent with angulate convergence".

12. Indentation at mid-point of lateral margins that diverge along their length (Ballantyne & Lambkin 2006 Fig. 1)
absent 0
present 1

13. Sinuousity of lateral margins (elevated in vertical direction, visible from the side)
no 0
yes (Fig. 40) 1

14 (2). Inclination of subparallel-sided lateral margins (Fig. )
margins straight ((Fig 493) 0
margins convex (Fig. 503, 505) 1

Character 2 split to reflect divergence or convergence of lateral margins; this character addresses the nature of the subparallel-sided margins; state 4 is subdivided here. Straight lateral margins are addressed above and will score 1 for both characters 8 and 9. The pronotum is widest across the middle in convex-sided margins which will also score 0 for characters 8 and 9.

15(8). Indentation of lateral margin of pronotum near posterolateral corner (Fig. 64)
not indented 0
slightly indented 1

(The indentation is slightly irregular and small)

16. Irregularities at apex of posterolateral corner (Fig. 341)
absent 0
present 1

17(6) Shape of posterolateral corners
rounded (Fig 542) 0
angulate (Fig. 64, 488, 491) 1

Character 6 split into 3 to distinguish angle and shape of posterolateral corners; shape is addressed here; state 1 here reflects states 1–3.

18(6). Angle of rounded posterolateral corners
obtuse 0
less than 90° 1

Character 6 split into 3 to distinguish angle and shape of posterolateral corners; angle is addressed here; states 2 and 3 become 1, state 0 here reflects the old state 0 and part of 1.

19. Inclination of angulate posterolateral corners
approximately 90 º to median line 0
oblique to median line (Fig. 64) 1

20(6). Angle of angulate posterolateral corners
approximately 90º 0
less than 90º but not very acute 1
very acute (Fig. 34) 2

Relates to character 6 states 1 and 3 only; 1 becomes 0, 3 becomes 2.

21. Projection of posterolateral corners beyond the line of the lateral margin (Fig. 40)
not projecting 0
projecting 1

22(7). Extension of posterolateral corners relative to the median posterior margin of the pronotum (Fig. 40, 64)
not extending as far as this margin 0
extending as far as this margin but not beyond 1
extending beyond this margin 2

Character 7 split to reflect two characters, depth of emarginations and posterior extension of the corners

23(7). Extent of emargination between posterolateral corners and median posterior margin of pronotum
scarce 0

developed (Fig. 64) 1

**Ventral surface**

24(1). Hypomera

open 0

closed in front 1

25. Elevation of median area of hypomeron (in vertical direction)

not 0

elevated (Fig. 40) 1

Pronotum viewed from the side.

26(9). Nature of anterior portion of hypomeron

flat to neck (Fig. 84) 0

not flat to neck (Fig. 13, 24) 1

Character 9 expanded to distinguish between anterior and posterior halves of the hypomeron; this character distinguishes the anterior half of the hypomeron; 4 and part of 3 become 0; 0, 1 and part of 2 become 1.

27(9). Nature of posterior portion of the hypomeron

flat to neck (Fig. 84) 0

not all flat to neck 1

Character 9 expanded to distinguish between anterior and posterior halves of the hypomeron; this character distinguishes the posterior half of the hypomeron; 3, 4 and part of 1 become 0; 0, part of 2 become 1.

28. Nature of entire area of hypomeron

not all flat 0

all flat 1

29. Nature of dorsal and ventral surfaces of flattened posterior part of hypomeron

closely approach but not strongly adpressed 0

strongly adpressed (Fig. 84) 1

Strongly adpressed dorsal and ventral surfaces are so closely adpressed that the thin lateral margin may appear semitransparent.

30. Pronotal width/GHW index measured from beneath

1.6 or greater 0

1.4–1.5 1

1.3 2

1.2 or less 3

*Elytron* (31–50)

31(11). Punctation

not as large as pronotal punctation 0

as large as pronotal punctation and regular is size and distribution (Fig. 57, 58) 1

Character 11 modified; descriptor for state 1‘punctation larger than pronotal punctation’ modified as above; no change to states or scoring.

32. Density of elytral punctation

not sparse 0

sparse (Fig. 118) 1

33. Punctation linear

not linear 0

linear (Thancharoen *et al*. 2007 Fig. 1) 1

34. Dorsal surface of elytral apex dimpled (Ballantyne, 2001, Fig. 32)

not dimpled 0

dimpled 1

35(12). Deflexion of elytral apex

not deflexed 0

deflexed (Fig. 496) 1

36(12). Shape of outline of deflexed elytral apex

rounded (Ballantyne & Lambkin 2000 Fig. 20 j, k) 0

| | |
|---|---|
| truncate (Ballantyne & Menayah 2000 Fig. 1a) | 1 |
| pointed (Ballantyne 1987a Fig. 8h) | 2 |

Character 12 state 1 becomes state 0; states 1 and 2 are new.

37. Length of truncate deflexed apex

| | |
|---|---|
| long | 0 |
| short | 1 |

38(16). Extent of epipleuron as a lateral ridge

| | |
|---|---|
| extends no further than half length of elytron (Lloyd & Ballantyne 2003 Fig 23) | 0 |
| extends to apex (Fig. 6, 10, 13) | 1 |

39(17). Extent of sutural ridge

| | |
|---|---|
| does not extend to apex | 0 |
| extends to apex (Figs 4, 5, 9, 10 11, 12) | 1 |

40. Epipleuron and suture continue around apex of elytra as a ridge (view from above)

| | |
|---|---|
| no | 0 |
| yes (Fig 9, 11) | 1 |

41. Nature of apex where epipleuron and suture continue around apex of elytra as a ridge

| | |
|---|---|
| not further expanded (Fig. 9, 11) | 0 |
| further expanded (Fig. 118, 119) | 1 |

42. Epipleuron and suture continue around apex of elytra as a ridge (view from below)

| | |
|---|---|
| no | 0 |
| yes (Fig. 9, 11, 118, 119) | 1 |

43(14). Thickening of epipleuron and sutural apex in apical half of elytron (Fig. 118, 119)

| | |
|---|---|
| no thicker than rest | 0 |
| considerably thicker than anterior portions | 1 |

44 (15). Interstitial line development measured as elevation and width similar to that of sutural ridge

| | |
|---|---|
| 4 well–defined lines (1, 2, 3, 4 including the humeral carina, line 3 arising at or near the humerus) | 0 |
| 3 well–defined lines (lines 1, 2, and 3 or 4) | 1 |
| 2 well–defined lines (lines 1, 2 closest to the suture) | 2 |
| only one line well–defined (humeral carina) | 3 |
| no lines well–defined | 4 |

Lines are compared in width and height to the sutural ridge, and are well–defined when both those parameters equal or exceed that of the suture. Lines are numbered 1 (nearest suture) to 4 (nearest lateral margin)

45. Interstitial line development that exceeds development of sutural ridge (excluding the humeral carina)

| | |
|---|---|
| no lines well–defined | 0 |
| no lines better defined than suture | 1 |
| some interstitial lines higher and thicker than suture (Fig. 177) | 2 |

46. Visibility of humerus from below at base of elytron

| | |
|---|---|
| widely visible (Fig. 30) | 0 |
| narrowly | 1 |
| not visible (Fig. 10, 13, 24) | 2 |

Specimen held horizontally; if the epipleuron arises widely at elytral base the humeral angle of the elytron is not visible from below

47. Visibility of origin of epipleuron from above in relation to the posterior margin of the MS (specimen horizontal)

| | |
|---|---|
| well behind posterior margin of the MS | 0 |
| level with or just behind posterior margin of the MS | 1 |
| arising before the posterior margin of the MS (Fig. 9) | 2 |

Specimen held horizontally; first point at which the epipleuron is visible at the sides of the elytron measured in relation to the posterior margin of the MS

48. Lateral margin of epipleuron developed as a ridge

| | |
|---|---|
| not (Lloyd & Ballantyne 2003 Fig. 23) | 0 |
| yes | 1 |

49. Extent of approximation of sutural margins in apical half when elytra closed

| | |
|---|---|
| contiguous along sutural margin for > half elytral length | 0 |

not contiguous in apical half (Fig. 118) 1

50(18). Margins
parallel-sided (may converge in posterior 1/3) 0
convex-sided (Fig. 186) 1

*Head, antennae, mouthparts* (51–85)

51(19). Depression of vertex
minimal 0
moderate–deep (Fig. 85) 1

Depression can be assessed by how closely the anterior margin of the pronotum follows the contours of the back of the head

52(4, 5). Degree of head exposure (governed by retraction into prothoracic cavity)
greatly exposed (either not retracted or slightly retracted into the prothoracic cavity; small area at back of head is covered) 0
scarce to moderately exposed (moderately retracted into the cavity; up to half of the posterior area of the head may be covered) 1
completely concealed (fully retracted into the cavity) 2

Wording modified to reflect retraction into prothoracic cavity eliminates uncertainty over extent of visibility from above if head is partially protruded. Character 5 is subsumed here as only the outgroup scored 0 and the head is not concealed by retraction into a prothoracic cavity, but by explanation of the anterior pronotal margin; the outgroup is now scored as an inapplicable (-). Character 4 state1 becomes 0, 2 becomes 1, 3 becomes 2.

53(20). Approximation of eyes on ventral surface of head (measured as eye separation taken just behind mouthparts/GHW measured ventrally)
wide separation (0.5 or greater) 0
close to moderate separation (0.4 or less) 1
contiguous or almost so 2

54(21). Posterolateral eye excavation (Ballantyne 1968 Figs 144, 147–150)
absent; if slightly developed not visible when head is retracted 0
well developed, visible when head is evenly retracted (Fig. 59) 1

A ‘developed’ excavation is visible when the head is completely retracted within the prothoracic cavity. A well developed posterolateral eye excavation is at least as wide as long when viewed from the side. *Luciola* (*Lampyroidea*) *syriaca* is scored 0 for this character here.

55(22). Antennal length
longer than twice GHW 0
> GHW–2 x GHW 1
subequal to GHW 2

56(23). Proximity of antennal sockets
contiguous 0
not contiguous 1

Character 23 split into two to reflect the extent of separation of non contiguous antennal sockets. Contiguous sockets have no separation.

57(23). Proximity of non contiguous antennal sockets
< ASW 0
subequal to ASW 1
> ASW but not twice ASW 2
> 2 X ASW but not 3 X ASW 3
3 X ASW or greater 4

58(24). Nature of frons-vertex junction
not acute (Ballantyne & Lambkin 2000 Figs 2 a, d, h) 0
acute (Fig. 84) 1

59(25). Nature of median area of frons-vertex junction
not elevated or indented 0
elevated and/or indented (Ballantyne & Lambkin 2000 Figs 2f, g) 1

60(26). Position of antennal sockets

on head between eyes (Fig. 84) 0
back margin level with anterior eye margin 1
antennal sockets in front of anterior eye margin on a prolongation of the head (Fig. 27, 29, 30, 32) 2

Reduction in eye size will inevitably result in an apparent prolongation of frontal and mouthpart area. Character 26 is expanded to define this prolongation relative to anterior margins of eyes and antennal sockets, with specimen held with labrum horizontal. State 1 becomes either 1 or 2 here.

61(28). Presence of clypeolabral suture visible as a distinct external suture
present (Fig. 84, 28, 31) 0
absent (Fig. 27, 30) 1

Character 28 expanded to reflect both position and nature of the suture. 28–2 scored 1 here.

62. Position of clypeolabral suture
in line with or behind anterior eye margins 0
a little in front of anterior eye margin (Fig. 507, 508) 1
well in front of anterior eye margins 2

Head held so labrum is horizontal as for 60 above.

63(28). Nature of clypeolabral suture
flexible (freely articulated) (Fig. 84, 28, 31) 0
inflexible (not freely articulated) (Fig. 507, 508) 1

Character 28 expanded to reflect flexibility of suture; 28 states 1 and 2 score 1 here

64(28). Nature of sclerotisation of labrum
not well sclerotised (labrum is flexible) 0
well sclerotised (labrum is inflexible) (Fig. 507, 508) 1

Character 28 expanded to reflect sclerotisation of suture; 28 states 1 and 2 score 1 here

65. Nature of anterior margin of inflexible labrum
lacking projections 0
with small rounded projections (Fig. 507, 508) 1

66(27) Length/ width of labrum
labrum reaching outer area of mandibular bases (mandibles in repose) 0
labrum reaching the inner edges of mandibular bases 1

Character 27 modified; Labral width measured relative to how far it reaches laterally; state 1 becomes 0 and 2, 1. State 0 is addressed in character 61 state 1.

67(29). Mouthparts
functional 0
non–functional 1

Possible functionality of mouthparts assessed relative to the size of both the mandibles and the apical segments of the palpi.

68 (41). Apical segment of labial palpi lunate
no 0
yes (Fig. 29) 1

Character 41 modified and expanded; states 0 and 1 become 0 here and state 2 becomes 1 here

69 (40). Nature of non–lunate apical segment of labial palpi–lateral flattening
not strongly flattened 0
strongly flattened 1

Character 40 modified; state 1 becomes 0 and 2, 1. State 0 is incorporated into 73 state 0.

70. Shape of strongly flattened apical segment of labial palpi
narrow triangle (longer than wide) 0
broad triangle (isosceles; as wide as long) 1

71(41). Nature of inner margin of strongly flattened apical segment of labial palpi
entire 0
irregular/dentate 1

Character 41 modified; states 2 and 3 become 1.

72(41). Nature of inner margin of strongly flattened apical segment of labial palpi that are irregular/dentate
irregular, not dentate 0

| | |
|---|---|
| dentate, 2 teeth or less | 1 |
| dentate, 3 or more teeth | 2 |

Character 41 modified; state 0 is part of state 0 here; state 1 is expanded here to 1 and 2.

73(40). Shape of apical segment of labial palpi that are not strongly flattened

| | |
|---|---|
| ovoid/fusiform | 0 |
| subtriangular | 1 |

Wording of states modified; no change to scoring.

74. L/W of ovoid apical segment of labial palpi

| | |
|---|---|
| L=W | 0 |
| L>W | 1 |

75. L/W of narrow triangular apical segment of labial palpi

| | |
|---|---|
| L=W | 0 |
| L up to 2–3 X W | 1 |
| L>4 X W | 2 |

76(30). Proximity of eyes above labrum (SIW/GHW)

| | |
|---|---|
| close (1/6–1/15) (Fig. 84) | 0 |
| moderately separated (>1/6) | 1 |
| widely separated (1/3–1/2) | 2 |

77(31). Antennal flagellar segment 1 (Fig. 494)

| | |
|---|---|
| shorter than pedicel | 0 |
| as long as or longer than pedicel | 1 |

States reordered; outgroup becomes state 0

78(32). Antennal flagellar segment 1 (Fig. 509)

| | |
|---|---|
| not expanded at its outer apex | 0 |
| expanded at its outer apex | 1 |

79(33). Median area of antennal flagellar segment 1

| | |
|---|---|
| not produced | 0 |
| produced (Ballantyne & McLean 1970 Fig 18b) | 1 |

80(34). Flagellar segments 7–9 (Fig. 105)

| | |
|---|---|
| not conspicuously shorter than rest of FS | 0 |
| conspicuously shorter than rest of FS | 1 |

81(35). Number of segments

| | |
|---|---|
| 11 | 0 |
| < 11 | 1 |

82. Expansion of flagellar segment 4 towards apex (Fig. 509)

| | |
|---|---|
| not expanded | 0 |
| expanded | 1 |

McLean in Ballantyne & McLean (1970:263, Plate 2l) correctly referred to the enlarged size of FS4; Ballantyne (2001:67) incorrectly recorded FS 2–9 as not expanded.

83(37). Flagellar segments 2–8 (Fig. 21, 22, 34)

| | |
|---|---|
| not expanded | 0 |
| expanded at anterior apical angle | 1 |

84(38). Antennal segments

| | |
|---|---|
| not flattened | 0 |
| flattened | 1 |

85(39). Shape of pedicel

| | |
|---|---|
| not produced at outer apex | 0 |
| produced at outer apex | 1 |

*Legs* (86–96)

86(42). Inner tarsal claw of each leg

| | |
|---|---|
| not split | 0 |
| split | 1 |

87(43). Presence of metafemoral comb (Ballantyne 1987a Fig 1j)

| | |
|---|---|
| absent | 0 |

present (Fig. 94, 95) 1
88. Swelling of femora 2
not swollen 0
swollen 1
89(44). Swelling of femora 3 (Ballantyne & McLean 1970 Fig. 4p)
not swollen 0
swollen 1
90(45). Curvature of femora 3
not curved 0
curved along their length (Ballantyne & Lambkin 2000 Fig. 26h) 1
91. Excavation of inner margin of basitarsus 2
not excavated 0
excavated 1
92. Expansion of basitarsus 3
not expanded 0
expanded 1
Expansion is in length and width relative to basitarsus 2.
93(46). Swelling of tibiae 3
not swollen 0
swollen/expanded at least at their apices (Ballantyne & Lambkin 2000 Fig. 26h)1
94(47). Curvature of tibiae 3
not curved 0
curved (Ballantyne & Lambkin 2000 Fig. 26h) 1
95 (48). Curvature of tibiae 2
not curved 0
curved 1
96(49). Curvature of tibiae 1
not curved 0
curved 1
*Abdominal segments–ventrites* (97–152)
97(50). Presence of V 8
present 0
absent 1
98. Presence of cuticular remnants in intersegmental membrane, dorsal to aedeagal sheath ((Jeng *et al.* 2003 Fig. 14)
absent 0
present 1
99. Presence of cuticular remnants in intersegmental membrane, ventral to aedeagal sheath (Jeng *et al.* 2003 Fig. 14)
absent 0
present 1
100. Shape of posterior margin of abdominal V3
not recurved 0
recurved 1
101. Shape of posterior margin abdominal V4 (Fig. 96)
not recurved 0
recurved 1
102. Protrusion of anterior margin of V4 into V3 (Fig. 96)
not protruding 0
protruding 1
103. Presence of LO in V7
present 0
absent 1
104. Nature of posterior margin of LO in V7
entire 0
emarginate (Fig. 24, 61) 1

bipartite 2
105. Nature of medial emargination of anterior margin of entire LO in V7
lacking 0
present (Thancharoen *et al.* 2007 Fig1b) 1
106(51) Nature of posterior half of V7
not arched or swollen 0
arched not swollen 1
arched and swollen (Fig. 24, 61, 62) 2
107. Nature of corners of V7 having arched and or swollen posterior halves
present 0
obliterated 1
108. Shape of corners in V7 having arched or swollen posterior halves
rounded 0
angulate 1
109(52). Intrusion of swollen posterior half of V7 into LO posterior margin
not reaching into LO 0
reaching into LO (Fig. 24, 61) 1
Descriptors modified to delete ‘arched or swollen’; no change to states or scoring.
110. Depth of intrusion into LO of swollen posterior half of V7
shallow 0
deep (Fig. 24, 61) 1
111(53). Extent of LO in V7
reaching sides and posterior margin 0
reaching sides but not posterior margin 1
not reaching sides or posterior margin 2
no LO 3
112. Presence of LOs in V6
present 0
absent 1
113. Size of LOs in V6
occupying most if not all of the area 0
restricted to anterolateral plaques (Fig. 178, 179) 1
114(54). Size of bipartite LOs in V7
half of the area or more 0
less than half the area 1
less than 10% (Ballantyne & McLean 1970 Fig 18c) 2
Character 54 modified to reflect whether the LO is entire or bipartite; state 1 becomes 2 here.
115(54). Size of entire LOs in V7
most of the area 0
half or less 1
Character 54 modified to reflect whether the LO is entire or bipartite; state 0 there becomes 1.
116(55). Presence of MPP
absent 0
present 1
Character 55 split into 4; presence absence addressed here; states 1–4 become 1.
117. Symmetry of apex of MPP
symmetrical 0
asymmetrical 1
118(55). Presence of medial emargination of MPP
absent 0
present (Fig. 98, 99, 100) 1
Character 55 split into 4; medial emargination addressed here; states 3 and 4 become 1. Specimen horizontal; emargination is visible from beneath.
119(55). Depth of medial emargination of MPP

| | |
|---|---|
| shallow (Fig. 24) | 0 |
| deep (Fig. 98, 99, 100) | 1 |

Character 55 split into 4; depth of medial emargination addressed here; state 3 becomes 0 and 4, 1.

120(55). Shape non-medianly emarginate apex MPP

| | |
|---|---|
| rounded (Fig. 10, 13, 16, 18, 20) | 0 |
| pointed (Fig. 387, 388) | 1 |
| squarely truncate (Fig. 351) | 2 |
| obliquely truncate (fig. 343) | 3 |

Character 55 split into 4; shape of non-emarginate MPP addressed here; states 1 becomes 2 or 3, state 2 becomes 0.

121. MPP laterally compressed

| | |
|---|---|
| no | 0 |
| yes (Fig. 45, 46) | 1 |

122. MPP bisinuate across posterior margin

| | |
|---|---|
| no | 0 |
| yes (Fig. 309, 310) | 1 |

123(56). Length/ width of MPP of V7

| | |
|---|---|
| short | 0 |
| L=W | 1 |
| L>W | 2 |

States 1 and 2 are combined to become state 1 and state 3 becomes state 2.

124. Length of MPP relative to PLP

| | |
|---|---|
| shorter than | 0 |
| subequal to | 1 |
| longer than | 2 |

Specimen horizontal.

125. Width of MPP relative to PLP

| | |
|---|---|
| narrower than | 0 |
| as wide as | 1 |
| wider than | 2 |

Specimen horizontal

126 (57). Apex symmetrical T8 engulfing posterior margin of V7

| | |
|---|---|
| V7 not enveloped by T8 | 0 |
| V7 enveloped by T8 (Fig. 452–454) | 1 |

Character 57 is modified to reflect symmetry/asymmetry of T8; 1 becomes 0 and 2, 1.

127. Lateral margins of symmetrical T8 enfold V7 at sides

| | |
|---|---|
| no | 0 |
| yes | 1 |

128 (58). Dorsal inclination of the apical area of a narrowed MPP

| | |
|---|---|
| not reflexed dorsally | 0 |
| reflexed dorsally strongly (Ballantyne & Lambkin 2006 Figs 18, 19, 23, 25, 26) (Fig. 60) | 1 |

Character 58 is modified to reflect whether MPP is narrowed; 1 becomes 0 in part, 2 becomes 1 in part. In many species an elongate MPP may be slightly curved or arched dorsally; this arching or curvature occurs along the length of the MPP and may reflect effects of dehydration. This new character refers to the tip of the MPP, which is actually inclined at right angles to the long axis of the body and is not a consequence of dehydration.

129. Relation of MPP or posterior margin of V7 to asymmetrical apex of T8

| | |
|---|---|
| not engulfed | 0 |
| engulfed (Fig. 6, 109) | 1 |

130 (59). Relation of MPP or posterior margin of V7 to symmetrical apex of T8

| | |
|---|---|
| not engulfed | 0 |
| engulfed (Fig. 60, 452–454) | 1 |

Character 59 modified to reflect relationship of MPP to a symmetrical apex of T8; 1 becomes 0 and 2, 1.

131. Emarginations at base of MPP

| | |
|---|---|
| absent | 0 |

| | |
|---|---|
| present (Fig. 470, 471) | 1 |
| 132. MPP prolonged into 2 elongate hooks | |
| not prolonged | 0 |
| prolonged into 2 long symmetrical hooks (Fig. 98, 99, 100) | 1 |
| prolonged into 2 long asymmetrical hooks (Fig. 510, 511) | 2 |
| 133. Presence of ridge on dorsal surface of MPP | |
| absent | 0 |
| present (Fig. 342–359) | 1 |
| 134. Nature of dorsal ridge on MPP | |
| median | 0 |
| to left of median | 1 |
| 135. Width dorsal ridge MPP | |
| narrow | 0 |
| broad (Fig. 304, 306) | 1 |
| 136. Dorsal ridge MPP with 2 elevated median projections | |
| absent | 0 |
| present (Ballantyne 2008 Fig. 5, 6) | 1 |
| 137(61). Presence median carina V7 | |
| absent | 0 |
| present (Fig. 98, 99, 100, 510) | 1 |
| 138. Width of the median longitudinal carina in V7 | |
| broad (Fig. 510) | 0 |
| narrow (Fig. 98, 99, 100) | 1 |
| 139. Height of median longitudinal carina in V7 | |
| low | 0 |
| high | 1 |
| 140(62). Presence of median longitudinal trough ventral face of V7 | |
| absent | 0 |
| present (Fig. 106, 107) | 1 |
| 141. Presence of median depression on anterior face of entire LO | |
| absent | 0 |
| present (Fig. 6) | 1 |
| 142 (63). Nature of margins of median longitudinal trough on ventral surface MPP | |
| trough absent | 0 |
| not margined | 1 |
| unevenly margined (Fig. 100) | 2 |
| evenly margined | 3 |
| 143. V7 very flat | |
| no | 0 |
| yes | 1 |

Dehydration may result in abdominal segments curving such that V7 is strongly curved at its edges; V7 may remain quite flat despite apparent effects of dehydration on more anterior abdominal segments.

| | |
|---|---|
| 144 (64). Expansion of V7 in posterior half | |
| flat, not arched or swollen | 0 |
| arched, often swollen (Fig. 24, 61, 62) | 1 |

Arching gives a gap at the sides between V7 and T8 which is wider the stronger the arching; this segment if arched is usually markedly narrower that the softer more anterior, and flatter ventrites; arching does not conform to the curvature of V5 (where the softer cuticle allows the lateral margins to curve dorsally) for example. The muscles that cause the arching are usually clearly visible through the cuticle posterior to the LO (see further interpretation in Discussion).

| | |
|---|---|
| 145 (65–67). Presence of PLP of V7 | |
| absent | 0 |
| present (Fig. 96, 98–100, 106, 107) | 1 |

Characters 65–67 modified, state 0 eliminated and presence/ absence developed here as a separate character.

Interpretation of the posterolateral corners of ventrite 7 as produced is exacerbated occasionally by dehydration, and overcome by soaking the dissected abdomen in hot water. Posterolateral corners were interpreted present if still produced after soaking e.g. *Atyphella scabra* and *Luciola owadai* are scored lacking, while *Missimia flavida* **sp. n** and *Pygatyphella okapa* **sp. n.** score positive.

146(65). Length of PLP of V7
- slightly produced (Ballantyne & Lambkin 2000 Fig. 26a) 0
- moderately produced, may extend beyond the tip of the MPP 1
- considerably produced (Ballantyne 1987b Fig. 2 a, b) 2

Character 65 modified; state 0 eliminated, 1 becomes 0, 2 1, and 3 2.

147(66). Width of PLP of V7
- narrower than MPP (Ballantyne & Lambkin 2000 Fig. 26a) 0
- as wide as or wider than MPP(may be obliquely inclined) (Ballantyne & McLean 1970 Fig. 9 a, b) 1

Character 66 modified; state 0 eliminated; 1 becomes 0, 2 and 3 are merged into 1. All measurements are taken in the same plane.

148(67). Inclination of PLP of V7
- horizontal 0
- oblique–vertical (Fig. 98–100) 1

(Ballantyne & McLean 1970 Fig 3 d, f; Ballantyne 1968 Figs 11, 13)

Character 67 modified, state 0 eliminated; 1 becomes 0 and 2, 1.

149(68). Presence of incurving hairy lobes along posterior margin of V7 (Ballantyne & Lambkin 2000 Fig. 26a)
- absent 0
- present (Fig. 106, 107) 1

150(69). Presence of pointed projection of V7 posterior margin (Ballantyne & Lambkin 2000 Fig. 26a)
- absent 0
- present (Fig. 106, 107) 1

151(70). Presence of dimple on V7 (Ballantyne & Lambkin 2000 Fig. 20k)
- absent 0
- present 1

152. Anterior margin of facing cuticle on dorsal face of V7 reflexed into paired lobes, which are visible from the side (Ballantyne, 1968 Fig. 44, 45)
- absent 0
- present 1

*Abdominal segments–tergites* (153–186)

153. Symmetry of T8
- symmetrical 0
- asymmetrical (Fig. 7) 1

154 (60). Ventral inclination of symmetrical apex of T8
- not inclined 0
- weakly 1
- strongly (Fig. 452–454) 2

Character 60 expanded; state 1 becomes 1 and 2 to distinguish degree of inclination.

155. Width of ventral inclination of symmetrical apex of T8 that is strongly inclined ventrally
- posterior half not strongly narrowed 0
- posterior half strongly narrowed (Ballantyne & Lambkin 2006 Figs 19, 20, 22, 23, 25, 26) 1

156. Width of posterior half of symmetrical apex of T8 that inclines ventrally and is not strongly narrowed
- very narrow shelf 0
- wide shelf (Fig. 452–455) 1

157. Thickness of posterior half of symmetrical apex of T8 that inclines ventrally and is not strongly narrowed in posterior half
- thin 0
- thick (Fig. 452–455) 1

158. Prolongation of posterior lateral corners of T8

| | |
|---|---|
| not | 0 |
| prolonged (Fig. 511, 512) | 1 |
| 159. Extent of prolongations of posterolateral corners of T8 | |
| weakly prolonged | 0 |
| strongly prolonged (Fig. 511, 512) | 1 |
| 160. Angle of strongly prolonged posterolateral corners of T8 | |
| horizontal | 0 |
| inclined ventrally (Fig. 511, 512) | 1 |
| 161. Length of prolongation of posterolateral corners of T8 | |
| very short | 0 |
| long (Fig. 511, 512) | 1 |
| 162(71). Presence of flanges on ventral surface of T8 | |
| absent | 0 |
| present (Fig. 93) | 1 |
| 163. Nature of apex of flanges on ventral surface of T8 | |
| rounded | 0 |
| acute | 1 |
| 164. Orientation of flanges on ventral surface of T8 | |
| both incline in same direction | 0 |
| incline in different directions (Fig. 104) | 1 |
| 165. Length/width of flanges on ventral surface of T8 | |
| short and wide | 0 |
| elongate slender | 1 |
| 166(72). Ventral face of T8 with depressed lateral troughs bearing spines and hairs (Ballantyne & Lambkin 2000 Fig. 26c, d ) | |
| absent | 0 |
| present | 1 |
| 167(73). Nature longitudinal trough ventral surface T8 | |
| absent | 0 |
| finely margined | 1 |
| slightly thickened margins | 2 |
| low ridges present in posterior half only | 3 |
| well developed lateral ridges | 4 |
| 168. Length of median trough on ventral surface of T8 | |
| very short | 0 |
| long | 1 |
| 169. Symmetry of margins of median trough on ventral surface of T8 | |
| symmetrically margined | 0 |
| asymmetrically margined | 1 |
| 170(74). Ventral face of T8 with asymmetrical projections (other than flanges), and/or transverse ridges and/or hooks | |
| absent | 0 |
| present (Fig. 472) | 1 |
| 171. Development of projections on ventral face of T8 in anterolateral left | |
| absent | 0 |
| present as low transverse ridge (Fig. 472) | 1 |
| 172. Development of projections on ventral face of T8 in posterolateral left | |
| absent | 0 |
| present (Fig. 472) | 1 |
| 173. Development of projections on ventral face of T8 in anterolateral right | |
| absent | 0 |
| present (Fig. 472) | 1 |
| 174. Development of projections on ventral face of T8 in posterolateral right | |
| absent | 0 |
| present (Fig. 472) | 1 |

| | |
|---|---|
| 175. Presence of median posterior ridge on ventral surface of T8 | |
| absent | 0 |
| present (Fig. 360, 361, 404, 423, 436–437, 439–440) | 1 |
| 176. Curvature of median posterior ridge on ventral surface of T8 | |
| not curved | 0 |
| curved | 1 |
| 177(75). Width of T8 (visible entire posterior half only; (does not include anterolateral prolongations) | |
| very short | 0 |
| W=L or W>L | 1 |
| L>W but not projecting considerably beyond MPP | 2 |
| L>W and projecting considerably beyond MPP | 3 |

States changed; 0 becomes 1, 1 becomes 0, 2 becomes 3 and 3, 2.

| | |
|---|---|
| 178(76). Nature of margins of visible posterior area symmetrical T8 | |
| if margins converge then not abruptly | 0 |
| abruptly narrowed (Ballantyne & Lambkin 2006 Figs 19, 20) | 1 |

Character expanded to refer only to the visible posterior half of T8; states expanded to reflect symmetry; no change to scoring.

| | |
|---|---|
| 179. Posterior margin of T8 with lobes extending to either side of median emargination | |
| absent | 0 |
| present (Ballantyne & Menayah 2000 Fig. 1b) | 1 |
| 180. Lateral margins of T8 indented before origin of elongate anterolateral projections | |
| no | 0 |
| yes | 1 |
| 181. Length of anterior concealed prolongations of T8 | |
| none | 0 |
| very short | 1 |
| not as long as posterior visible area of T8 | 2 |
| as long as, if longer less than 2 x length of posterior visible portion | 3 |
| > 2 x as long as posterior portion | 4 |
| 182. Width of anterior prolongations of T8 (in horizontal plane) | |
| absent or very short | 0 |
| narrow | 1 |
| wide (Fig. 47) | 2 |

Prolongations may appear narrow when viewed from beneath; they are often expanded in a D–V plane to afford greater surface area for attachment of muscles.

| | |
|---|---|
| 183. Width anterior prolongations T8 in vertical plane | |
| not expanded D–V (Fig. 47) | 0 |
| expanded D–V (Fig.273, 274, 311–314, 410, 421) | 1 |
| 184. Inner area of anterior area of prolongations of T8 with bifurcation | |
| absent | 0 |
| present (Fig.249, 250, 254) | 1 |
| 185. Presence of ventrally directed pieces on ventral area of base ofprolongations of T8 | |
| absent | 0 |
| present (Fig. 360, 361) | 1 |
| 186. Emargination of median posterior margin of T8 | |
| absent | 0 |
| present | 1 |

*Aedeagal sheath* (187–211)

The significance of the 'aedeagal sheath' (abdominal segments 9 and 10 which are retracted within the abdomen) was not realised until 1987 and certain specimens dissected before then may not have this feature described. Collectors often partially extracted the aedeagus so it protrudes beyond the abdomen, but this process can sometimes destroy the integrity of the sheath.

187. Aedeagal sheath symmetry
symmetrical 0
asymmetrical 1
188(77, 78). Aedeagal sheath sternite symmetry in posterior area i.e. posterior to point of articulation with the sheath tergite
symmetrical (Ballantyne & Lambkin 2000, Fig. 21 b, d, e) 0
asymmetrical 1
Character 78 is partly subsumed into this character; no change to states.
189. Angulation of right side of sheath sternite posterior to tergite articulation
not angulate 0
angulate (Fu & Ballantyne 2006 Fig. 4) 1
190. Angulation of left side of sheath sternite posterior to tergite articulation
not angulate 0
angulate (Fu & Ballantyne 2006 Fig. 4) 1
191. Sheath sternite bent to right
no 0
yes (Fu & Ballantyne 2006 Fig. 4) 1
192(78). Extent of subparallel-sided sheath sternite posterior to tergite articulations
not subparallel-sided 0
yes in basal 1/3–1/2 (Fig. 360, 362, 363) 1
yes in basal 2/3 (Fig. 41–44) 2
yes along whole length (Fig. 115–117) 3
Character 78 is partly incorporated here; state 1 is state 3 here.
193. Nature of anterior half of sheath sternite (anterior to lateral attachment of tergal arms)
gradually narrowing to a very narrow anterior end 0
if narrowing then anterior end not extremely narrow 1
194. Nature of expansion of posterior half of symmetrical sheath sternite
expands posteriorly well behind the lateral articulation of the tergal arms (Ballantyne & Lambkin 2006 Figs 15–17) 0
does not expand posteriorly, or any expansion is an even one along the entire length of the sternite 1
195. Nature of expansion of symmetrical posterior half of sheath sternite
gradual expansion along length 0
expanding gently to widely, often abruptly, in posterior 1/3–2/3 (Ballantyne & Lambkin 2006 Figs 15–17)1
196. Nature of expansion of symmetrical sheath sternite in posterior area
gentle expansion in posterior 1/3–2/3 0
wide often abrupt expansion in posterior 1/3 (Ballantyne & Lambkin 2006 Figs 15–17) 1
197(80). Nature of posterior margin of sheath sternite
entire 0
medially emarginated (Fig. 115–117) 1
Character 80 split to reflect two different characters; here emargination is addressed; 1 and 2 become 1.
198. Width of medial emargination of posterior margin of sheath sternite
narrow 0
wide (Fig. 115–117) 1
199. Position of narrow medial emargination of posterior margin of sheath sternite
centred 0
off–centre 1
200. Presence of pointed projections to either side of narrow emargination of posterior margin of sheath sternite
absent 0
present 1
201(80). Symmetry of wide medial emargination of posterior margin of sheath sternite
symmetrical 0
asymmetrical 1

Character 80 split to reflect two characters; here symmetry of posterior margin is addressed; 1 becomes 0 and 2, 1.

202. Nature of posterior margin of sheath sternite that is not medially emarginate
 lacking rounded projection 0
 with rounded projection (Fig. 181, 183) 1

203. Emargination of both sides of lateral margins of posterior 1/3 of sheath sternite
 no 0
 yes (Fig. 41–44) 1

204. Irregular emargination of preapical area right side sheath sternite
 no 0
 yes (Fig. 477, 478) 1

205(81). Width of aedeagal sheath sternite in anterior area
 Broad 0
 if narrowed then this is a gradual narrowing anteriorly that progresses from the point of articulation of the tergal arms 1
 abruptly narrowed, anterior prolongation much narrower than posterior half of sternite, and narrowing commences posterior to the point of articulation of the tergal arms (Ballantyne & Lambkin 2006 Figs 15–17) 2

State 0 split into 0 and 1; state 1 becomes 2

206(82). Length/width of aedeagal sheath
 never more than about 4 times as long as wide 0
 very long and narrow (about 7 times as long as wide) (Fig. 103) 1

207(83). Presence of bulbous paraprocts on lateral margins of aedeagal sheath
 lacking (Fig. 90–93) 0
 present (Fig. 86–89)) 1

Descriptor 'bulbous' added to paraprocts

208. Lateral arms of tergite widely visible at sides of sternite
 not 0
 visible and joining anteriorly to sternite (Ballantyne & Lambkin 2006 Figs 15–17) 1

209. Tergite 9 of sheath split into two pieces
 no 0
 yes 1

210. Posterior margin of tergite 9 with downwardly projecting pieces
 no 0
 yes (Fig. 41–44) 1

211. Presence of transverse band anterior to sheath tergite (Ballantyne 2008 Fig. 9)
 no 0
 yes 1

*Aedeagus* (212–261)

212. L/W aedeagus
 3/1 or greater 0
 < 3/1 1

213(85). Maximum width across lateral lobes/ maximum width of median lobe
 wide (4–6/1) (Ballantyne 1968 Fig. 171) 0
 moderate (2/1–3/1) (Ballantyne & Lambkin 2000 Fig. 5) 1
 narrow (less than 2/1) (Ballantyne & Lambkin 2000 Fig. 21 o, r, u; 26e) 2

214(92). Median lobe symmetry
 symmetrical 0
 asymmetrical (Fig. 48–54, 286–289) 1

Character 92 is incorporated into this character; no change to states

215. Median lobe asymmetry due to curvature of ML in horizontal plane
 no (Fig. 48–50) 0

| | |
|---|---|
| yes (Fig. 286–289) | 1 |
| 216. Median lobe asymmetry due to asymmetrical projections of ML | |
| no | 0 |
| yes (Fig. 48–50) | 1 |
| 217. Nature of ventral face of asymmetrical ML | |
| lacking median longitudinal groove | 0 |
| with median longitudinal groove (Fig. 48–50) | 1 |
| 218. Presence of lateral teeth of median lobe | |
| absent | 0 |
| present (Fig. 364–376, 428–435) | 1 |
| 219. Width of lateral teeth of median lobe | |
| narrow (Fig. 364–376) | 0 |
| wide(Fig. 428–435) | 1 |
| 220. Shape of apices of lateral teeth of median lobe | |
| pointed (Fig. 364–376) | 0 |
| rounded (Fig. 428–435) | 1 |
| 221(86). Inclination of apex of median lobe | |
| not curving ventrally | 0 |
| curving ventrally (Ballantyne 1968 Figs 164, 168) | 1 |
| 222. Median lobe strongly arched | |
| no | 0 |
| yes (Fig. 514) | 1 |
| 223(87). Extent of preapical ventral area of median lobe | |
| not produced | 0 |
| produced and rounded (Fig. 248) | 1 |
| produced and pointed (Ballantyne 1968 Figs 162, 164, 168) | 2 |
| ML viewed from side. | |
| 224. Width of symmetrical ML at apex relative to width at base | |
| as wide as or wider than base | 0 |
| much narrower than at base (Ballantyne 1968 Figs 162, 164, 168) | 1 |
| Aedeagus horizontal, ML viewed from beneath. | |
| 225. Apex of median lobe in arrowhead shape | |
| absent | 0 |
| present (Fig. 48–50) | 1 |
| 226(88). Length of LL relative to length of ML (measured from beneath) | |
| much shorter than ML | 0 |
| ML subequal or slightly longer or shorter | 1 |
| ML considerably longer than LL | 2 |

Character 88 modified to relate length of LL relative to ML rather than the opposite; measurement of LL and ML taken from beneath in horizontal specimen; 0 becomes 2, and 2 and 3 become 0.

| | |
|---|---|
| 227. Equality of length LL | |
| same length | 0 |
| unequal length (Jeng *et al.* 1998 Fig. 32–42) | 1 |
| Aedeagus horizontal. | |
| 228. Divergence of LL along inner margins | |
| not divergent along most of their length | 0 |
| divergent along their length | 1 |
| 229(89). Separation of LL (view from above) | |
| separated by>half their length | 0 |
| separated by < half their length (Fig. 48, 49, 101, 102) | 1 |
| 230. LL base width=LL apex width | |
| no | 0 |
| yes | 1 |
| 231(89). Separation of LL that are visible from beneath | |

separated by>half their length 0
separated by < half their length 1

232(90). Width LL at apices
much wider than widest point of ML 0
subequal to ML 1
narrower than ML (Fig. 184, 185) 2

233. Width of apices of LL that are visible from beneath, in horizontal plane
not wide 0
wide (Fig. 518) 1

234(91). Separation of lateral lobes into broad basal section and narrowed widely separated apical section
absent 0
present (Ballantyne & Lambkin 2000 Fig. 21k) 1

235. Ventrobasal area of LL produced into lobes that may overlap base of ML
no 0
yes (Lloyd & Ballantyne 2003 Fig. 18) 1

236. Anterior margin of base of LL asymmetrically produced
no 0
yes (Fig. 286–295) 1

237. Excavation of anterior margin of symmetrical base of lateral lobes
not excavated 0
excavated 1

238. Nature of anterior projection of symmetrical base of LL
broadly rounded 0
broadly truncate (Fig. 145, 146) 1
pointed medially entire (Fig. 212–216) 2
pointed medially emarginated (Fig. 172, 173) 3

239(93). Presence of fleshy leaf–like lobes on inner margins LL
absent 0
present (Ballantyne 1968 Figs 165, 166, 168, 169) 1

240(94). Visibility from beneath of LL at sides of ML
visible (Fig. 35) 0
almost visible (Fig. 48–51) 1
not visible (Fig. 36, 101, 102) 2

The ML may conceal one or other of the apices of the LL in *Pygat. uberia* so both may not be visible in the same plane and this situation is scored 1.

241. Visibility from beneath of LL at sides of asymmetrical ML
visible 0
not both visible in the one plane 1
not visible 2

242(95). Lateral appendages of lateral lobes
absent 0
present (Lloyd & Ballantyne 2003 Fig. 17, 18, 21) 1

243. Basal piece strongly sclerotised
no 0
yes (Fig. 518) 1

244(96). Shape of basal piece of aedeagus
not hooded 0
hooded (Fig. 212–216) 1

245. Preapical lateral margin LL produced
no 0
yes (Fig. 286–303) 1

246. Shape of expanded preapical lateral margin
rounded 0
angulate (Fig. 293, 294, 302, 303) 1

247. Production of inner apical margin LL
    no 0
    yes (Fig. 286–303) 1
248. Length inner apical margin LL
    short 0
    medium 1
    long (Fig. 302, 303) 2
249. Width of inner apical production
    wide (Fig. 270, 271) 0
    narrow (Fig. 302, 303) 1
250. Preapical inner margin LL obliquely truncate
    no 0
    yes (Fig. 212–216) 1
251. Inner preapical margin of LL that are obliquely truncate on their inner margins with strong tooth
    no 0
    yes (Fig. 242, 243) 1
252. Entire apices of LL out–turned
    no 0
    yes 1
253. Shape of outer margin of out-turned apices of LL
    rounded 0
    angulate 1
254. Apices of LL inturned (meet or nearly so in midline
    no 0
    incline towards each other 1
    strongly bent towards each other, and meet or nearly so in the midline (Fig. 513, 515, 516) 2
255. Presence of asymmetrical flap like projection to left side of ML
    absent 0
    present (Fig. 48–54) 1
256. Presence of projection on left LL
    Absent 0
    Present (Fig. 48–54) 1
257. Presence of apparently bulbous tip to the ML
    absent 0
    present (Fig. 188, 189) 1
In *C. wolfi* the ML is constricted preapically giving the appearance of a bulbous tip.
258. Emargination of median anterior apex of BP
    absent 0
    present (Fig. 518) 1
259. Width of BP
    not very narrow 0
    very narrow (Fig. 5513, 515) 1
260. Inner margins of LL approach closely and narrowly
    no 0
    yes (Fig. 513, 515, 516) 1
261. Longitudinal emarginate hair bearing area on outer margin LL
    no 0
    yes (Fig. 246, 247) 1
FEMALE CHARACTERS (262–290)
262. Presence of irregularities in posterolateral areas dorsal pronotal surface
    absent 0
    present 1
263. Punctation in lateral areas of disc

moderate to dense 0
small sparse 1

264. Pronotal dimensions
A= width anterior 1/3; B= width across middle; C= width across posterior
A==C 0
B>A or C 1
C>A or B 2
B==C 3
C< A or B 4

265. Width across posterior portion of pronotum relative to width across elytral humeri (elytra closed)
less than 0
subequal to 1
greater than 2

266. Indentation of lateral margin of pronotum near posterolateral corner
not indented 0
slightly indented 1

267. Irregularities at apex of posterolateral corner
Absent 0
Present 1

268. Elytral punctation
not conspicuously larger than pronotal punctation 0
conspicuously larger than pronotal punctation 1

269(112). Density of pronotal punctation
not sparse 0
Sparse 1

Descriptors wording changed; no change to states

270(103). Development of fore wings of female
fully developed (or covering all but two terminal abdominal segments) (Fig. 25, 130) 0
elytra longer than pronotum but shortened such that they cover approximately ½–2/3 of the abdomen 1
elytra subequal to or shorter than pronotum (more than half as long as pronotum) and contiguous in the median line (Fig. 132) 2
elytra shorter than half pronotal length and often contiguous or closely approaching in the median line (Fig. 133) 3
elytra shorter than half pronotal length and widely separated in the median line (Fig. 136) 4

Macropterous gravid females may have one to two abdominal segments protruding beyond the elytral apices (see discussion for interpretation of aptery in the Luciolinae).

271(104). Development of hind wings of female
fully developed 0
always shortened, usually at least half as long as macropterous state but lacking apical fold 1
vestigial or absent 2

Descriptor for state 1 amplified; no change to states or scoring.

272(110). Interstitial line development as elevation similar to that of sutural ridge
4 well–defined lines (1, 2, 3, 4 including the humeral carina, line 3 arising at or near the humerus) 0
3 well–defined lines (lines 1, 2, and 3 or 4) 1
2 well–defined lines (lines 1, 2 closest to the suture) 2
only one line well–defined 3
no lines well–defined 4

Character 110 expanded; state 0 remains the same; state 1 becomes 1–4.

273(111). Elytral carina

| | |
|---|---|
| absent | 0 |
| present | 1 |

274. Size of eyes

| | |
|---|---|
| not greatly reduced | 0 |
| considerably reduced | 1 |

275(113). Position of antennal sockets on head relative to eyes (labrum horizontal)

| | |
|---|---|
| on head between eyes | 0 |
| on short anterior prolongation of head | 1 |
| on long anterior prolongation of head | 2 |

Character 113 is subdivided into two to distinguish more completely the difference between heads of winged and wingless females, and the particular situations in *Missimia* and *Photinus* females where the antennal sockets are on an anterior prolongation of the head. 113(1) is both state 0, and 1 here; 113(2) is either state 1 or 2 here. Lateral margins of prolongation in state 1 are subparallel, in state 2 the margins converge anteriorly and this is characterised as a wingless or flightless female head in character 276.

276(113). Nature of anterior prolongation of head

| | |
|---|---|
| not developed | 0 |
| with sides parallel | 1 |
| sides converge anteriorly | 2 |

Further subdivision of character 113; 113(2) is state 2 here; 113(1) becomes 0, and 113(0), 1. Wingless or flightless females have head scored 113, state 2.

277. Clypeolabral suture

| | |
|---|---|
| present, junction flexible | 0 |
| present, junction inflexible | 1 |
| absent | 2 |

278. Curvature of tibiae 3

| | |
|---|---|
| not curved | 0 |
| curved (Ballantyne & Lambkin 2000 Fig. 26h) | 1 |

279. Curvature of tibiae 2

| | |
|---|---|
| not curved | 0 |
| curved | 1 |

280. Curvature of tibiae 1

| | |
|---|---|
| not curved | 0 |
| curved | 1 |

281(105). Extent of female LO

| | |
|---|---|
| occupying V6 and 7 | 0 |
| restricted to V6 | 1 |

282(106). Presence of anteromedian elevations on abdominal T7

| | |
|---|---|
| absent | 0 |
| present (Ballantyne & Lambkin 2001 Figs 18, 19) | 1 |

Ballantyne & Lambkin (2006:42) incorrectly attributed the elevation to T8 and this is corrected here. Descriptor modified to add ‘anteromedian elevation’.

283(107). Presence of median transverse ridge on abdominal V7

| | |
|---|---|
| absent | 0 |
| present(Ballantyne & Lambkin 2001 Fig. 16) | 1 |

Descriptor modified to add ‘median transverse ridge’.

284 (108). Presence of lateral elevated areas on ventral face of V7

| | |
|---|---|
| absent | 0 |
| present (Ballantyne & Lambkin 2001 Fig. 30) | 1 |

285(109). Presence of depressed lateral areas on V7 ventral face (corresponding to dorsoventral muscles)

| | |
|---|---|
| absent | 0 |
| present | 1 |

286. Presence of bursa plates

| | |
|---|---|
| absent | 0 |
| present | 1 |

287. Bursa plates appear as paired strips
no 0
yes (Fu & Ballantyne 2006 Fig. 8) 1
288. Bursa plates appear as paired hooks
no 0
yes (Ballantyne & Lambkin 2006 Fig. 37) 1
289. bursa plates appear as wide (paired)plates
no 0
yes 1
290. Presence of plate at base of median oviduct
no 0
yes (Fu & Ballantyne 2006 Fig. 8) 1

## Larval characters (291–321)

291(118). Production of lateral margins of terga
not explanate (laterotergites usually visible from above) (Ballantyne & Lambkin 2000 Fig. 22) (Fig. 517) 0
narrowly explanate especially at posterolateral corners (Ballantyne 1968 Figs 158–160) 1
widely explanate (laterotergites not visible from above) (Ballantyne & Lambkin 2000 Figs 12, 15, 36B) 2
292. Visibility of laterotergites from above
no (Ballantyne & Lambkin 2000 Fig. 36B) 0
yes (Fig. 517) 1
293(119). Length/width of pronotum
longer than wide 0
about as long as wide 1
wider than long 2
294(120). Nature of tergal margins
not ridged 0
ridged 1
295. Nature of antennal segment 3
short 0
long 1
296. Nature of sense cone larval antenna
wide 0
slender 1
297. Length of sense cone larval antenna
short 0
long 1
A long sense cone is usually as long as segment3; a short cone is considerably shorter than segment 3.
298(121). Presence of paired dorsal and ventral tubercles on protergum along anterior margin
absent 0
present (Ballantyne & Lambkin 2000 Fig. 15a, c) 1
299(122). Shape of posterolateral corners of protergum
not narrowly produced (Ballantyne & Lambkin 2000 Fig. 36B) 0
narrowly produced 1
300. Shape of posterolateral pronotal corners that are not produced
rounded (Ballantyne & Lambkin 2000 Fig. 15 a–c, 36B) 0
acute (Ballantyne & Lambkin 2000 Fig. 12 c) 1
301. Shape posterolateral corners protergum that are narrowly produced
entire 0
bifurcate 1

302. Shape posterolateral corners pronotum that are narrowly produced
- rounded 0
- pointed 1

303. Shape posterolateral corners meso and metaterga
- not narrowly produced (Ballantyne & Lambkin 2000 Fig. 36B) 0
- narrowly produced 1

304. Inclination of narrowly produced posterolateral corners of meso and metaterga
- oblique to median line (Ballantyne, 1968 Figs 158–161) 0
- parallel to median line 1

305. Median line with lateral margins
- no 0
- yes 1

306(123). Ridges along margins of median line on terga 1–10
- absent 0
- present 1

307. Median line extends to anterior and posterior margins of most terga
- yes (Ballantyne & Lambkin 2000 Fig. 36B) 0
- no 1

308(124). Size of punctures in anterior half of terga 2–10
- no larger than rest 0
- larger than rest 1

309(125). Extent of posterolateral corners of tergum 12
- not produced (Ballantyne & Lambkin 2000 Fig. 7a, 15b) 0
- produced (Ballantyne & Lambkin 2000 Fig. 12a–c, 15 a, c) 1

310. Posterior margins of abdominal terga 1–7 or 8 with projections to either side of median line
- absent 0
- present 1

311. Nature of projections along posterior margins of terga 1–7 or 8
- rounded 0
- pointed 1

312. Presence of dense brush of white hairs arising from the apex of the tibia and enveloping apical (tarsungulus) claw from above
- absent 0
- present 1

313. Presence of thickened lateral margin of protergum especially in posterior 3/4
- absent 0
- present 1

314. Mandibles with two strong inner teeth
- absent 0
- present 1

315. Tergal plates sclerotised to margins
- absent 0
- present (Ballantyne & Lambkin 2000 Fig. 36B) 1

316. Posterolateral corners of penultimate tergite broadly produced posteriorly
- no 0
- yes (Jeng *et al.* 2003 Fig 41) 1

317. Mode of life
- terrestrial 0
- semi-aquatic 1
- aquatic 2

318. Presence of tracheal gills
- absent 0
- present in some stages 1
- present in all stages (Jeng *et al.* 2003 Fig 39) 2

319. Presence of tergum 8 spiracles

| | |
|---|---|
| absent | 0 |
| present (Jeng *et al*. 2003 Fig 41) | 1 |

320. Presence of laterosternal plates to either side of median sternal plate in abdominal segments 1–8

| | |
|---|---|
| absent | 0 |
| present | 1 |

321. Presence of filaments along posterior margins most terga

| | |
|---|---|
| absent | 0 |
| present | 1 |

*Male colour patterns* (322–337)

322(98). Colour of elytra

| | |
|---|---|
| elytra concolourous pale | 0 |
| elytra concolourous dark | 1 |

Character 98 had become unwieldy and did not accommodate many of the species scored herein. State 0 becomes either 0 or 1 here, state 7 becomes 0, and states 2–6 are scored inapplicable here and are elaborated in characters 329, 330, 331–333,335.

323. Elytra dark with paler randomly scattered spots

| | |
|---|---|
| no | 0 |
| yes (Fig. 137, 138) | 1 |

324(99). Elytra striped male

| | |
|---|---|
| no | 0 |
| yes (Fig. 11, 122, 123, 124, 150, 151, 153) | 1 |

Character 99 is partially incorporated here; 2 becomes 1.

325. Number of pale interstitial lines in striped elytra

| | |
|---|---|
| <3 | 0 |
| 3 | 1 |
| >3 | 2 |

326. Extent of pale lateral margin in striped elytra

| | |
|---|---|
| narrow does not extend to line 4 | 0 |
| wide extends to line 4 | 1 |

327. Fat body contributes to pale line colour in striped elytra

| | |
|---|---|
| no | 0 |
| yes (Fig. 150) | 1 |

328. Striped elytra with additional stripes due to lines of fat body

| | |
|---|---|
| no | 0 |
| yes (Fig. 150) | 1 |

329(99). Base of elytra with dark area adjacent to MS

| | |
|---|---|
| no | 0 |
| yes (Fig. 23, 69, 70) | 1 |

Character 99 state 0 is partly incorporated here; 0 becomes 1.

330. Extent of dark elytral marking adjacent to MS

| | |
|---|---|
| restricted to base of elytron, not a wide triangle (Fig. 166, 167, 169) | 0 |
| wide triangle (Fig. 23, 69, 70) | 1 |

331(98). Elytra with pale margin/s (different colour)

| | |
|---|---|
| no | 0 |
| yes (Fig. 5, 12, 17, 66, 67, 128) | 1 |

Character 98 modified, states 1–4 become state 1 here.

332(98). Extent of pale elytral margins

| | |
|---|---|
| lateral margin only excluding apex | 0 |
| lateral margin including apex | 1 |
| humerus to MS excluding apex | 2 |
| humerus to MS including apex | 3 |
| sutural margin including apex | 4 |

Character 98 modified; state 1 becomes 0 or 1, 2 and 3 become either 2 or 3 here; character 98 did not specify colour of elytral apex.

333(98). Dark elytra with paler base

| | |
|---|---|
| no | 0 |
| yes (Ballantyne & Lambkin 2000 Fig. 19 g–j) | 1 |

Character 98 state 3 and 4 partly incorporated into state 1 here.

334. Pale elytra with darker margins

| | |
|---|---|
| no | 0 |
| yes (Fig. 467) | 1 |

335(98). Presence of pale basal area of dark elytra

| | |
|---|---|
| no | 0 |
| yes (Ballantyne & Lambkin 2000 Fig 19 h) | 1 |

Character 98 state 3 and 4 partly incorporated into state 1 here.

336(97). Colour of pronotum

| | |
|---|---|
| pronotum concolourous | 0 |
| pronotum not concolourous | 1 |

337(100). Colour of terminal abdominal tergite

| | |
|---|---|
| As dark as or darker than preceding terga | 0 |
| Pale (as pale as preceding terga or paler) | 1 |

Female colour patterns (338–339)

338(115). Colour of elytra

| | |
|---|---|
| concolourous | 0 |
| not concolourous | 1 |

339(114). Colour of pronotum

| | |
|---|---|
| concolourous | 0 |
| not concolourous | 1 |

*Nature of dorsal colour patterns, male and female* (340–343)

340(101). Nature of dorsal colouration pattern female

| | |
|---|---|
| crypsis | 0 |
| mimicry | 1 |

341(117). Type of crypsis female

| | |
|---|---|
| background matching | 0 |
| disruptive colouration | 1 |

State 1 omitted (covered in character 341 above); 1 becomes 0 and 2, 1.

342(116). Nature of dorsal colouration pattern male

| | |
|---|---|
| crypsis | 0 |
| mimicry | 1 |

343(102). Type of crypsis male

| | |
|---|---|
| background matching | 0 |
| disruptive colouration | 1 |

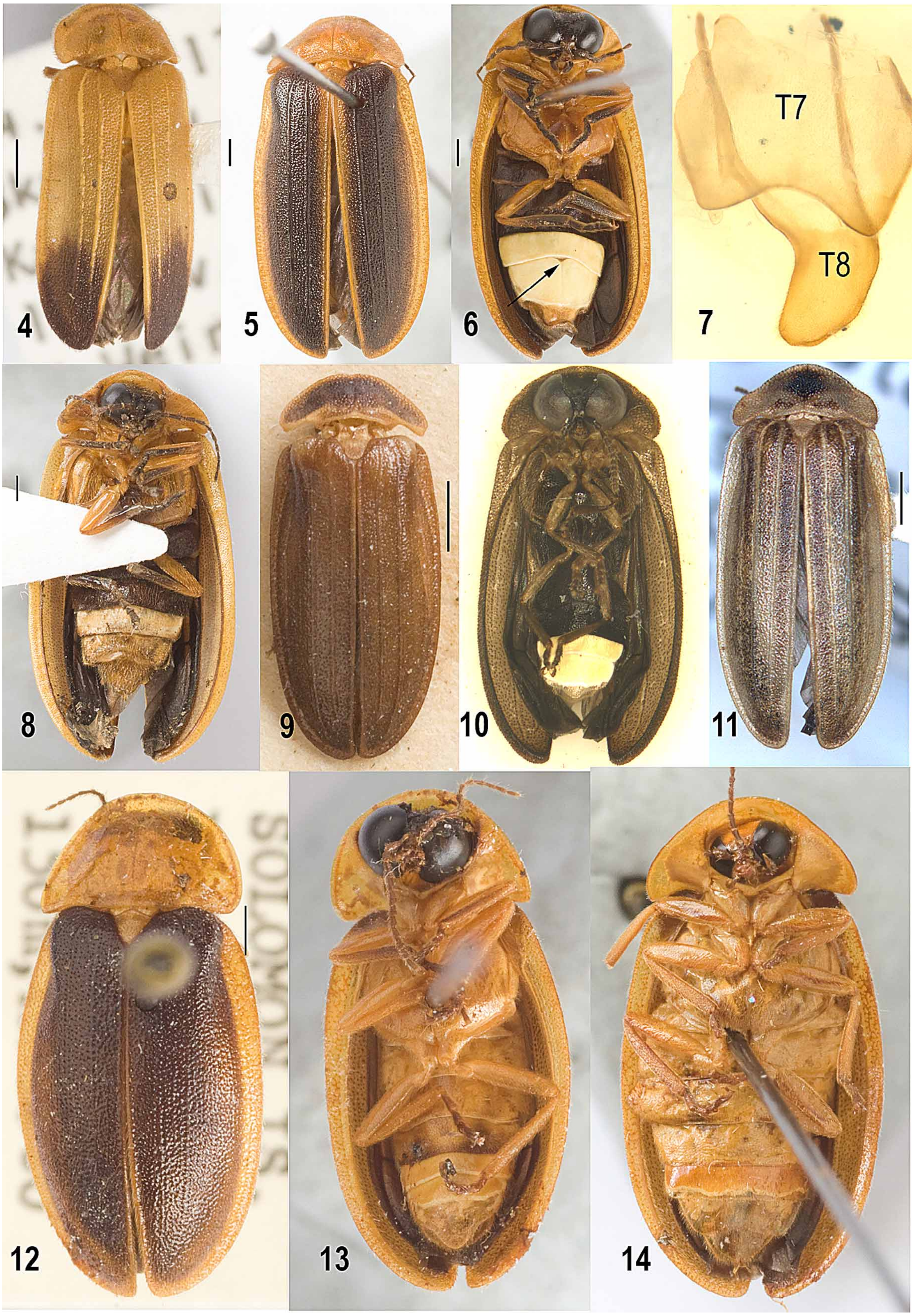
State 1 omitted (covered in character 342 above); 1 becomes 0 and 2, 1.

## Appendix 2. Origin of colour photos

Jenni Horsnell of Charles Sturt University Wagga Wagga took the following colour photos using a Canon 30D 100 mm camera mounted on a tripod in natural light: 4–6, 8, 9, 12–26, 39, 40, 65–72, 118, 119, 122–131, 137–139, 142, 144, 150–157, 167–169, 177, 178, 186, 192–194, 204–206, 211, 225–227, 231, 232, 251, 264–268, 278–282, 315, 316, 329–337, 340, 377–386, 397, 398, 405, 406

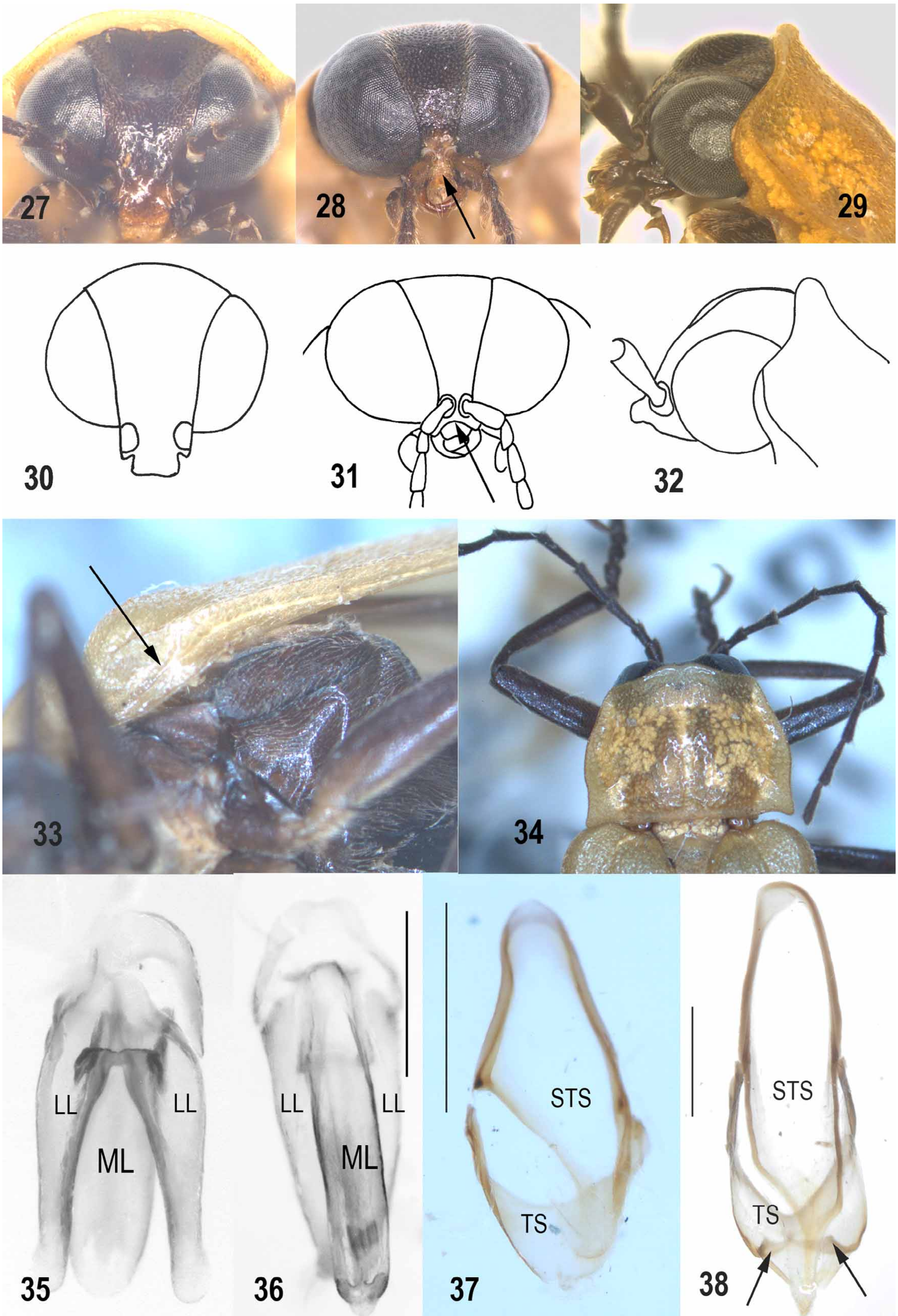
Ballantyne used Helicon Focus 4.30 to reassemble multiple levels of these pictures: 10, 27–29, 61, 62, 79, 83, 84, 98, 100, 393, and 394.

For Figures 4–518 scale lines are 1 mm unless indicated otherwise. Specimen listing includes locality and museum of origin.

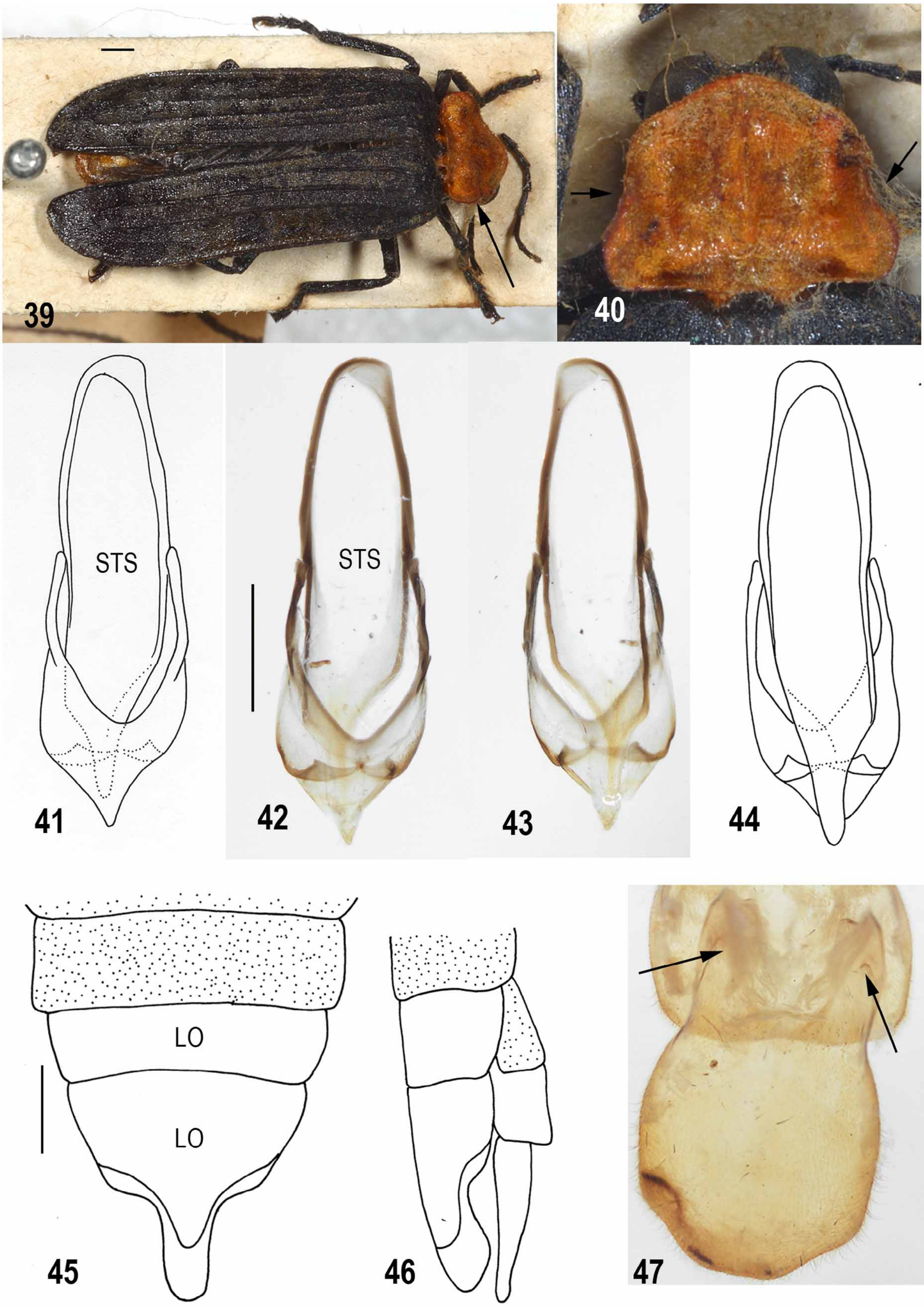



**FIGURES 4–14.** Habitus Genera 1. *Aquilonia costata* male dorsal (Katherine NT, ANIC). 5, 6, 8, *Asymmetricata circumdata*, 5, 6 males dorsal ventral, 8 female ventral (Thailand, ANIC). 9, 10 *Atyphella atra* males dorsal, ventral (9 paratype National Park Q; 10 Springbrook Q, ANIC). *Atyphella lychnus* male dorsal (Lansdowne State Forest, ANIC). *Convexa wolfi* males 12, 13 dorsal, ventral, 14 female ventral (Kukugai, BPBM).

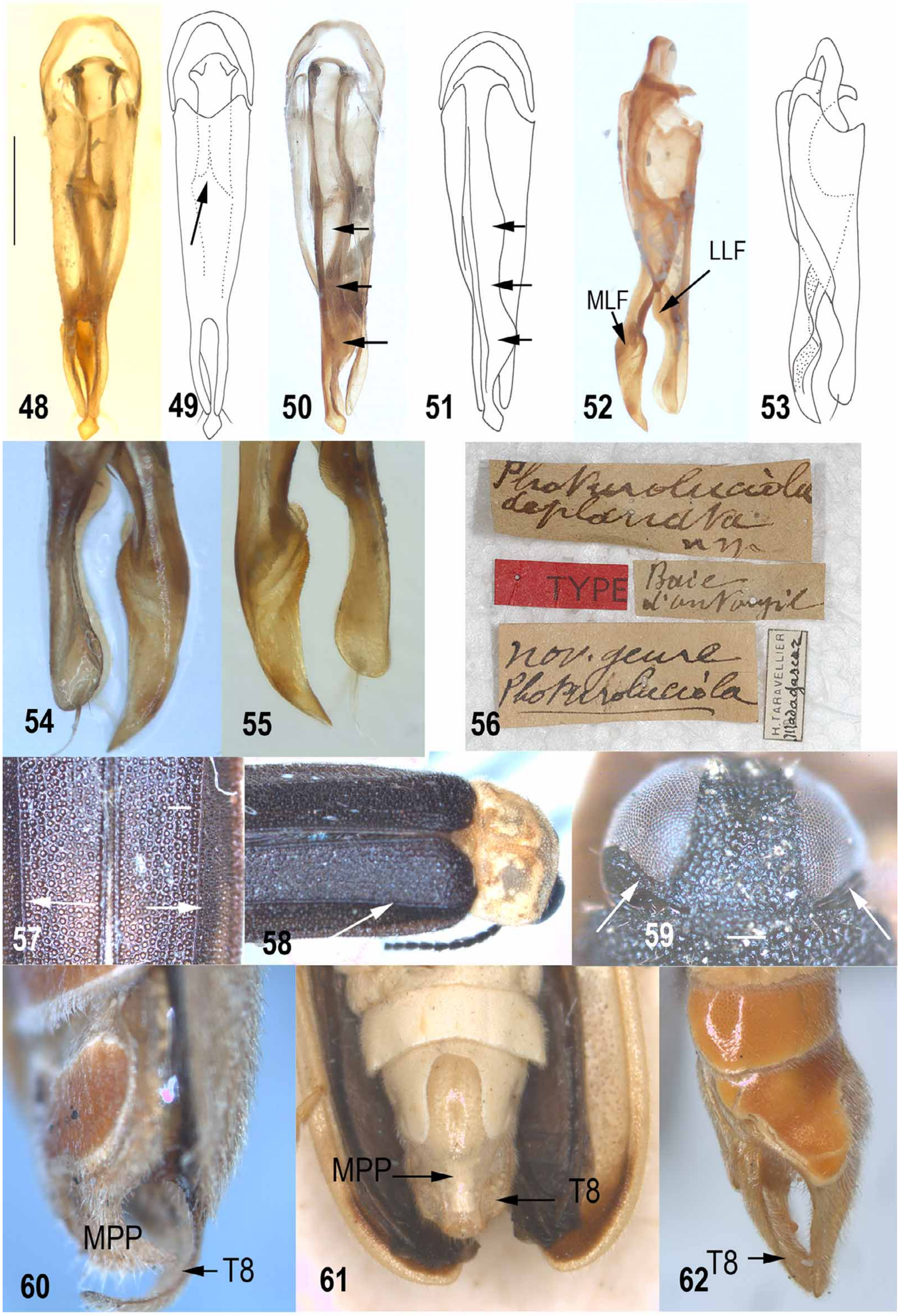

**FIGURES 15–26.** Habitus Genera 2. 15, 16 *Atyphella messoria* holotype male, dorsal, ventral (MNHN). 17, 18 *Magnalata limbata* male, dorsal, ventral (Kira Kira, BPBM). 19, 20 *Lloydiella wareo* paratype males, dorsal, ventral (Wareo, SAM). 21, 22 *Missimia flavida* males, holotype, paratype (BPBM). 23–26 *Pygatyphella huonensis* males dorsal, ventral (23, 24), females dorsal, ventral (25, 26) (Wareo, BPBM).



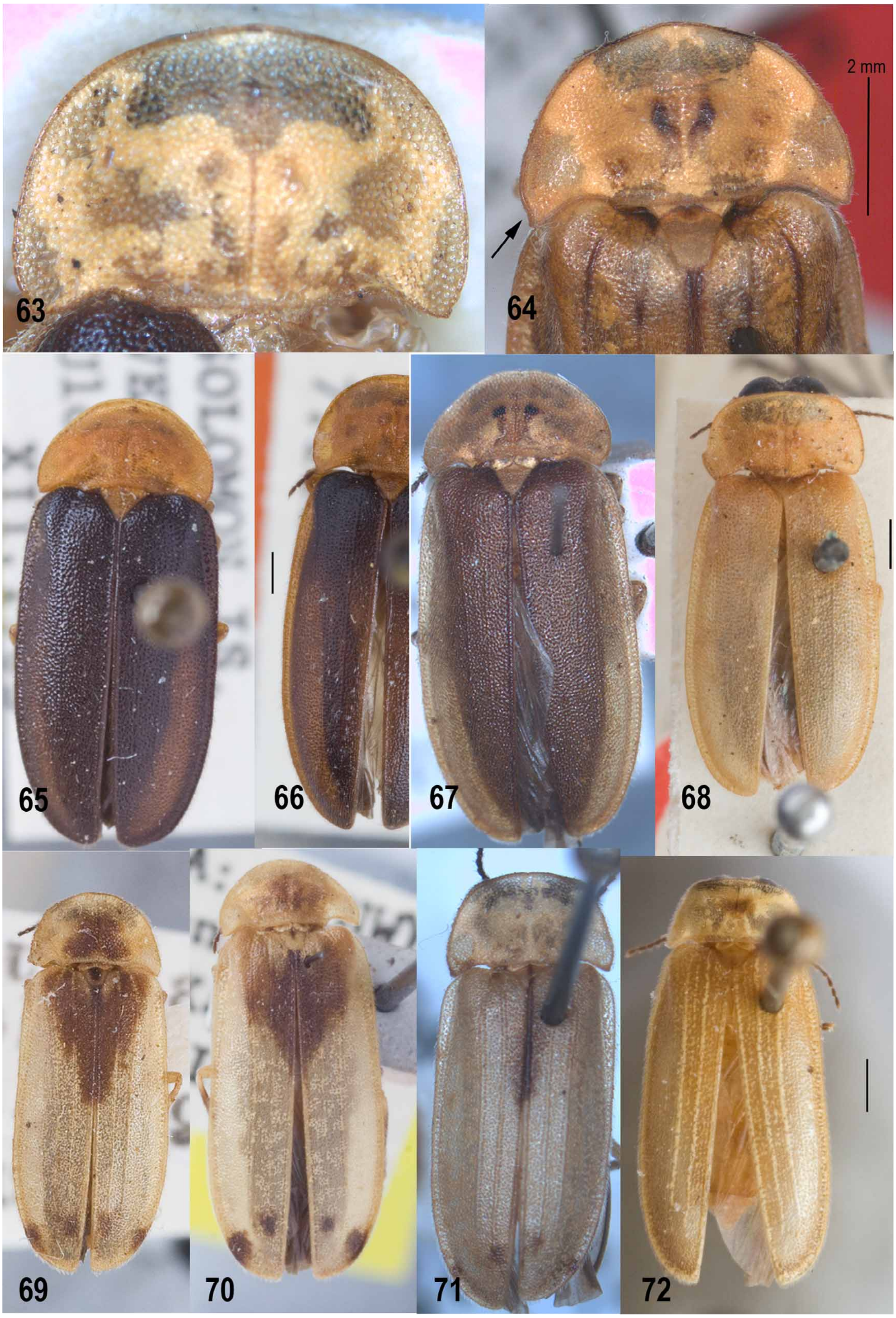

**FIGURES 27–38.** Characters key to genera of Luciolinae using males. 27, 29, 30, 32, 33, 34 *Missimia flavida* 27, 29, 30, 32 head, anterior, left lateral; 33 ventrolateral aspect base of L elytron (arrow indicates epipleuron); 34 pronotum and head. 28, 31 *Luciola substriata* (China, ANIC) head, anterior. 35 *Atyphella scabra* aedeagus, dorsal (Sea Falls, BPBM). 36 *Luciola nigra* aedeagus, ventral (Queensland, ANIC). 37 *Luciola cruciata* aedeagal sheath, ventral (Japan, ANIC). 38 *Photuroluciola deplanata* holotype male, aedeagal sheath, ventral (Madagascar, MNHN).



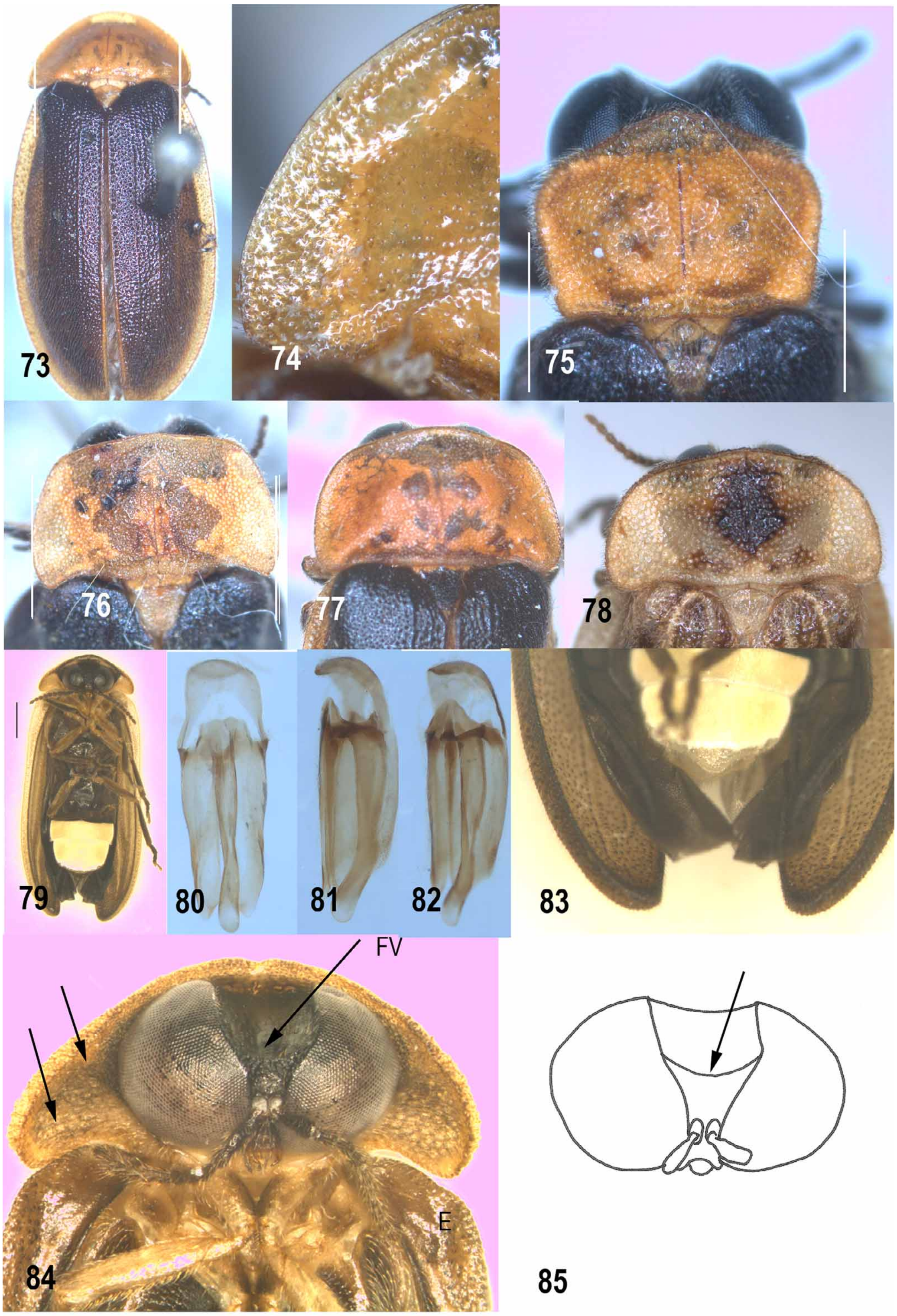

**FIGURES 39–47.** Characters key to genera of Luciolinae using males. *Photuroluciola deplanata* holotype male (Madagascar). 39, 40 dorsal whole body (39), pronotum (40) arrows indicate position of vertical sinuousity. 41–44 aedeagal sheath, dorsal (41, 42), ventral (43, 44). 45–47 abdomen, ventral, ventrites 5–7 (45), lateral ventrites 5–7 (46), ventral tergites 7, 8 (arrows indicate anterior prolongations of T8).



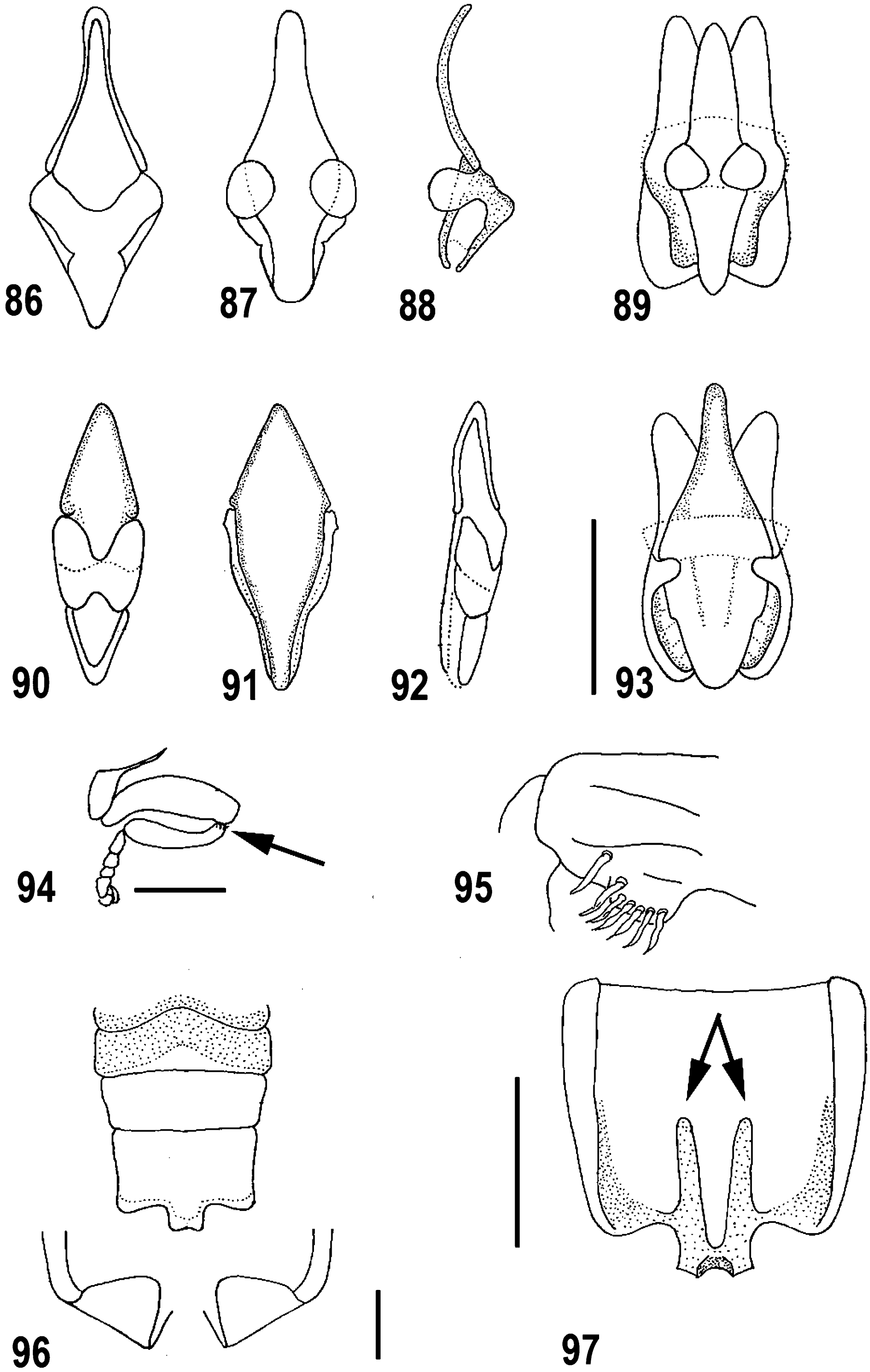

**FIGURES 48–62**. Characters key to genera of Luciolinae using males. 48–56 *Photuroluciola deplanata* holotype male (Mauritius, MNHN).48–55 aedeagus dorsal (48, 49 arrow indicates junction of ML with inner surface of LL), ventral (50, 51 arrows indicate groove in ML), left lateral (52, 53 stippled area on 53 indicates extent of groove on ML). 54, 55 detail apex ML and LL, right lateral (55), left lateral (56). 57 type labels. 57, 58 *Curtos okinawanus* male (Japan, ANIC). 57 dorsal elytra (arrows indicate elytral carina); 58 left dorsolateral pronotum and basal half of elytra (arrow indicates elytral carina). 59 *Bourgeoisia antipoda* male head, dorsal (Nin Reu, (SAM) eye emarginations arrowed. 60 *Pygoluciola hamulata* lectotype male abdomen left lateral (Sarawak, MCSN). 61, 62 *Pygatyphella huonensis* male (Huon Pen., BPBM), terminal abdomen, ventral (61), right lateral (62). Figure legends: MLF lateral flap on median lobe; MPP median posterior projection ventrite 7; LLF lateral flap left lateral lobe; T8 tergite 8.



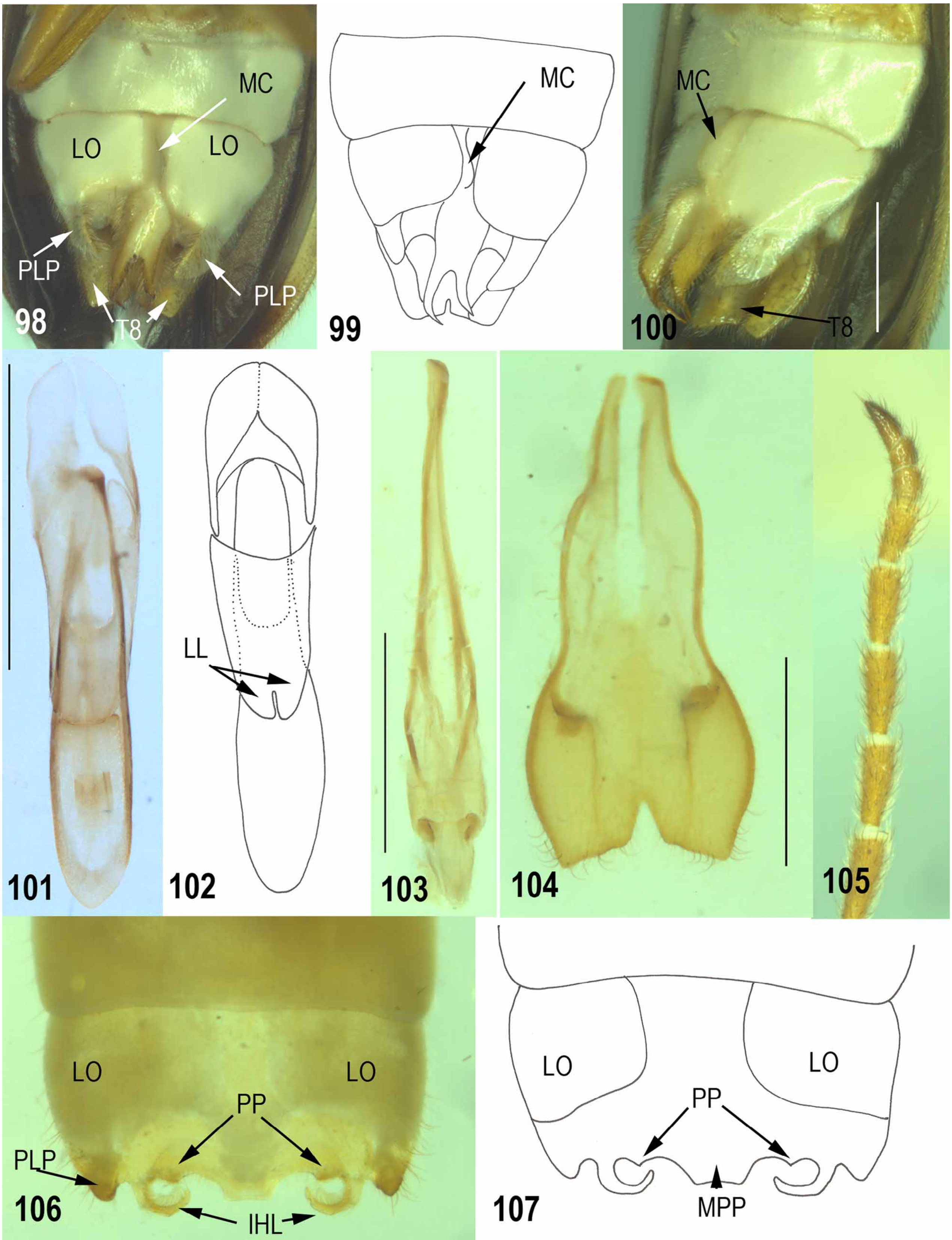

**FIGURES 63–72.** Characters key to genera of Luciolinae using males. 63 *Atyphella limbatipennis* holotype male, pronotum (Solomon Is., NHML). 64 *Pygatyphella eliptaminensis* holotype male, pronotum (Eliptamin Valley, BPBM). 65 *Pygatyphella salomonis* male (Vella Lavella, BPBM). 66 *Pygatyphella limbatipennis* male (Choiseul, BPBM). 67 *Pygatyphella limbatifusca* paratype male (Wugiroga, BPBM). 68 *Pygatyphella russellia* paratype male (Russell Island, NHML). 69, 71 *Pygatyphella obsoleta* male (69 Bulolo, 71 Lae BPBM). 70 *Pygatyphella wisselmerenia* paratype male (Wisselmeren, BPBM). 72 *Pygatyphella uberia* holotype male (Uberi, ANIC).



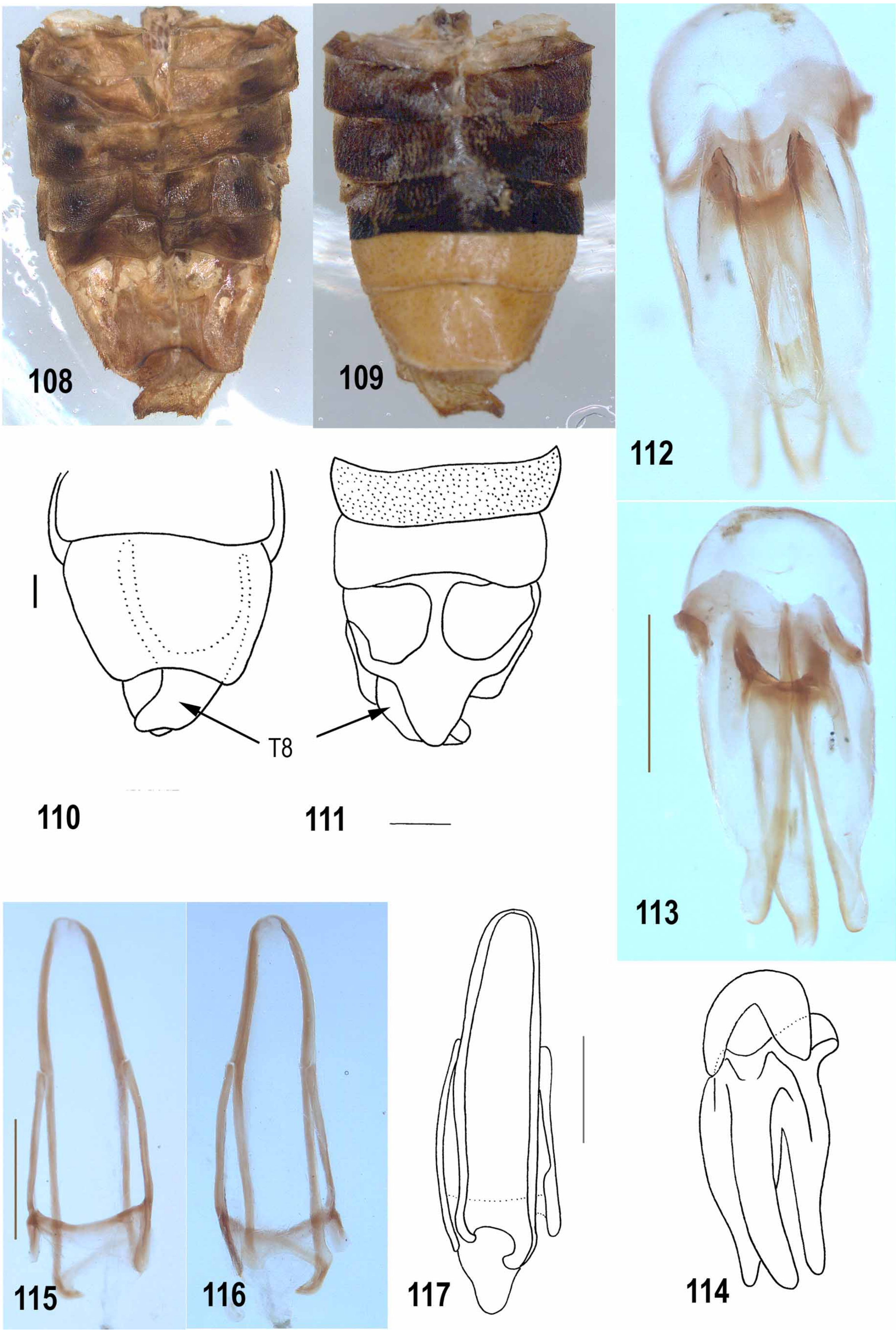

**FIGURES 73–85.** Characters key to genera of Luciolinae using males. 73, 74 *Convexa wolfi* male dorsal (lines indicate width across elytral humeri; 74 detail left pronotal surface (Kukugai, BPBM). 75 *Luciola nigra* pronotum lines indicate width across elytral humeri (Kuranda, ANIC). 76 *Lloydiella uberia* paratype male pronotum (lines indicate width across elytral humeri) (Uberi, BPBM). 77 *Magnalata limbata* male pronotum (Kira Kira, BPBM). 78, 79 *Atyphella lychnus* 78, male pronotum (Lansdowne State Forest, ANIC), 79 ventral aspect (Springbrook, ANIC). 80–82 *Lloydiella* sp. Paratypes, aedeagus ventral, left lateral and right dorsolateral (80 *Ll. wareo*, 81, 82 *Ll. japenensis*; BPBM). 83–85 *Atyphella atra*. 83 ventral terminal abdomen and elytral apices, 84, 85 anterior head (Springbrook, ANIC). Figure legends: arrows on left of 84 indicate strongly adpressed hypomeron; E epipleuron; FV frons–vertex junction (acute in this figure).



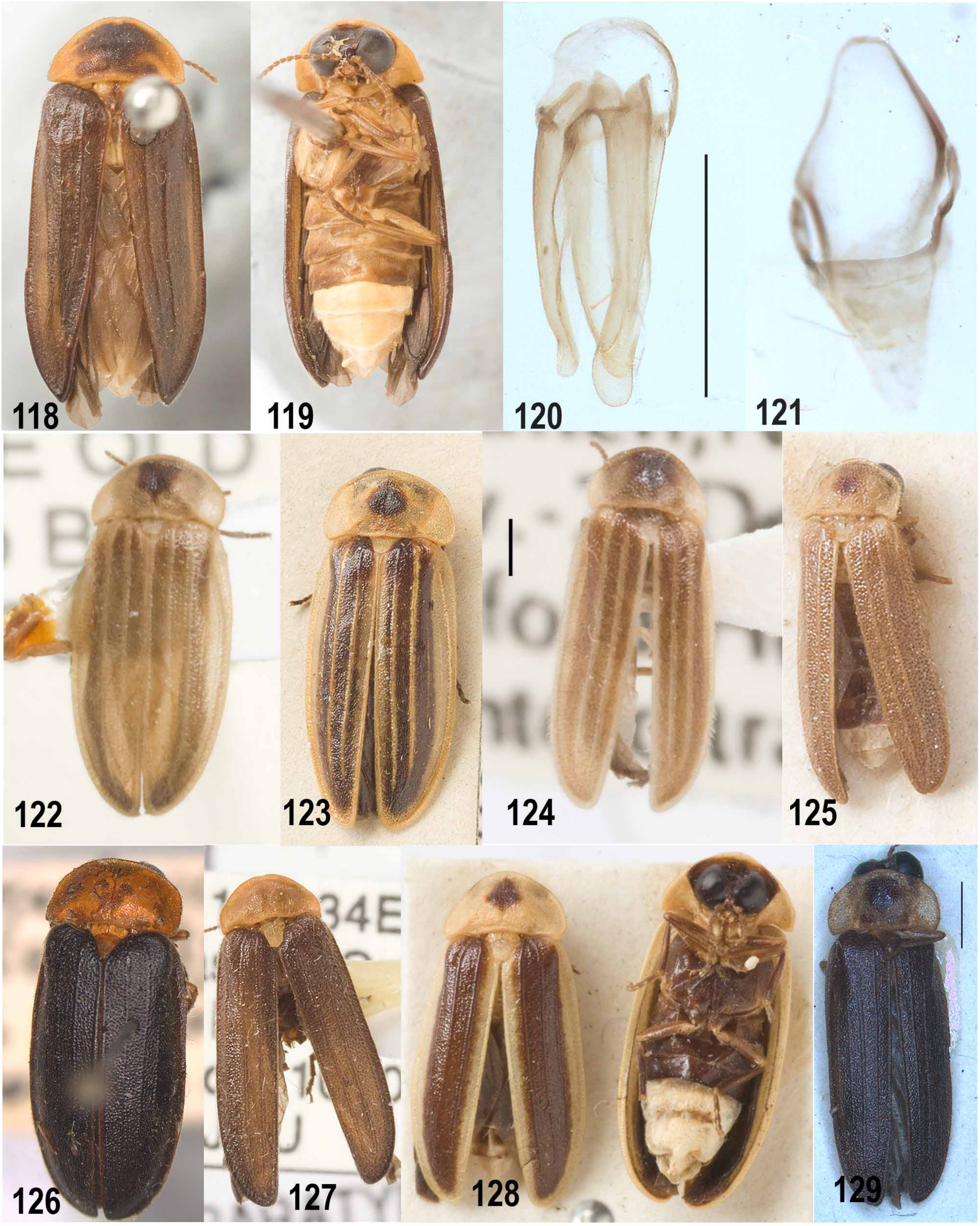

**FIGURES 86–97.** Characters key to genera of Luciolinae using males. Figures 86–93 redrawn with modification from Ballantyne 1987a. 86–89 *Pteroptyx malaccae* 86–88 aedeagal sheath dorsal, ventral and left lateral; 89 ventral tergite 8 with aedeagal sheath in situ. 90–93 *Pteroptyx effulgens* 90–92 aedeagal sheath dorsal, ventral and left lateral; 93 ventral tergite 8 with aedeagal sheath in situ. 94 *Pyrophanes appendiculata* left hind leg with metafemoral comb arrowed. 95 *Pteroptyx valida* male detail metafemoral comb. 96 *Pteroptyx torricelliensis* holotype male, ventral aspect terminal abdomen and elytral apices. 97 *Pteroptyx antennata* male dorsal surface ventrite 7 with cuticular strips arrowed.



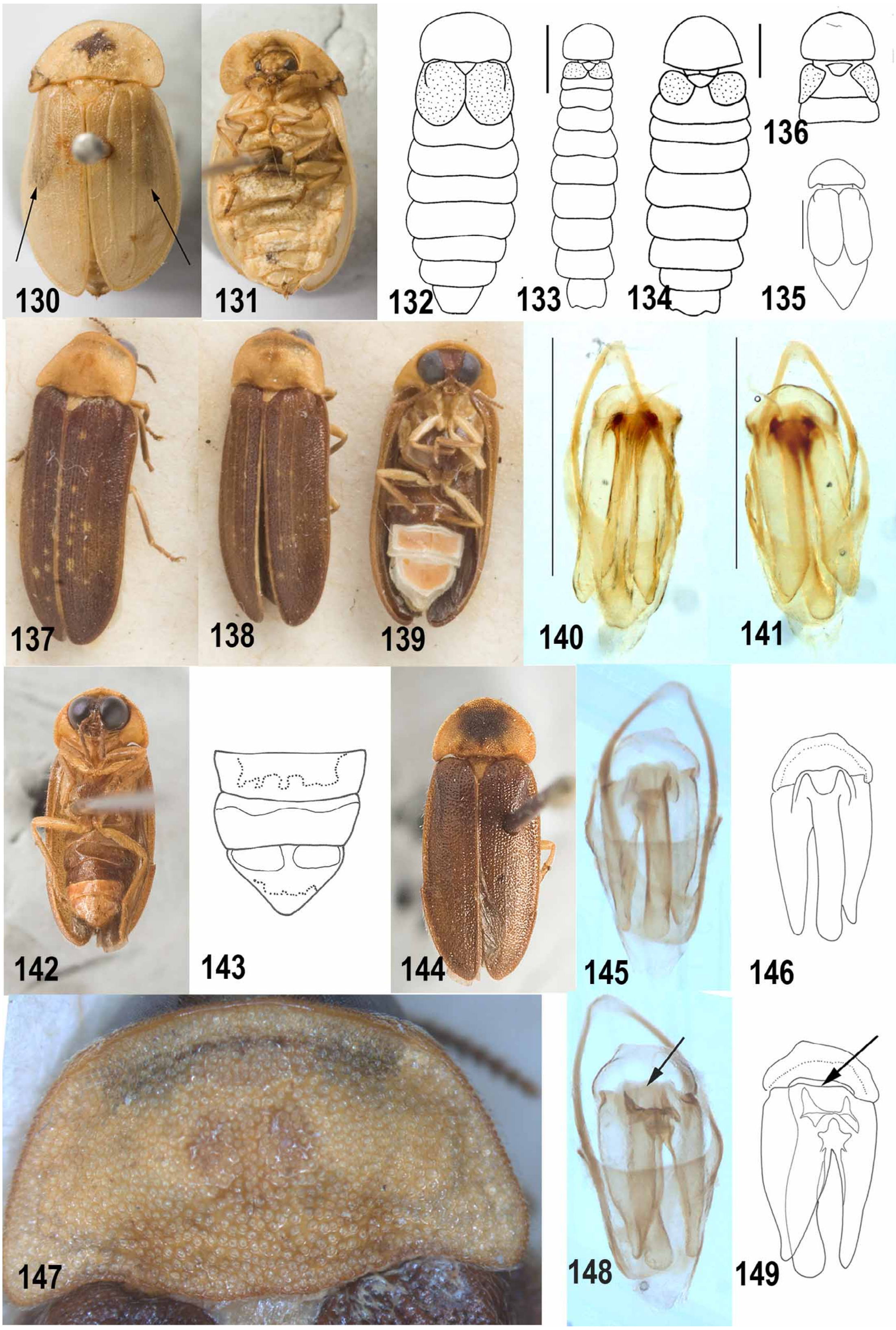

**FIGURES 98–107.** Characters key to genera of Luciolinae using males. 98–105 *Colophotia praeusta* (Philippines, USNM) 98–100 abdomen, ventral and left ventrolateral; 101, 102 aedeagus ventral, dorsal; 103 aedeagal sheath dorsal; 104 tergite 8 ventral; 105 right antenna FS 2–9. Figure legends IHL incurving hairy lobe; LL lateral lobes; LO light organs; MC median carina; MPP median posterior projection; PLP posterolateral projections; PP pointed projection; T8 tergite 8.



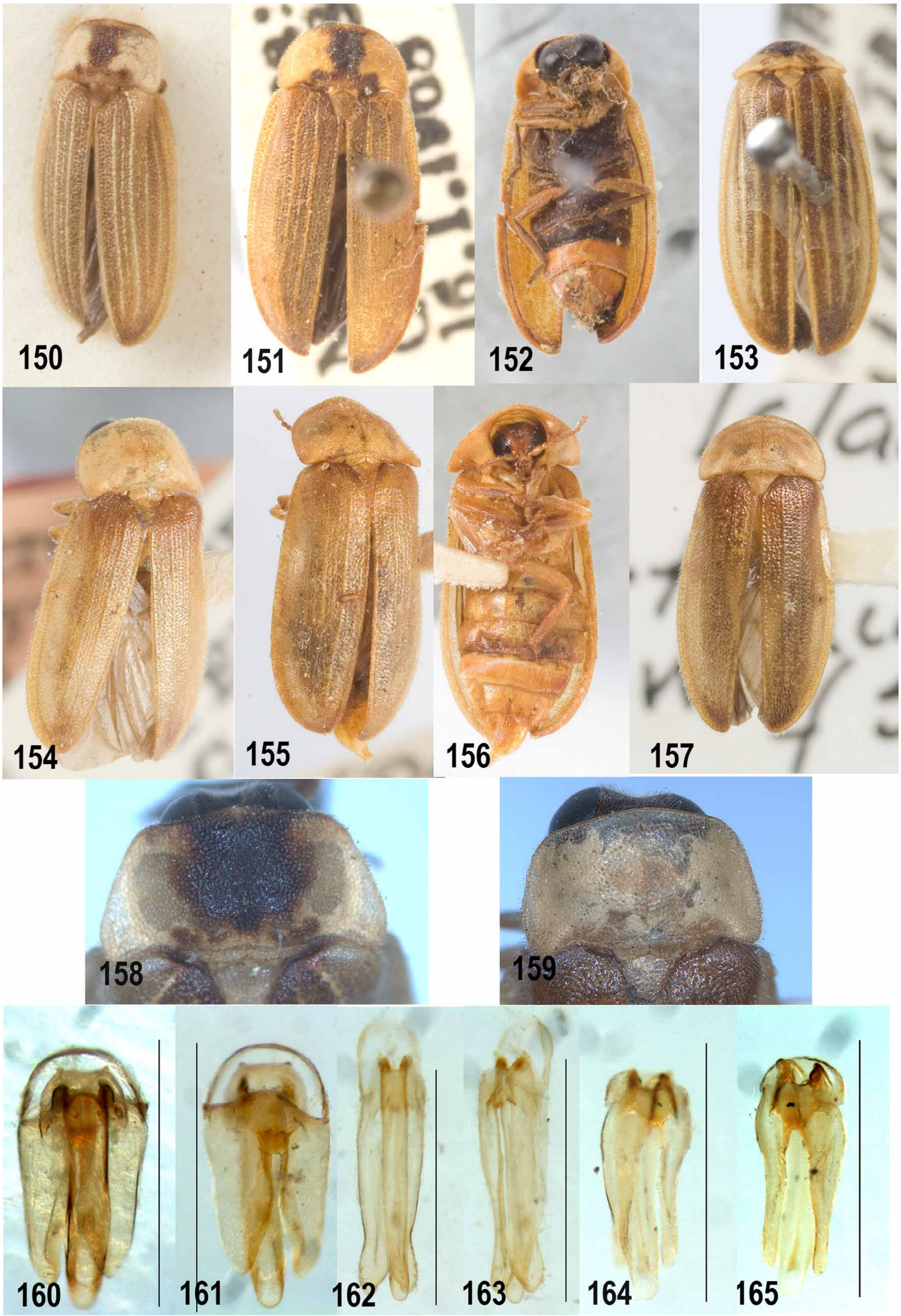

**FIGURES 108–117.** *Asymmetricata circumdata* 108, 109, 112–117; *As. ovalis* 110, 111. 108, 110 abdomen dorsal; 109, 111 abdomen ventral; 112–114 aedeagus ventral, dorsal, ventrolateral; 115–117 aedeagal sheath dorsal, ventral (Thailand, ANIC).



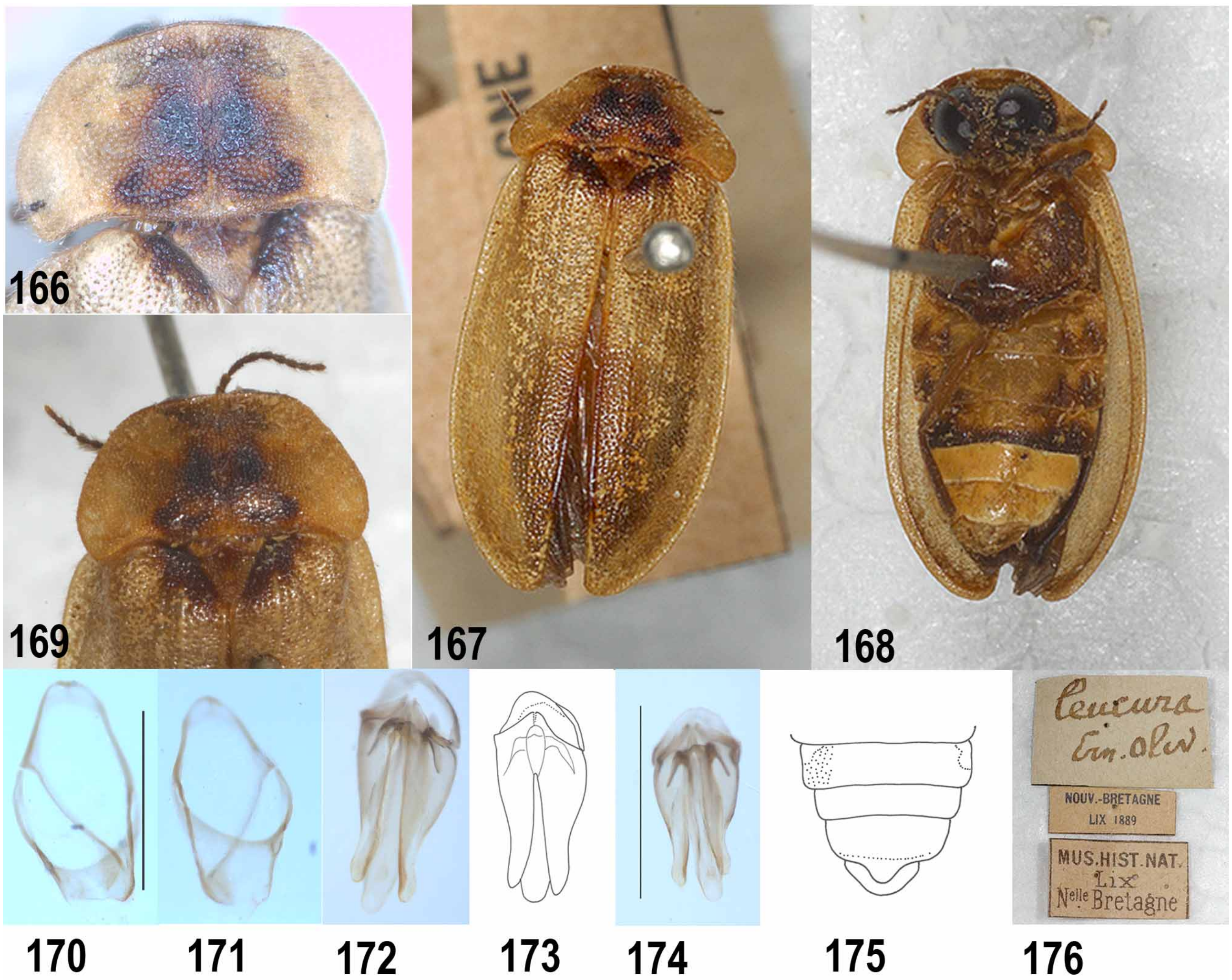

**FIGURES 118–129.** *Atyphella* sp. Males. 118–121 *A. aphrogeneia* dorsal, ventral, aedeagus ventrolateral, aedeagal sheath dorsal (Malekula, BPBM). 122 *A. brevis* (Longlands Gap, ANIC). 123 *A. flammans* (Cairns, BPBM). 124 *A. lewisi* paratype (abdomen dissected) (Mt Lewis, ANIC). 125 *A. inconspicua* paratype (Cairns, ANIC). 126 *A. guerini* (Kavieng, BPBM). 127 *A. immaculata* paratype (abdomen dissected) (Mt Fisher, ANIC). 128 *A. olivieri* 'syntypes' dorsal, ventral (Cairns, NHML). 129 *A. scintillans* (Acacia Plateau, ANIC).



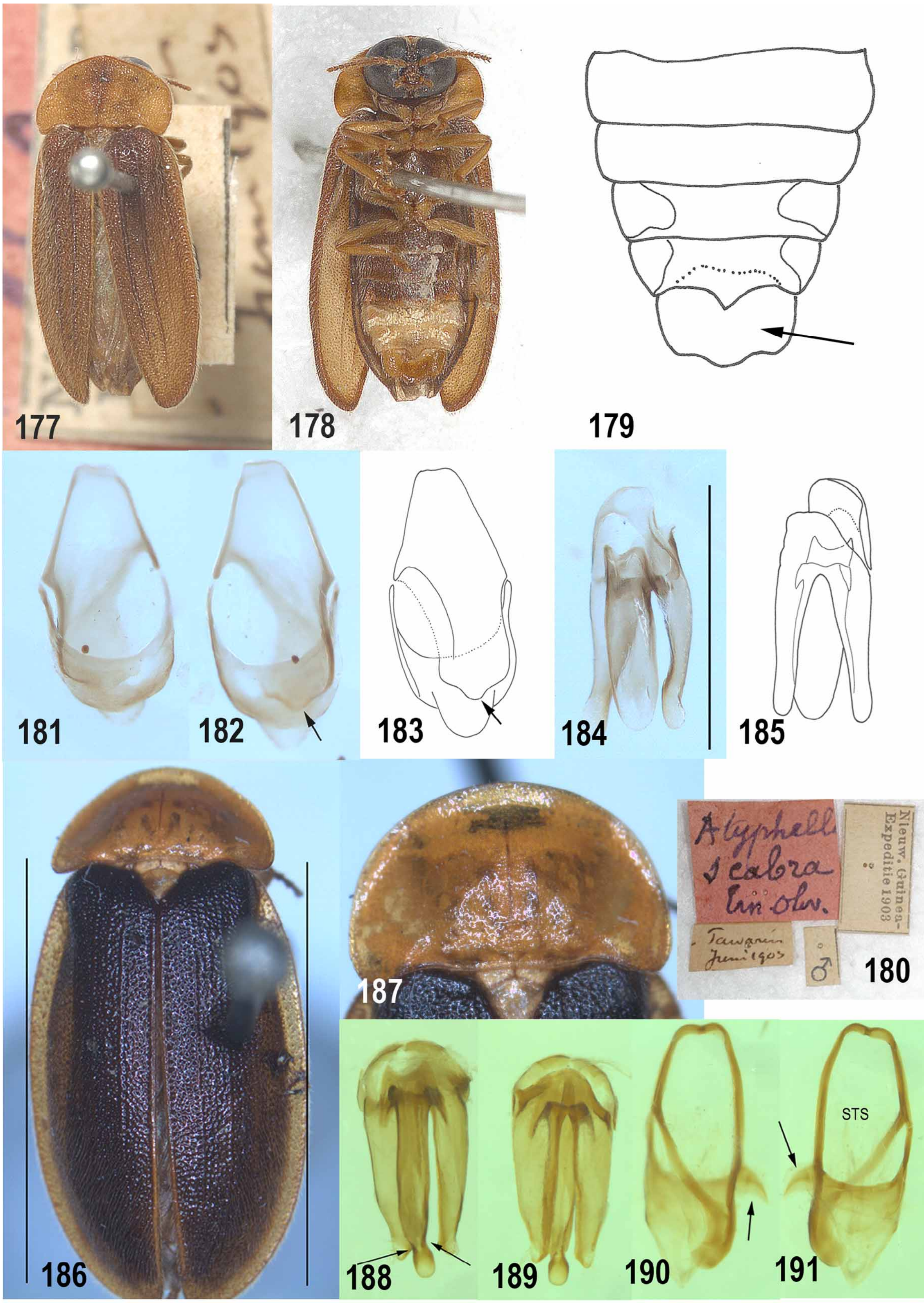

**FIGURES 130–149**. *Atyphella* spp. 130, 131 *A. flammans* female, dorsal ventral (emerged from larvae taken at Mt Blackwood, QMBA). 132–136 diagrammatic representation flightless *Atyphella* females; 132, 135 *A. scintillans*, 133 *A. inconspicua*; 134 *A. similis*; 136 probably *A. lewisi*. 137–141, 147 *A. dalmatia* **sp. n.** 137–139 dorsal and ventral paratype males; 140, 141 aedeagus in sheath, ventral (140) and dorsal; 147 pronotum paratype male. 142–146, 148, 149 *A. kira-kira* **sp. n.** 142, 144 dorsal, ventral; 143 ventral terminal abdomen ventrites 5–7; 145, 148 aedeagus in sheath ventral (145) and dorsal; 146, 149 aedeagus ventral (146) and dorsal.



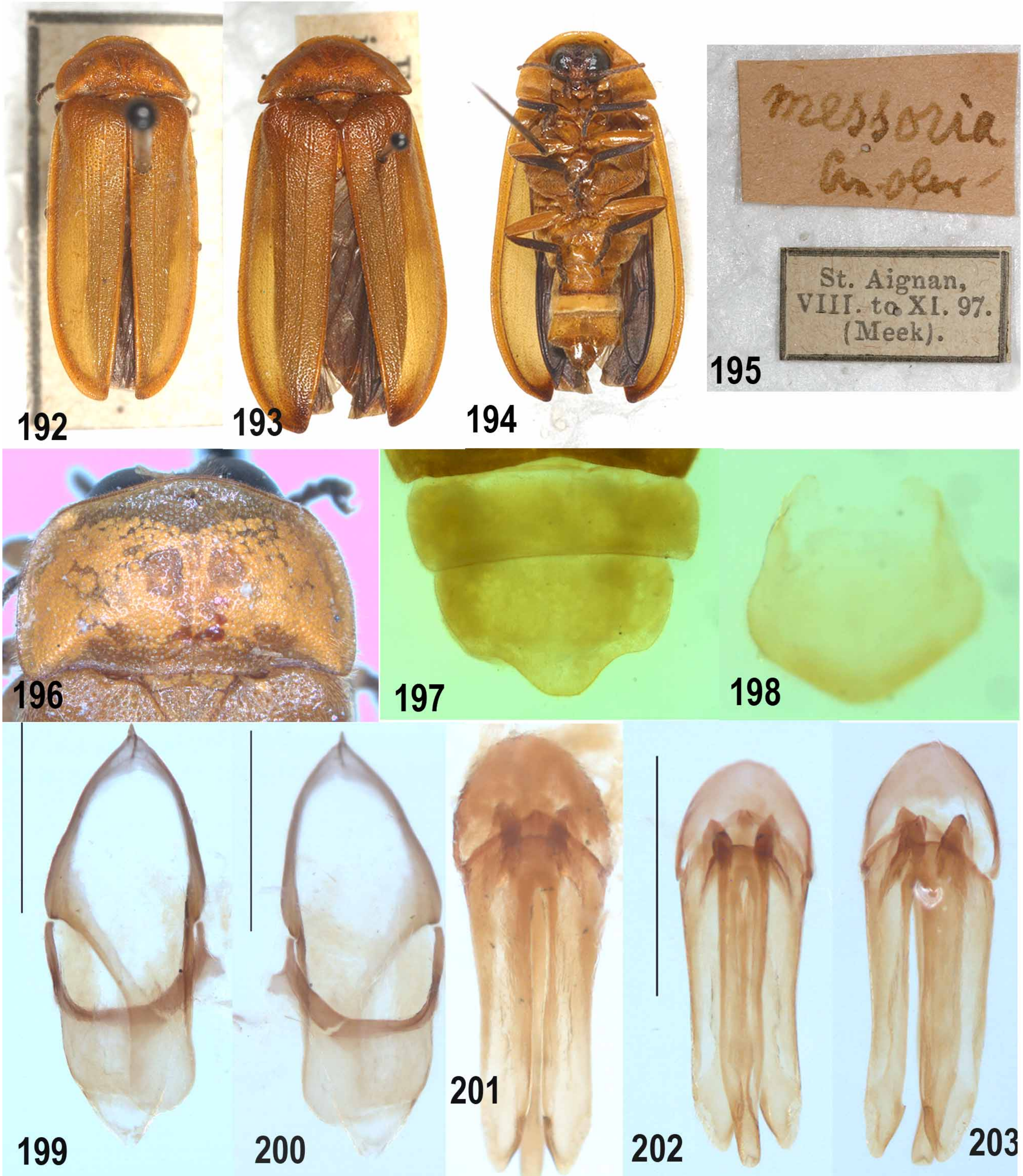

**FIGURES 150–165.** *Atyphella* spp. 150–152, 160, 161 *A. lamingtonia* **sp. n.** 150, 151 dorsal paratype males (150 SAM; 151 Garaina, BPBM); 152 ventral Garaina male; 160, 161 aedeagus, ventral, dorsal. 153, 158, 164, 165 *A. testaceolineata*. 153 dorsal male (Erume, BPBM); 154 pronotum male (Etrume, BPBM); 164, 165 aedeagus ventral, dorsal. 154–157, 159, 162, 163 *A. palauensis*. 154, 157 dorsal [154 paratype male BPBM; 157 male (Babelthaup, BPBM)]; 155, 156 dorsal, ventral paratype female (BPBM); 159 pronotum male (Palau, BPBM).



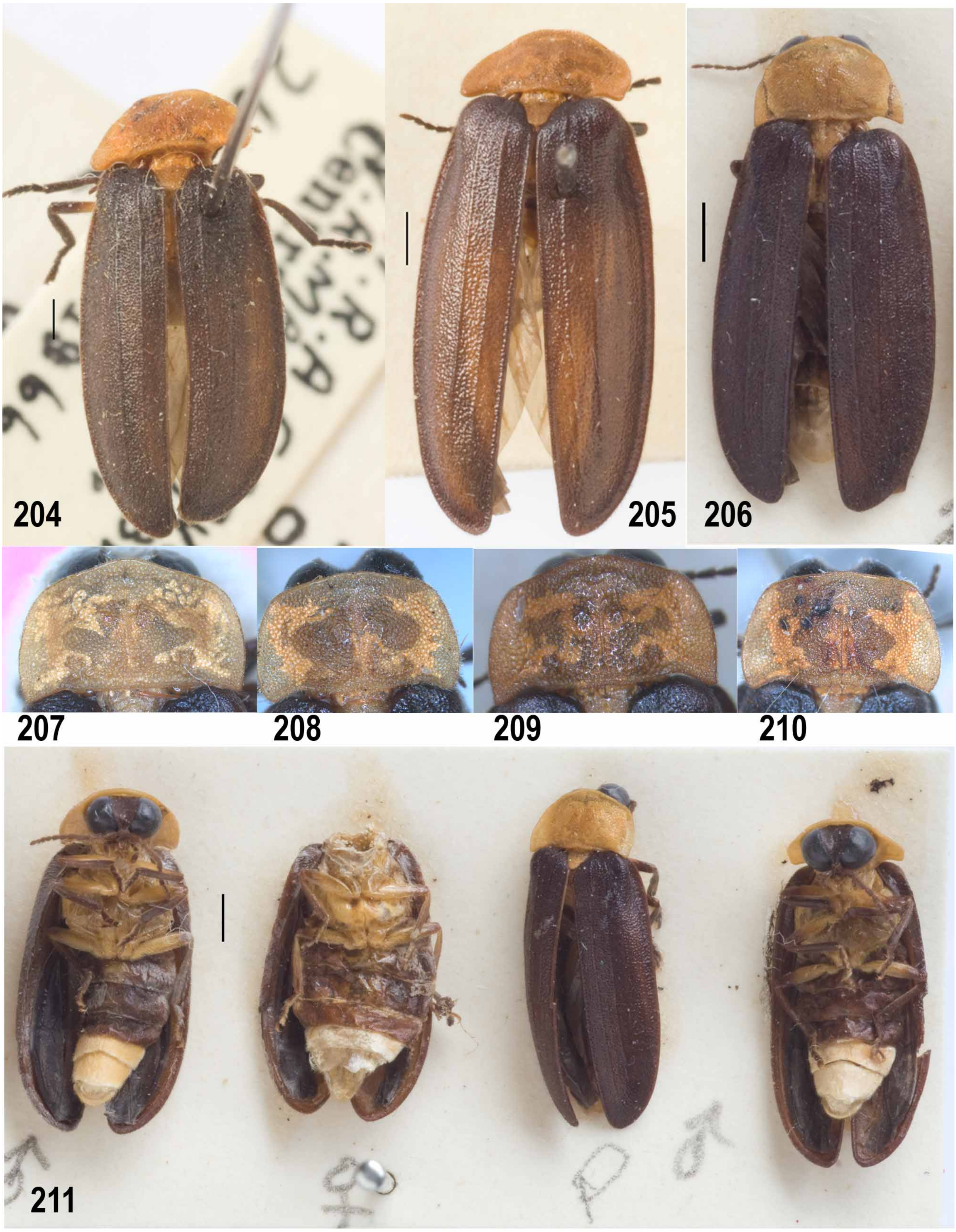

**FIGURES 166–176.** *Atyphella leucura*. 166, (Kerevat male, BPBM) 167–176 type male (MNHN). 169 detail pronotum; 167, 168 dorsal, ventral, male; 170, 171 aedeagal sheath ventral, dorsal; 172–174 aedeagus dorsal and ventral (174); 175 ventral terminal abdomen; 176 type labels.



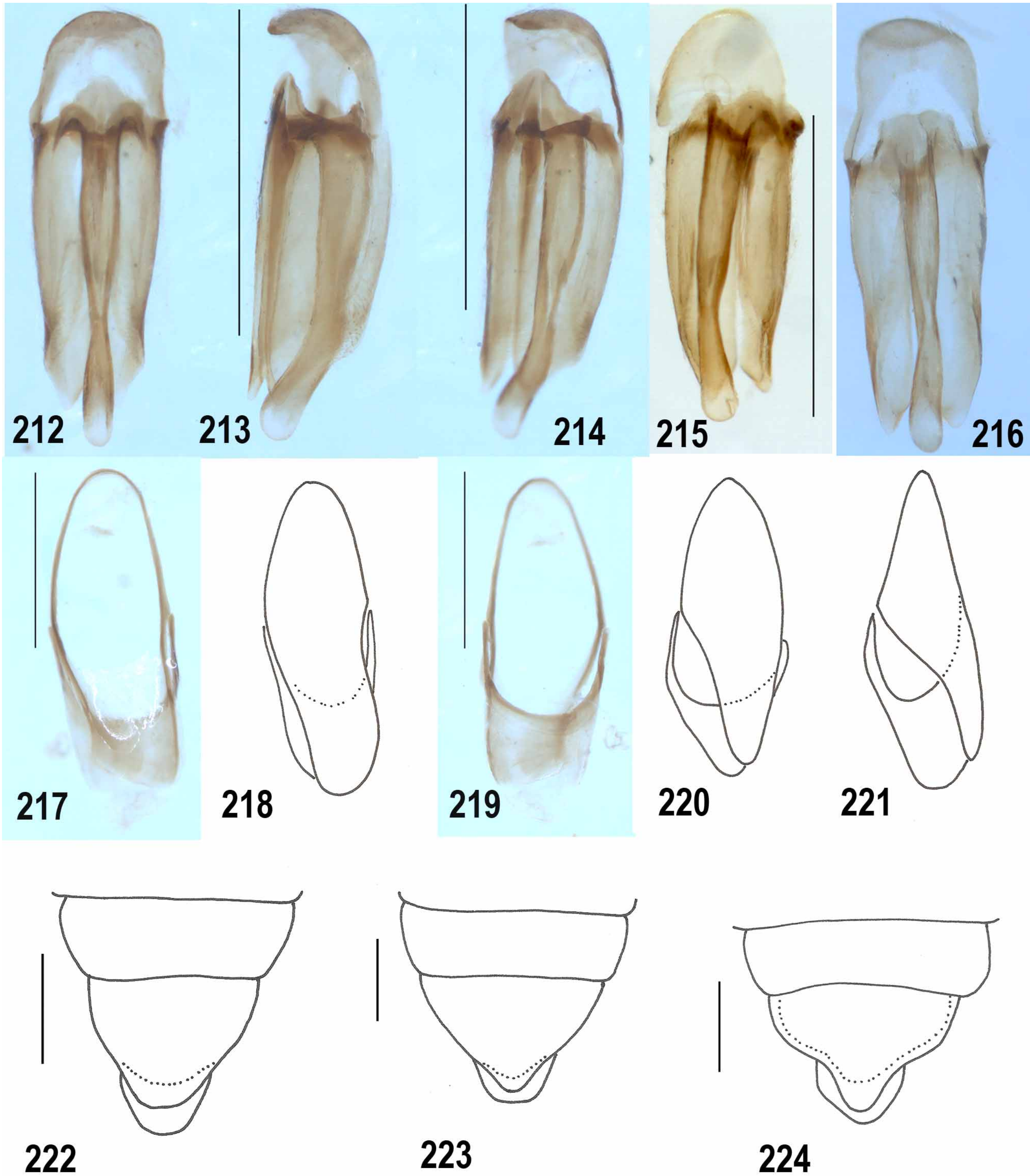

**FIGURES 177–185** *Atyphella scabra* type male (MNHN). **Figures 186–191** *Convexa wolf* male (Kukugai, BPBM). 177, 186 dorsal body (lines on 186 are parallel); 178 ventral; 179 ventral abdominal ventrites 4–7 and tergite 8 (arrowed); 180 type labels; 181–183, 190, 191 aedeagal sheath dorsal (181, 191) and ventral (arrows on 182, 183 indicate protrusion on posterior margin of sheath sternite); 184, 185, 188, 189 aedeagi ventral (184, 188) and dorsal; 187 detail pronotal surface male (Kukugai, BPBM).




**FIGURES 192–203**. *Gilvainsula messoria* type male (MNHN) 192, 195, 196, 199–203; *G. similismessoria* paratype females 193, 194, paratype male 197, 198. 192, 193 196 dorsal; 194 ventral whole body; 195 type labels; 197, 198 terminal abdomen ventral ventrites 6, 7 (197); 198 ventral tergite 8; 199, 200 aedeagal sheath dorsal, ventral; 201–203 aedeagus dorsal, ventral, ventrolateral.

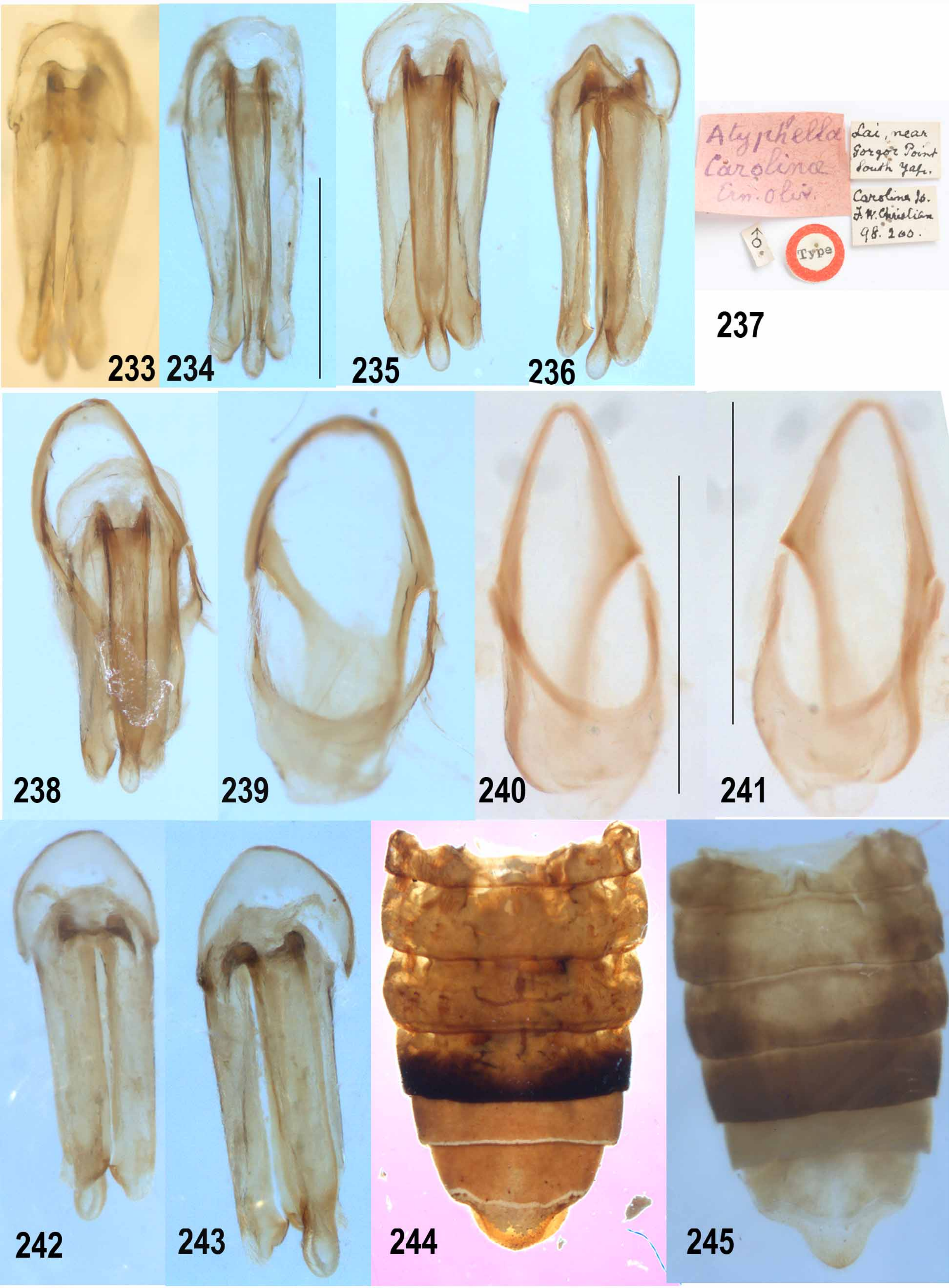



**FIGURES 204–211**. *Lloydiella* spp. paratype males. 204, 208, 210 *Ll. uberia*; 205, 209 *Ll. japenensis*; 206, 207, 211 *Ll wareo* (BPBM). 204–206 dorsal whole body (204, 206 have abdomen dissected); 207–210 dorsal pronota; 211 four specimens on one card, L to R male ventral, female ventral (no head or pronotum), male dorsal, male ventral.

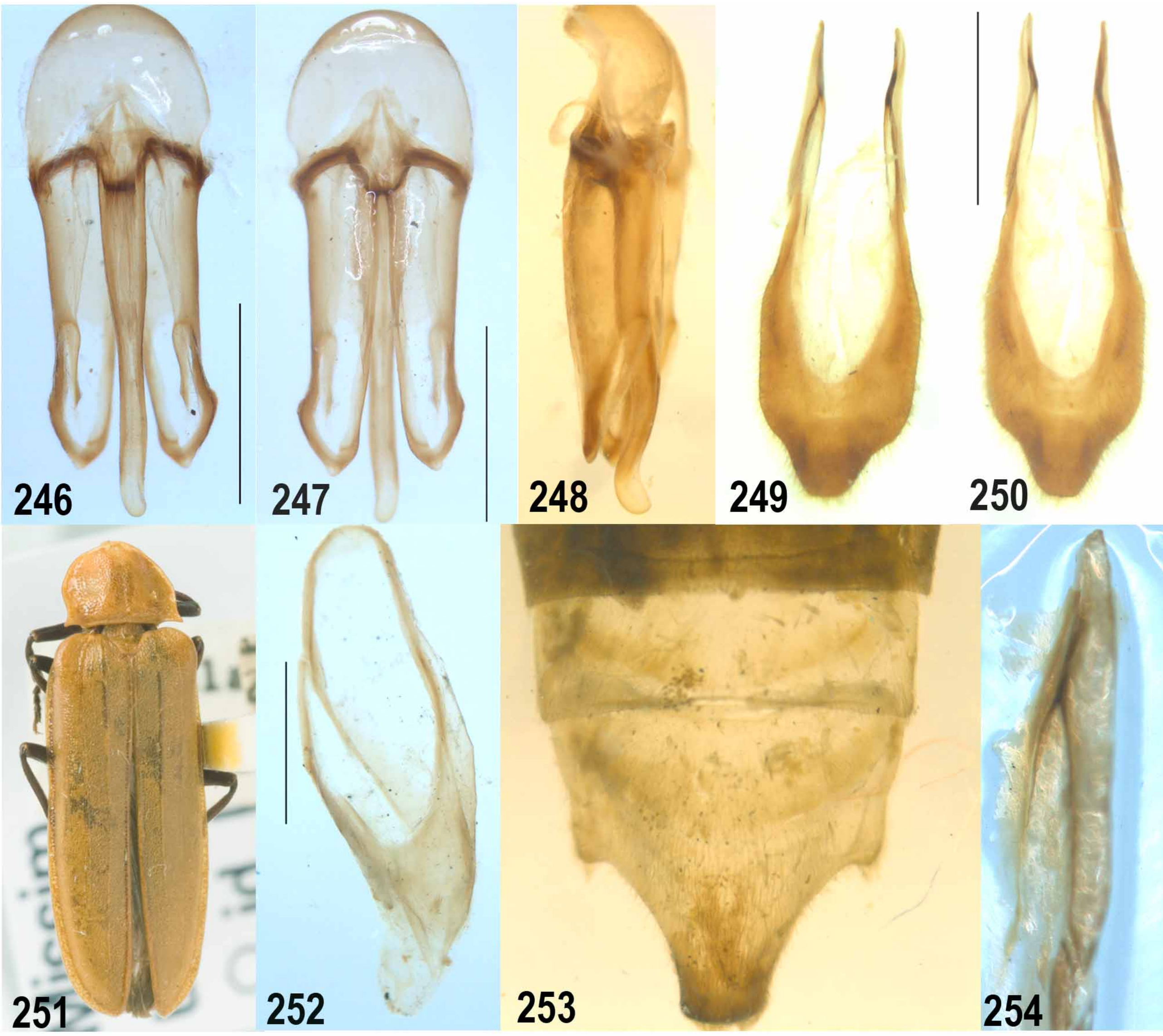



**FIGURES 212–224.** *Lloydiella* spp. paratype males. *Ll. japenensis* 212–214, 217–219, 222. *Ll. majuscula* holotype 223. *Ll. uberia* 215, 220, 224. *Ll. wareo* 216, 221, 224. 212, 215, 216 aedeagi ventral; 213 aedeagus left laterodorsal; 214 aedeagus slightly laterodorsal; 217, 218, 220, 221 aedeagal sheath, ventral; 219 aedeagal sheath dorsal; 222–224 abdominal ventrites 6, 7 and tergite 8 ventral.

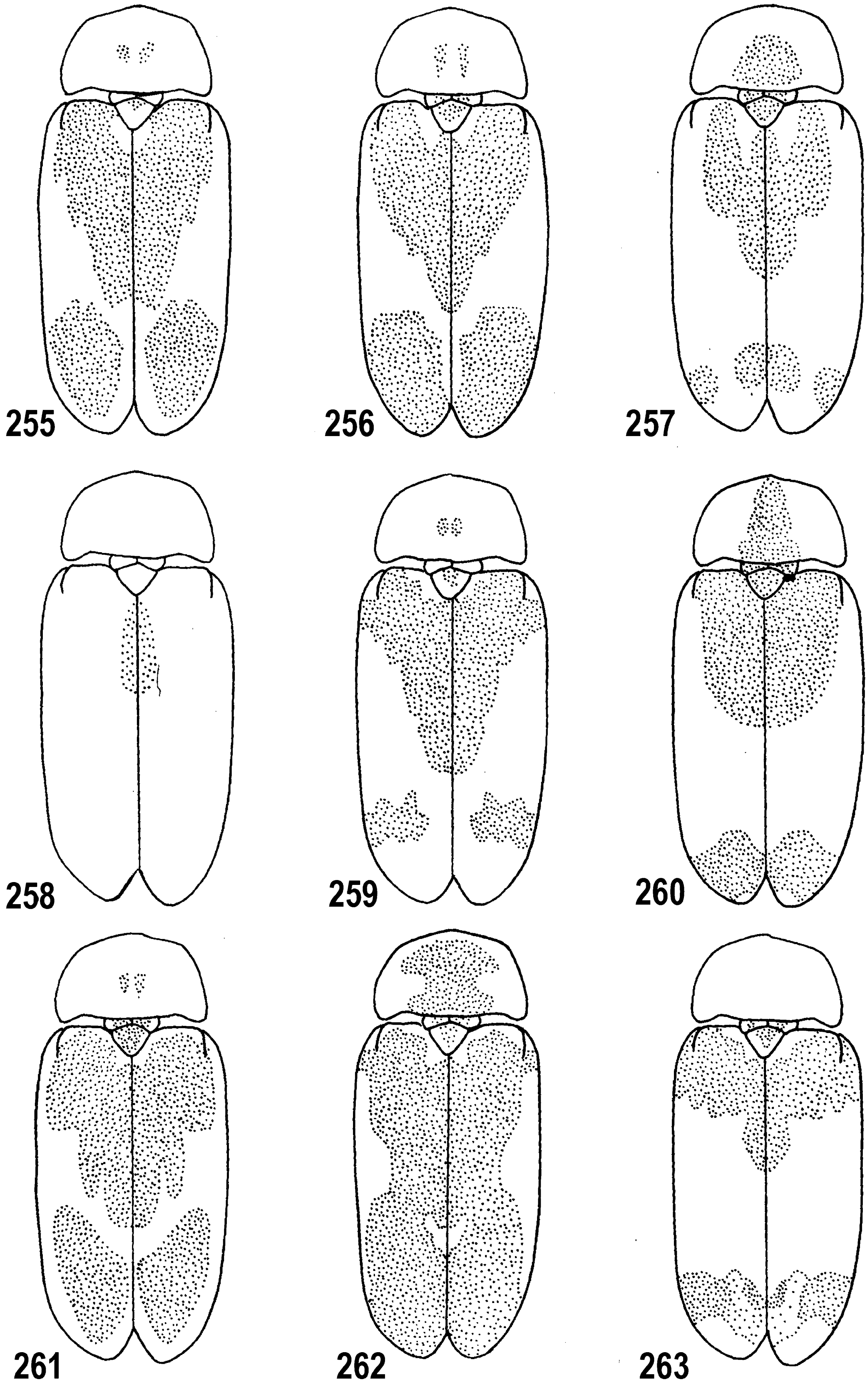

**FIGURES 225–232.** *Magnalata* spp. 225, 226 *M. carolinae* (225 type male, NHML, 226 Yap male, BPBM). 227–230 *M. limbata* (227, 228 female dorsal and ventral, Florida Group, BPBM; 229, 230 pronota, 229 Kira Kira male BPBM; 230 San Cristobal male BPBM). 231, 232 *M rennellia* paratype male, ventral and dorsal.



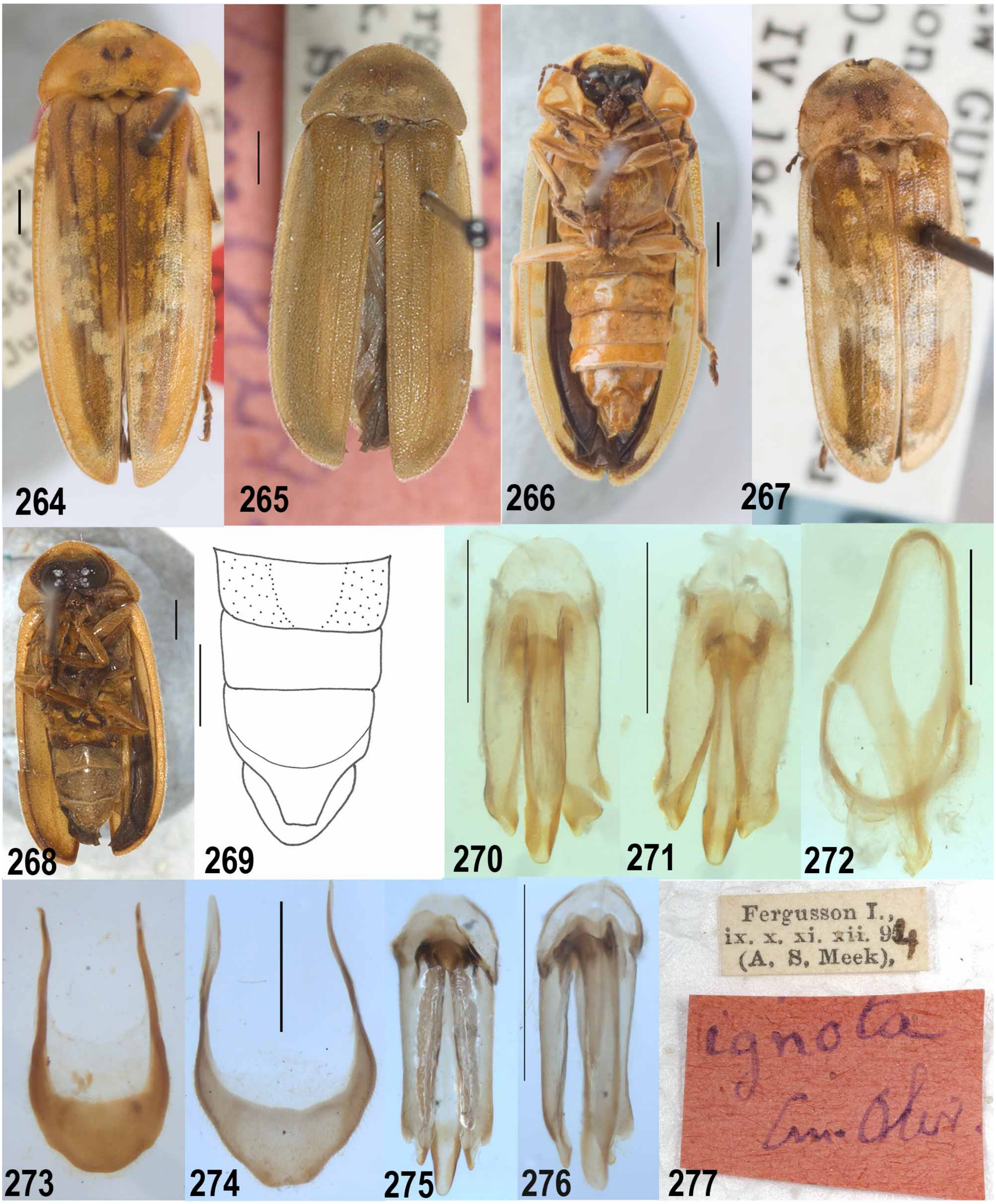

**FIGURES 233–245**. *Magnalata* spp. 233, 234, 237, 240, 241 *M. carolinae* type male NHML. 234–236, 238, 239, 244 *M. limbata* (all Kira Kira males except for 244 Manipwena male, BPBM). *M. rennellia* paratype male 242, 243, 245. 233, 236, 242 aedeagus dorsal; 234, 235, 243 aedeagus ventral; 237 type label; 238 aedeagus in sheath ventral; 239–241 aedeagal sheath ventral (239, 241) and dorsal; 244, 245 ventral abdomen ventrites 2–7, tergite 8 removed.



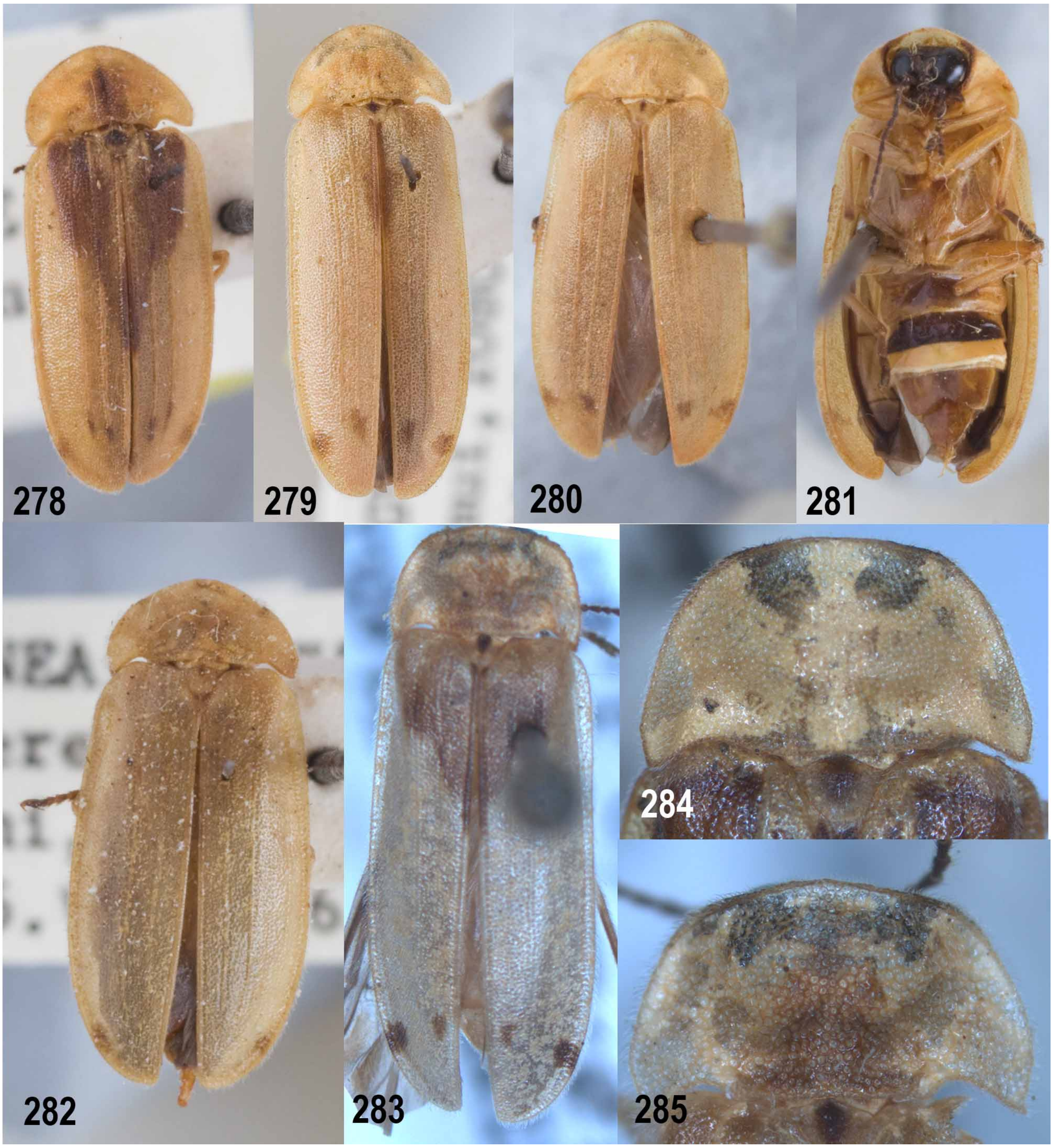

**FIGURES 246–254.** *Missimia flavida*, 246–250, 252–254 type male; 251 female (Mt Shungol, QM). 246–248 aedeagus, ventral, dorsal, left lateral; 249, 250, 254 tergite 8 (254 detail tip of left prolongation); 252 aedeagal sheath ventral; 253 abdominal ventrites 5–7, softened in hot water, tergite 8 removed.



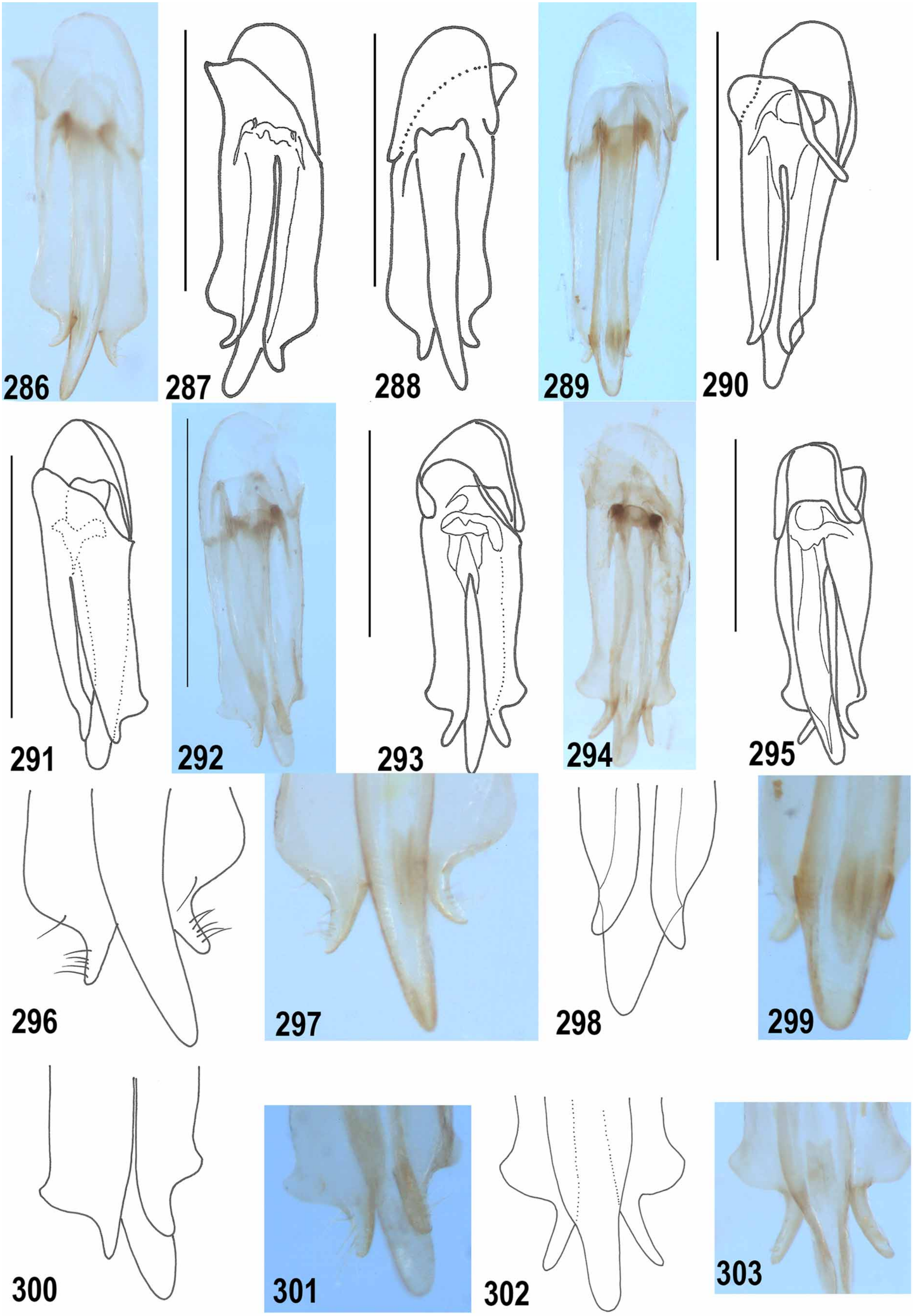

**FIGURES 255–263.** *Pygatyphella* males, semidiagrammatic representation of dorsal colour patterns, not to scale. 255 *Pygat. eliptaminensis*. 256 *Pygat. huonensis*. 257, 258 *Pygat. obsoleta*. 259 *Pygat. peculiaris*. 260 *Pygat. pulcherrima*. 261, 262 *Pygat. tagensis*. 263 *Pygat. undulata*.



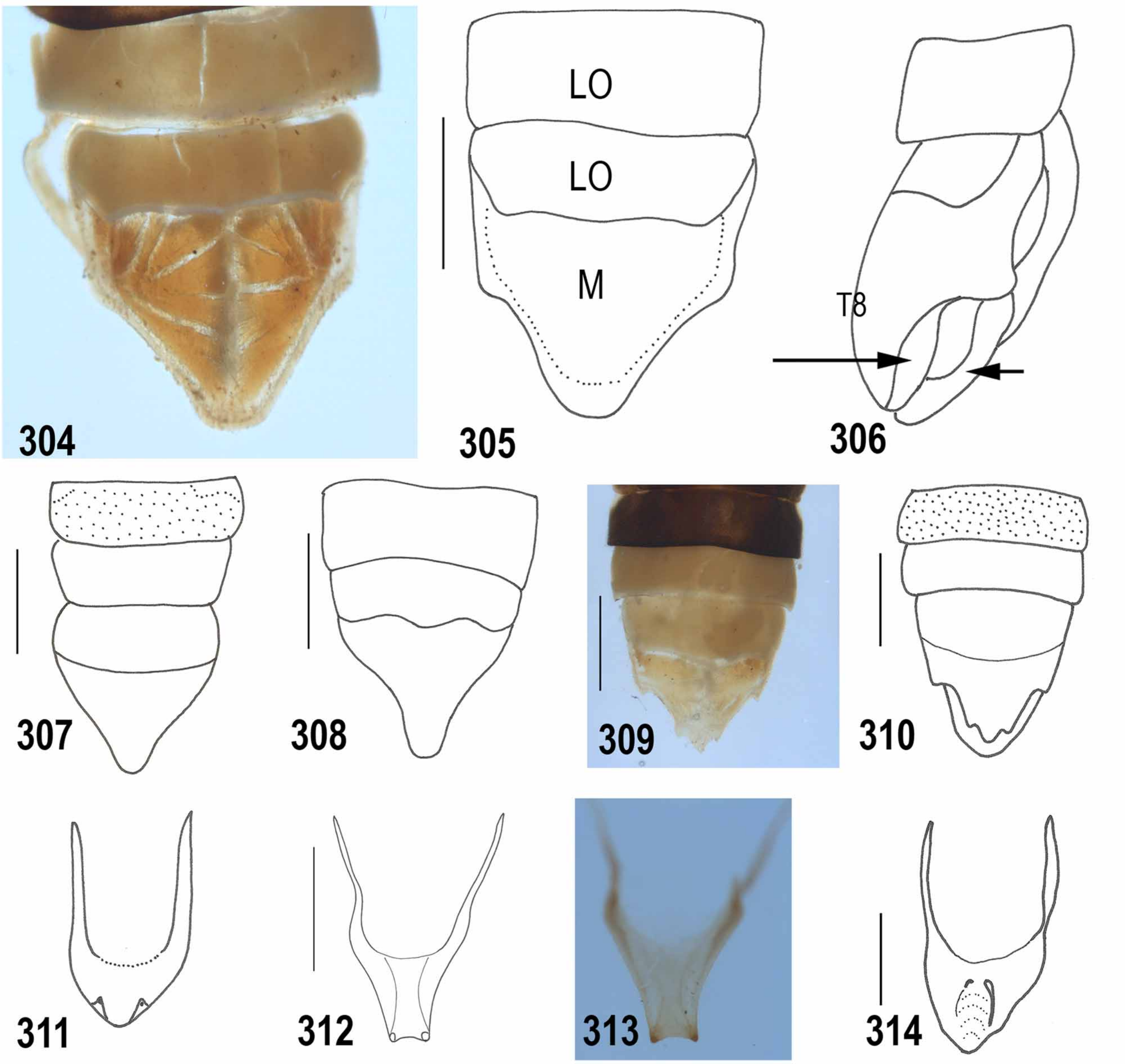

**FIGURES 264–277**. *Pygatyphella* spp. 264, 270–273 *Pygat. eliptaminensis* holotype male (Eliptamin Valley, BPBM), 266 paratype female (BPBM). 265, 268, 269, 274–277 *Pygat. ignota* holotype male (Fergusson Is., MNHN). 267 *Pygat. huonensis male* (Huon Pen., BPBM). 264, 265, 267 dorsal whole body, 266, 268 ventral whole body. 269 ventral abdominal ventrites 5–7 and tergite 8; 270, 271, 275, 276 aedeagi (ventral 270, 276, and dorsal); 272 aedeagal sheath ventral; 273, 274 tergite 8; 277 type labels.



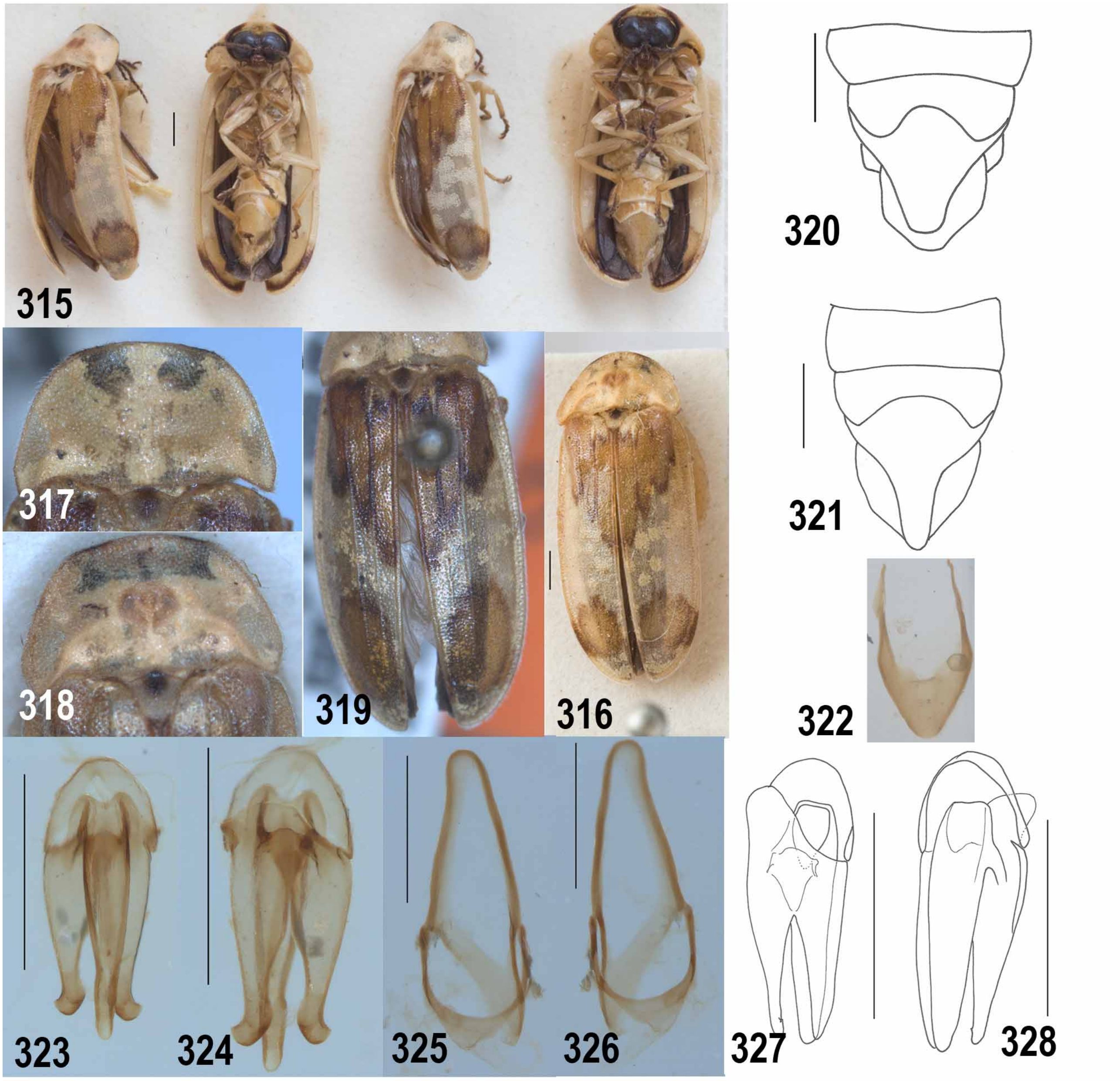

**FIGURES 278–285**. *Pygatyphella* spp. 278 *Pygat. japenensis* paratype male. 279–281, 284 *Pygat. karimui* paratype male (279, 284 pronotum), paratype female (280, 281 ventral). 282 *Pygat. nabiria* paratype male. 283, 285 *Pygat. okapa* paratype male (285 pronotum) (BPBM).



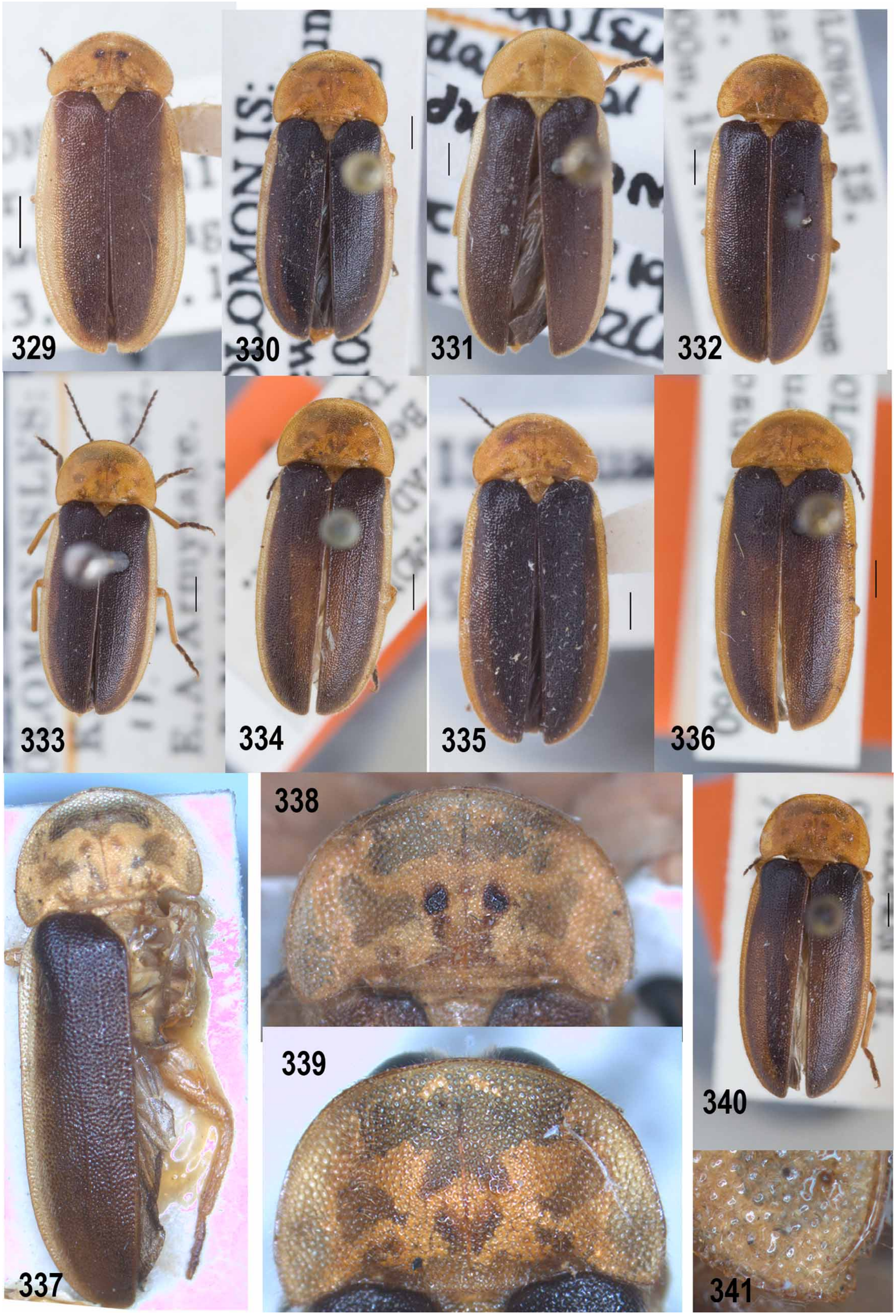

**FIGURES 286–303.** *Pygatyphella* spp. Aedeagi, paratype males. 286–288, 296, 297 *Pygat. japenensis*. 289, 290, 298, 299 *Pygat. karimui*. 291, 292, 300, 301 *Pygat. nabiria*. 293–295, 302, 303 *Pygat. okapa*. 286, 287, 289, 292, 295, dorsal; 288, 289, 292, 294 ventral; 296–303 ventral detail apices of LL and ML.



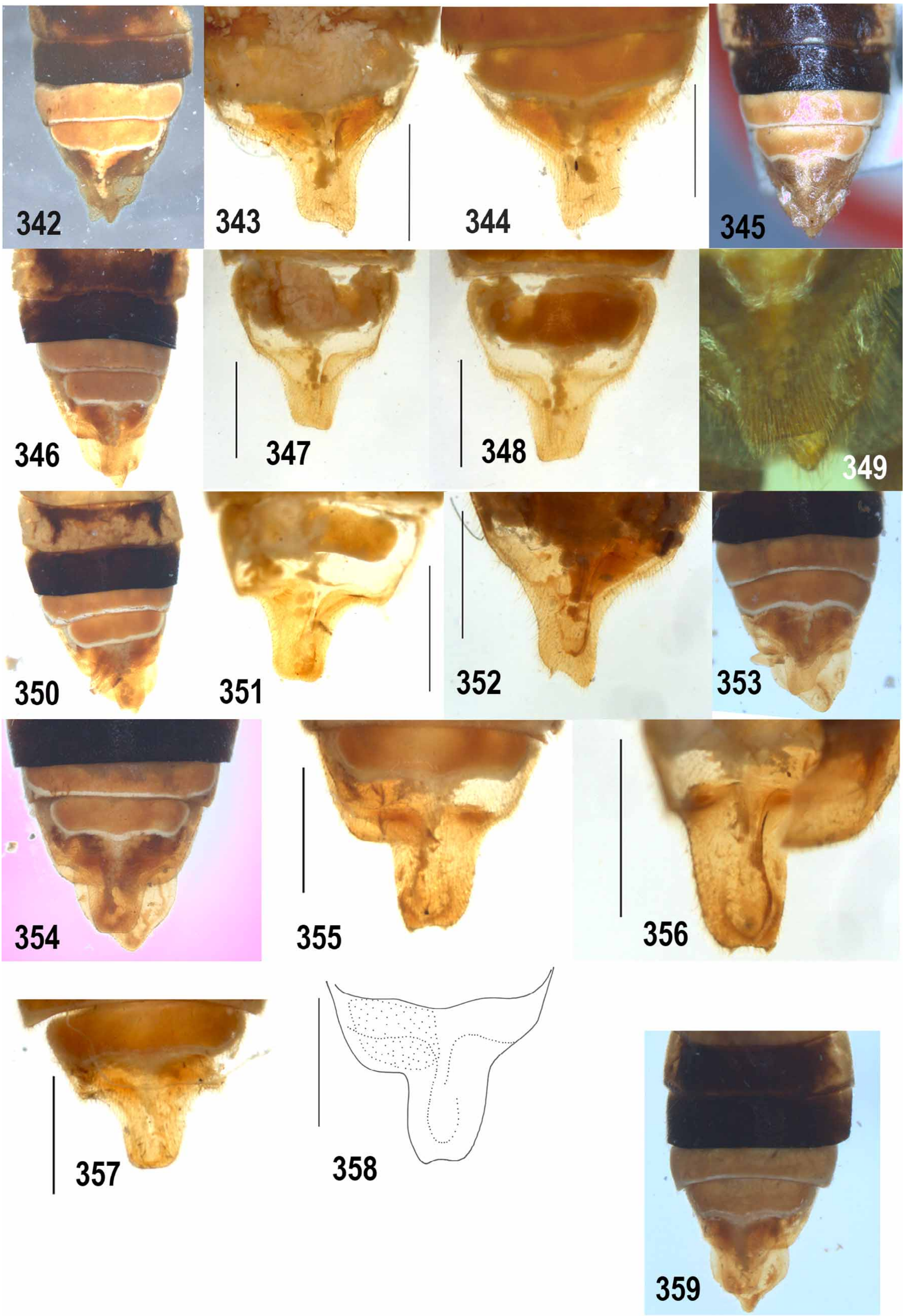

**FIGURES 304–314**. *Pygatyphella* spp. Abdomens, paratype males. 304–306 *Pygat. karimui*. 307, 311 *Pygat. japenensis*. 308, 312, 313 *Pygat. nabiria.* 309, 310, 314 *Pygat. okapa*. 304, 305, 307–310 ventral terminal abdomen (310 with tergite 8, 304, 309 after softening in hot water); 306 lateral with tergite 8; 311–314 ventral tergite 8.



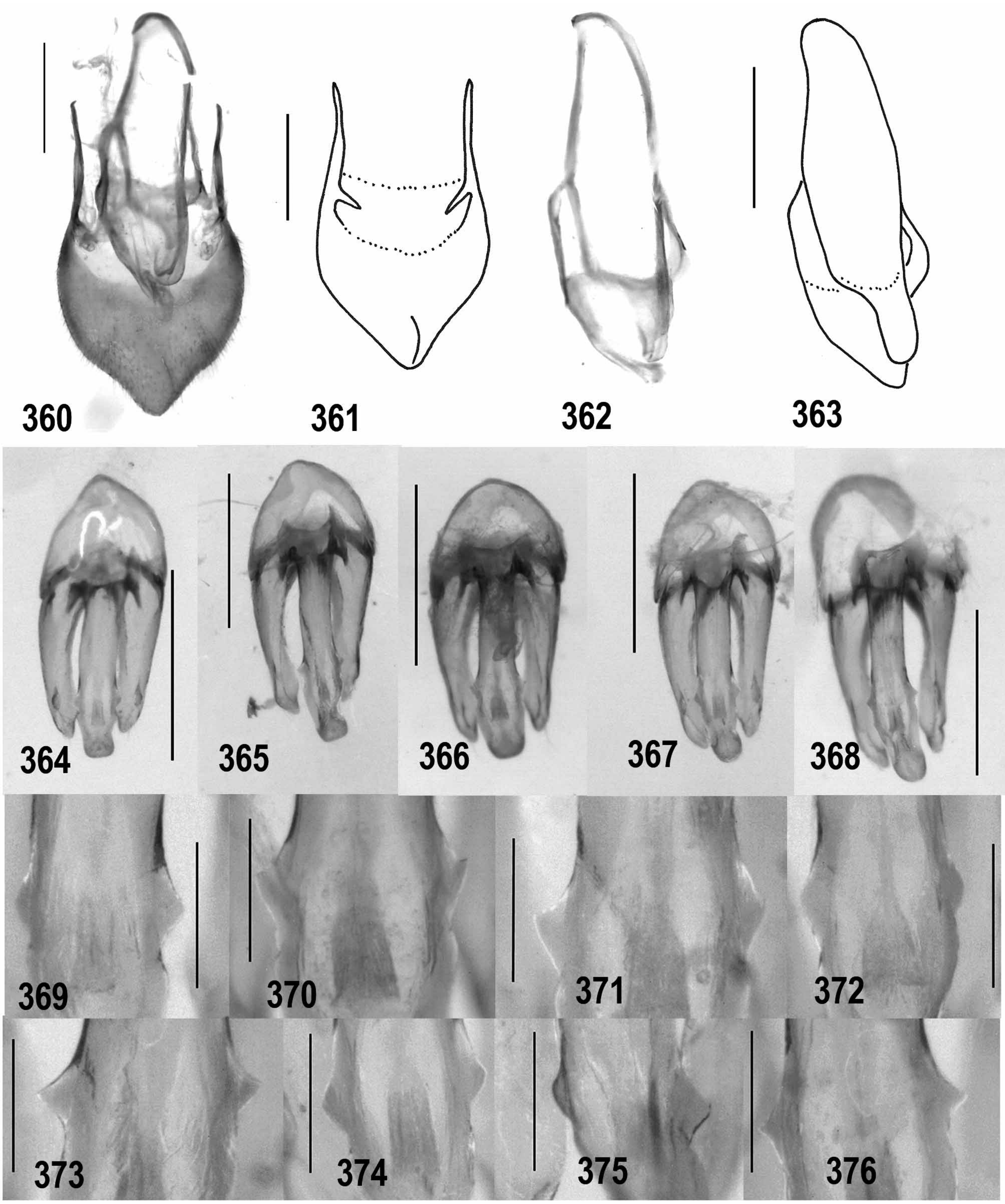

**FIGURES 315–328.** *Pygatyphella* spp. 315, 316, 318, 321–328 *Pygat. peculiaris* (315, 321 Mt Lamington, SAM; 316, 316 Kokoda, NHML; 322–326 Near Port Glasgow, BPBM). 317, 319, 320, 327, 328 *Pygat. kiunga* paratype males. 315, 316, 319 dorsal (315 dorsal and ventral aspects four males on card; 317, 318 dorsal pronotum; 320–322 abdomen (320, 321 ventral terminal sternites and tergite 8; 322 ventral tergite 8); 323, 328 aedeagus ventral; 324, 327 aedeagus dorsal; 325, 326 aedeagal sheath, ventral and dorsal.



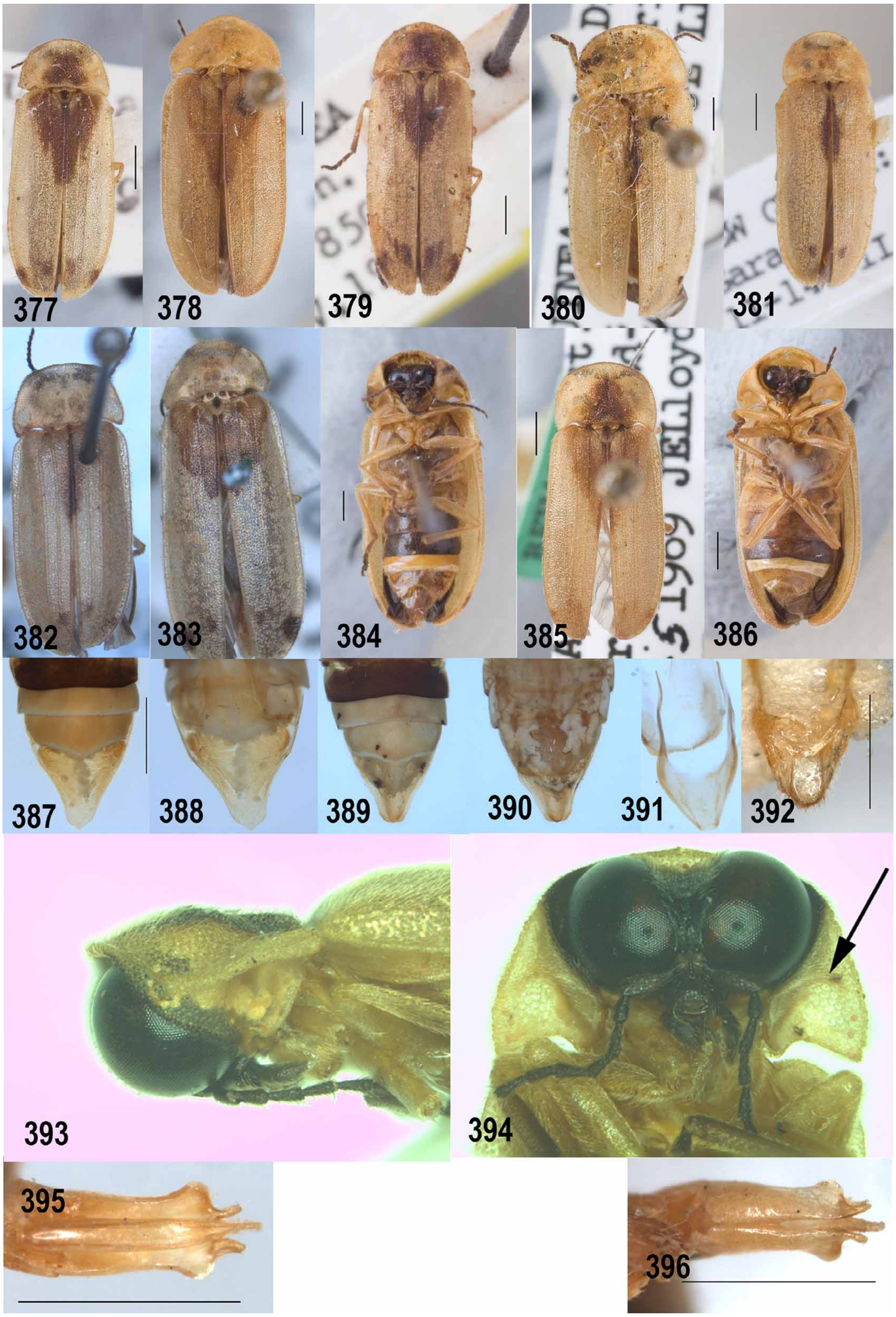

**FIGURES 329–341**. *Pygatyphella* spp. 329, 338, 341 *Pygat. limbatifusca* paratype males. 330–337, 339, 340 *Pygat. limbatipennis* males (330 New Georgia Munda, BPBM; 331 Guadalcanal Mt Gallego, BPBM; 332 Guadalcanal Lame, BPBM; 333 Guadalcanal Kolombangara, BPBM; 334 Guadalcanal Betikama River, BPBM; 336 Guadalcanal Kolosulu, BPBM; 337 holotype male, NHML; 340 Choiseul, BPBM). 329–337 340 dorsal; 338, 339 pronota; 341 detail right pronotal corner.



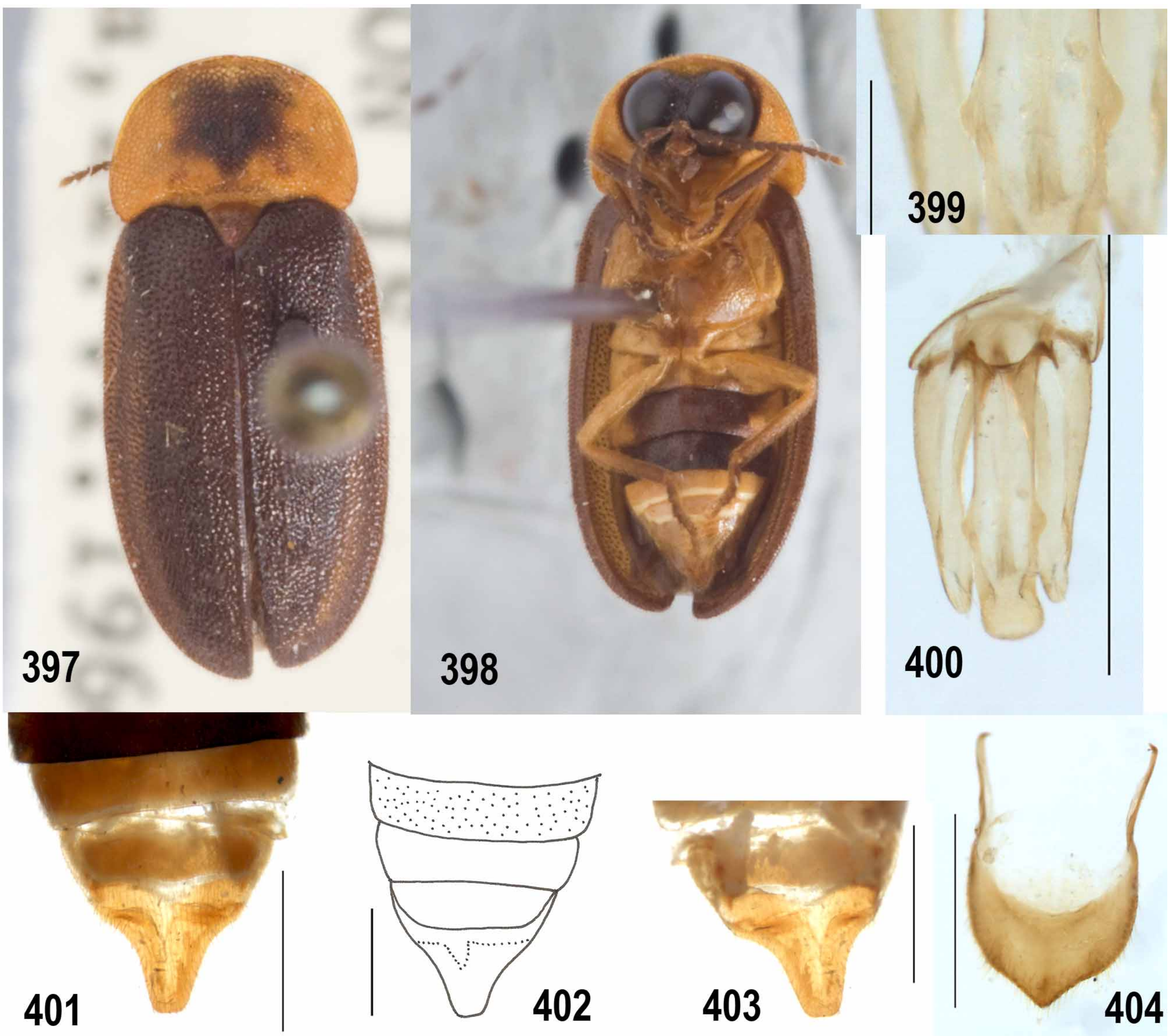

**FIGURES 342–359**. *Pygatyphella limbatipennis* Male abdomens (342–344 Gairava, BPBM; 345 type, NHML; 346–348 Kolosulu, BPBM; 349 Honiara, BPBM; 350, 351 Paripao, BPBM; 352, 353 Choiseul, BPBM; 354–356, 358 Betikama River, BPBM; 357 Guadalcanal, BPBM; 359 Honiara, BPBM). 349 detail MPP ventral. 343, 347, 351, 356 dorsal terminal abdomen, remainder ventral, terminal abdomen (all but 345 softened in hot water).



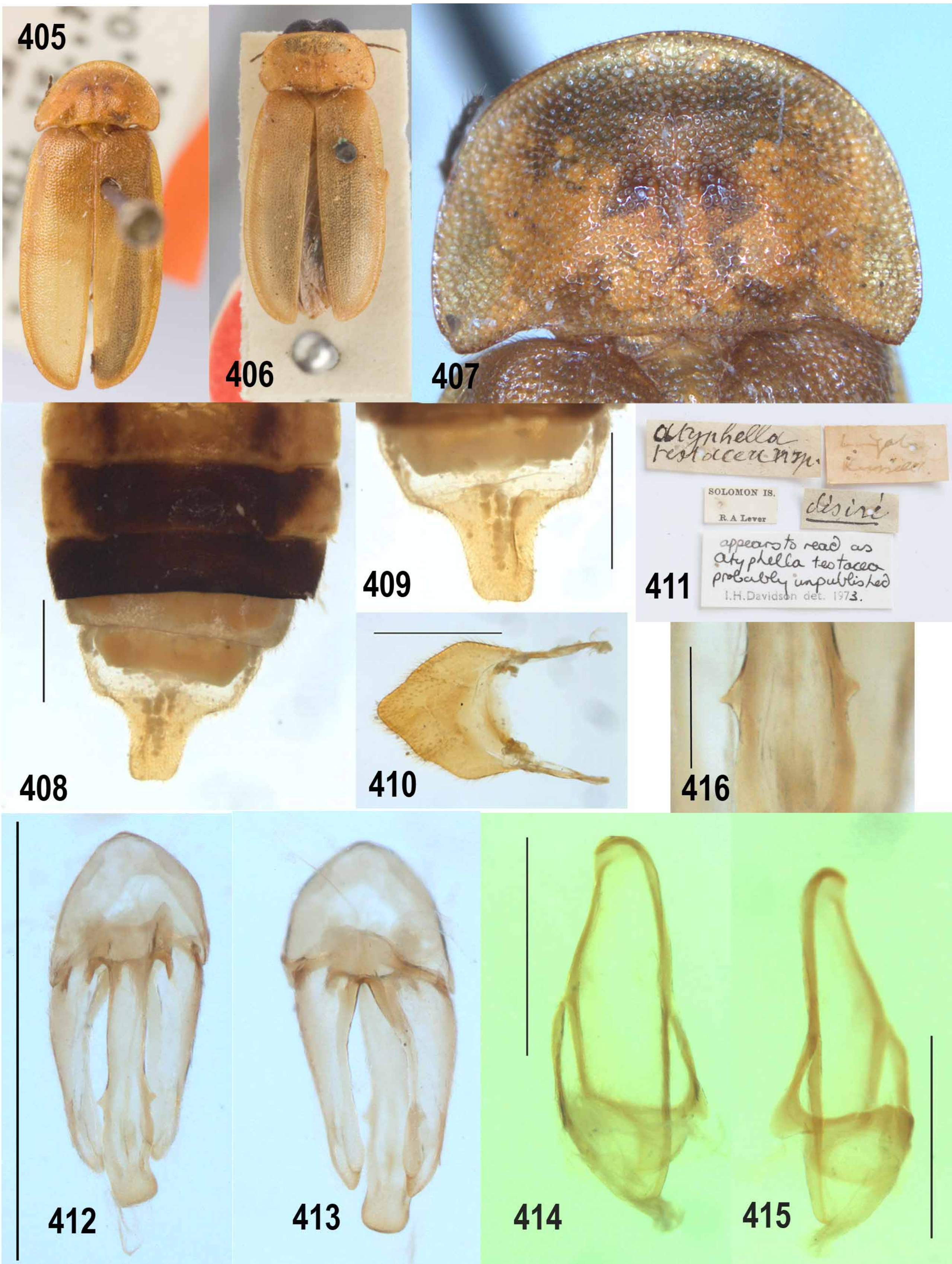

**FIGURES 360–376.** *Pygatyphella* spp. Males. *Pygat. limbatipennis* 360, 361, 364–369, 372–376. *Pygat. limbatifusca* paratypes, 362, 363, 370, 371. 360, 361 tergite 8 (360 with aedeagal sheath still incorporated); 362, 363 aedeagal sheath ventral; 364–368 aedeagus ventral; 369–376 detail teeth on median lobe. Scale lines 0.25 mm for 369–376.



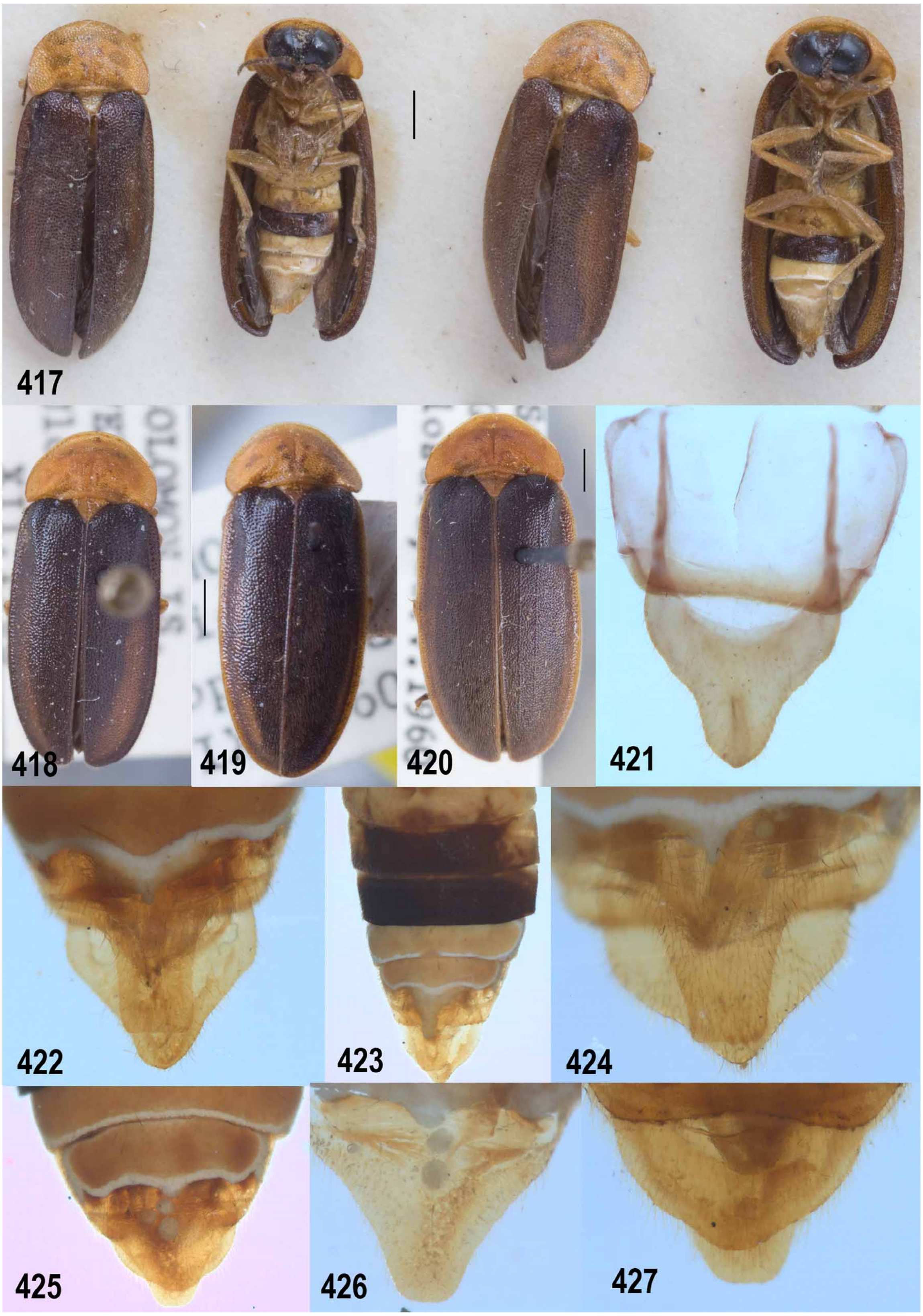
**FIGURES 377–396.** *Pygatyphella obsoleta*. 377–383, 385 dorsal, males; 384, 386 ventral females; 387, 389 ventral terminal abdomen, 388, dorsal softened and partly cleared terminal ventrites; 390 dorsal terminal abdomen; 391. 392 ventral tergite 8 (391 softened and cleared in KOH); 393, 394 head lateral and anterior; 395, 396 aedeagus dorsal, ventral. (377 Bulolo, BPBM; 378 Sek Harbor, G230 Lloyd; 385 Sek Harbor, G118 Lloyd; 379 Huon Pen., BPBM; 380 Lae, G230 Lloyd; 381, 384, 391 Garaina, BPBM; 382 Markham River, G238 Lloyd; 383 Aiyura, DAPM; 386 Lae, BPBM; 387, 388 Wau, BPBM; 389, 390 Kokoda, BPBM; 392 Sek Harbor, G260 Lloyd; 395, 396 Sek Harbor, G47 Lloyd). Specimens in Lloyd bear lettered and numbered labels relating to behavioural and ecological data kept by Lloyd.



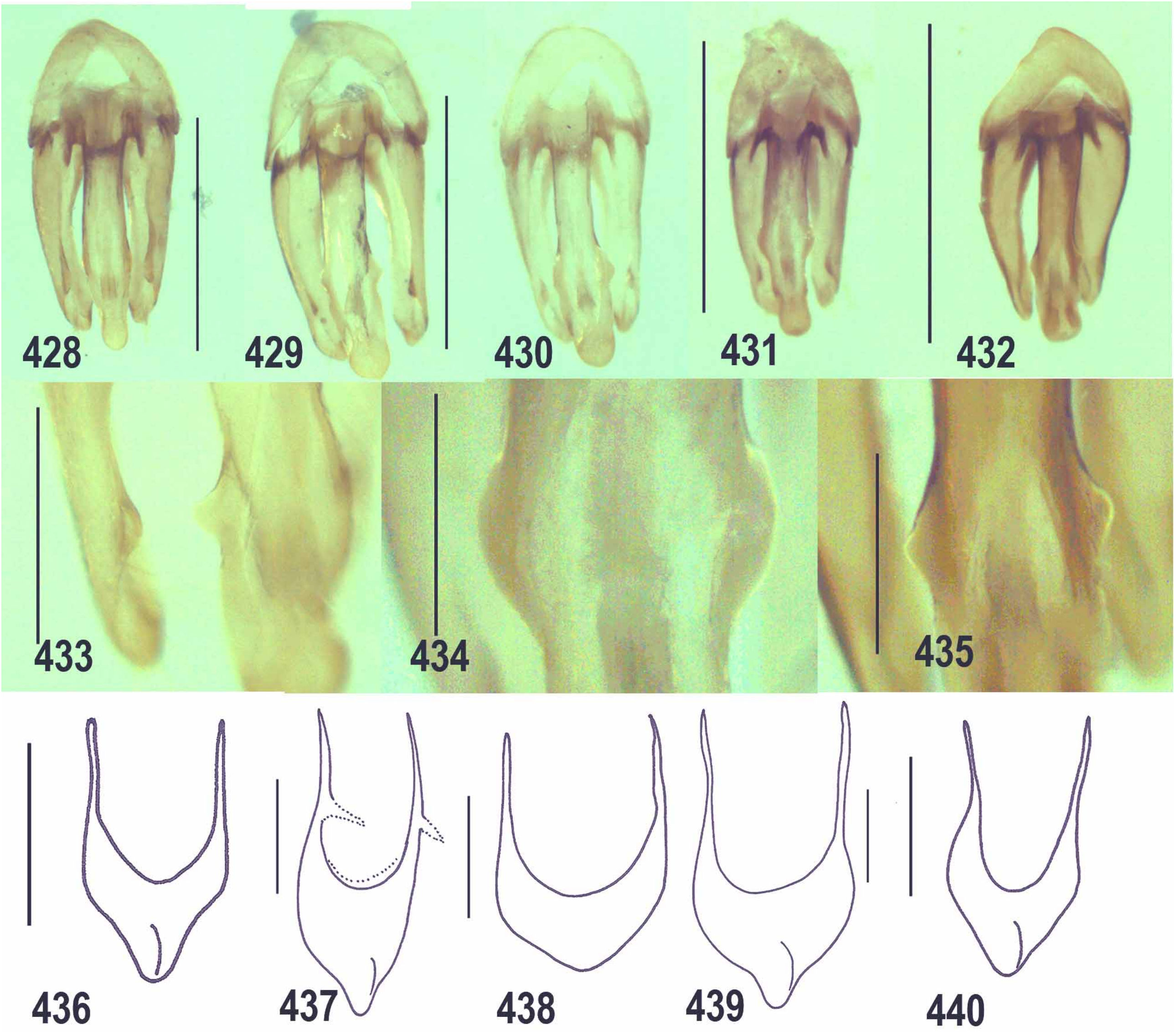

**FIGURES 397–404**. *Pygatyphella plagiata* paratype males. 397, 398 dorsal, ventral; 399, 400 aedeagus ventral (399 detail ML teeth); 401–404 abdomen, 401, 402 ventral terminal ventrites only (after softening in hot water with T8 removed); 403 terminal ventrites dorsal after softening in hot water T8 removed; 404 T8 ventral. Scale line for 399 is 0.25mm



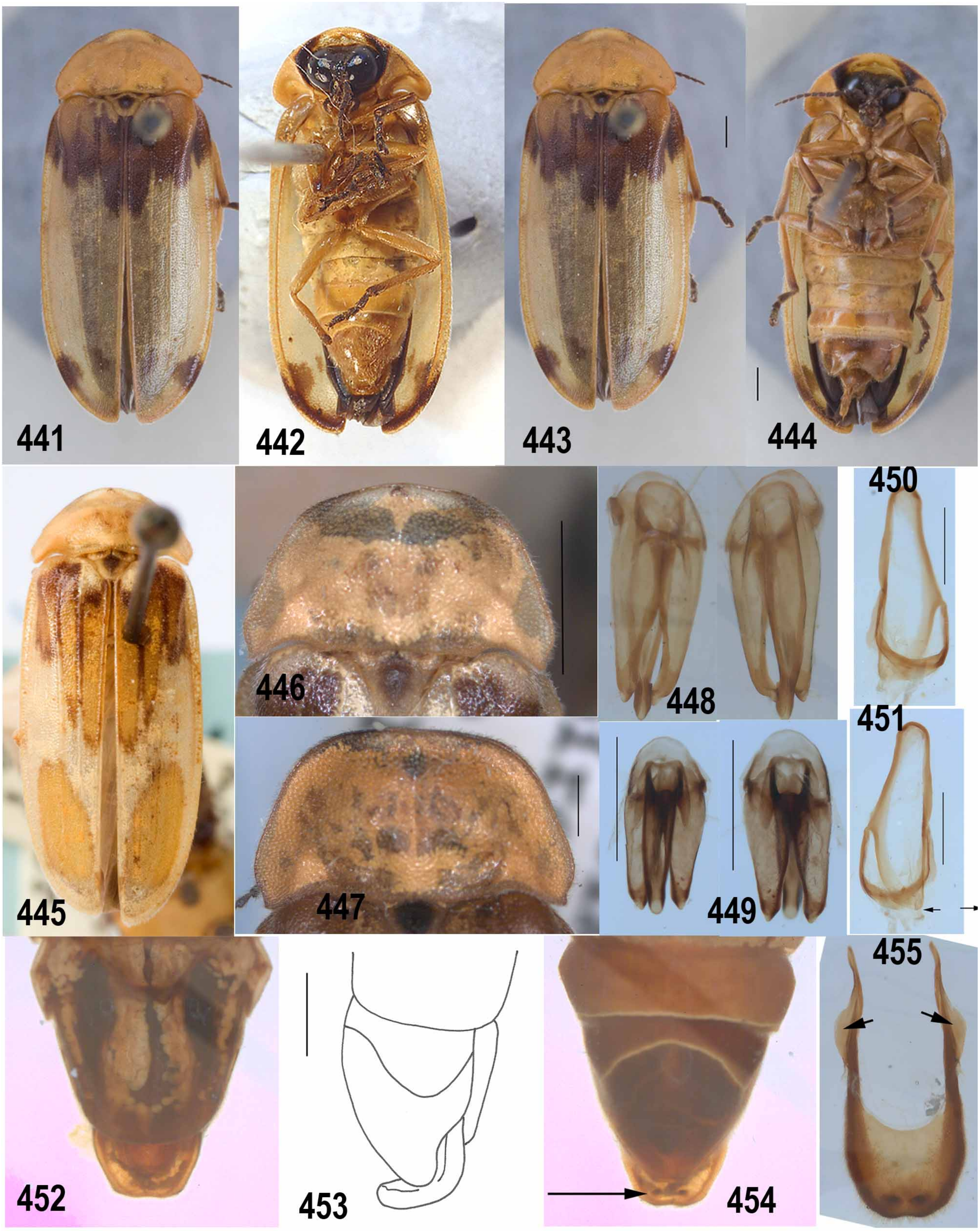

**FIGURES 405–416.** *Pygatyphella russellia* holotype male (paratype male 406). 405, 406 dorsal; 407 pronotum dorsal; 408 ventral abdominal ventrites 3–7 after soaking in hot water, T8 removed; 409 abdominal ventrite 7 dorsal after soaking in hot water; 410 tergite 8 ventral; 411 label on holotype; 412, 413, 416 aedeagus ventral, dorsal and detail aedeagal teeth ventral; 414, 415 aedeagal sheath ventral, dorsal. Scale line for 416 is 0.25 mm.



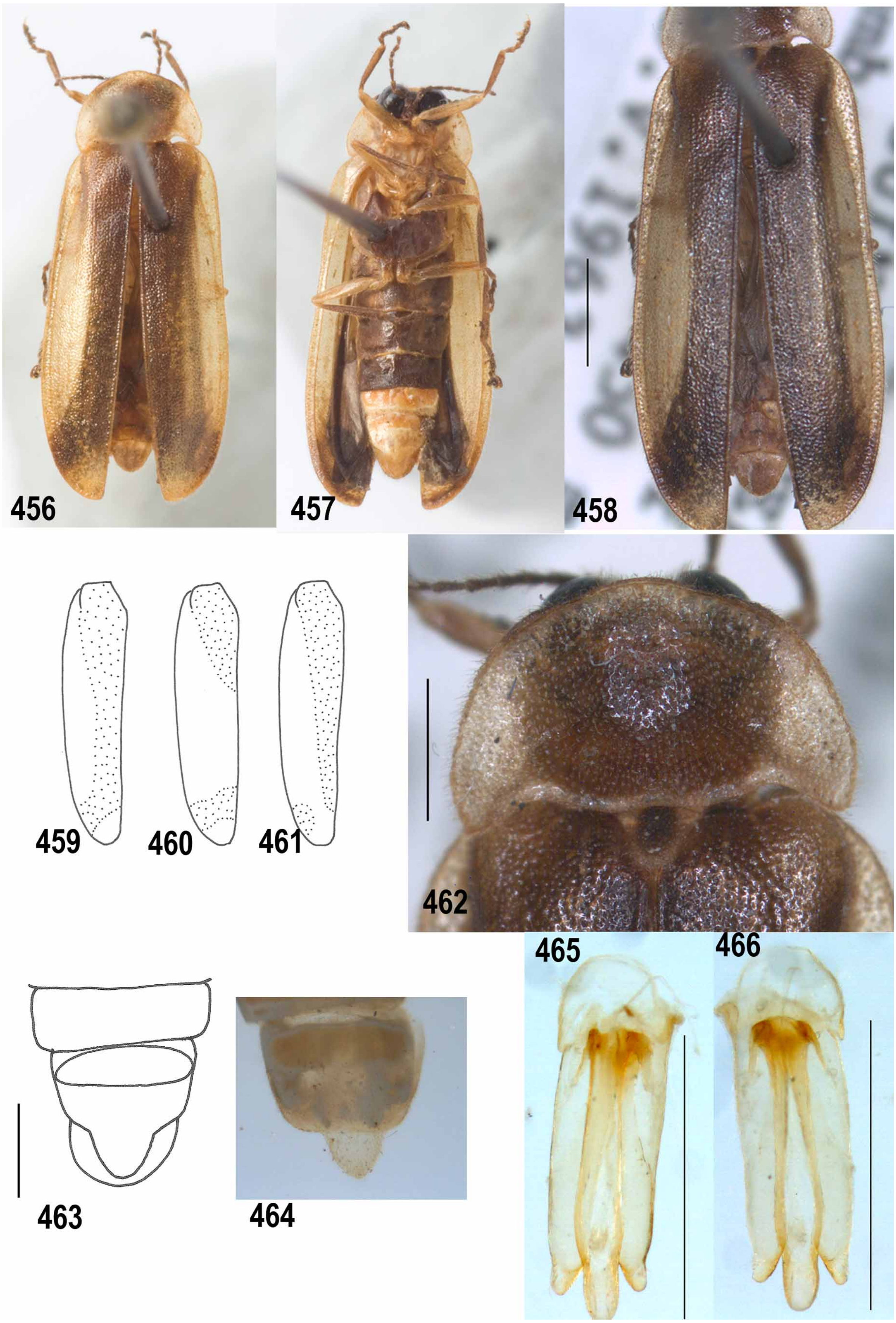

**FIGURES 417–427.** *Pygatyphella salomonis* spp. Males, female (420). (417 Solomon Islands, NHML; 418, 423 Vella Lavella, BPBM; 419 Takopekope, BPBM; 420, 421 Kolosulu, BPBM; 422 Sahuluatea, BPBM; 424 Gizo, BPBM; 425–427, Malaita, BPBM). 417 dorsal and ventral; 418–420 dorsal; 421 ventral tergites 7, 8 softened and partly cleared in KOH; 422, 424, 427 ventral ventrite 7 and tergite 8, softened in hot water; 423 abdomen ventrites 3–7 and tergite 8; 428 dorsal posterior half of ventrite 7 only, softened in hot water; 429 dorsal, tergite 8 and MPP of ventrite 7, softened in hot water.



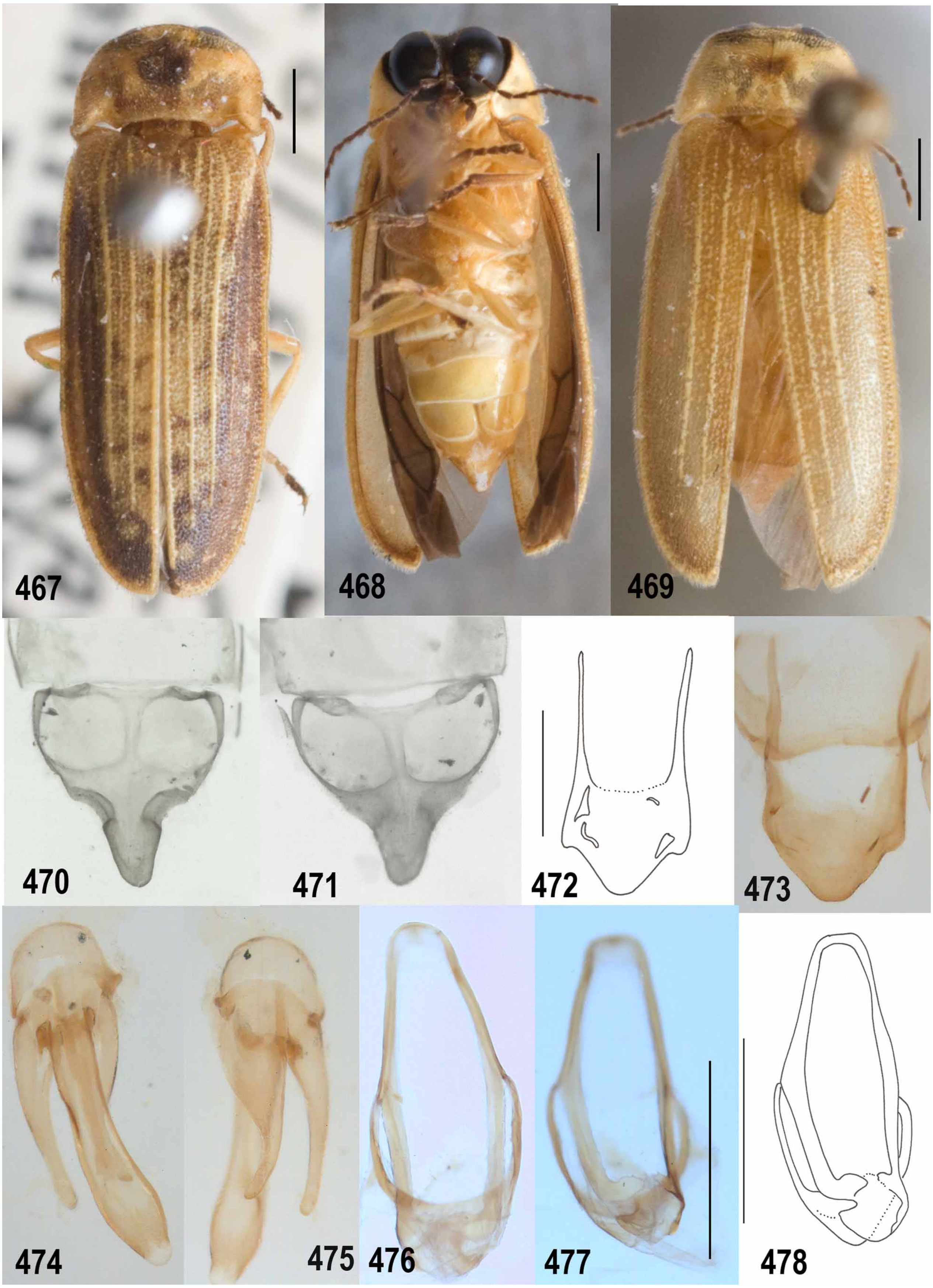

**FIGURES 428–440.** 428–439 *Pygat. limbatipennis* males; 440 *Pygat. limbatifusca* paratype males (all BPBM). (430, 436, 439 Kolosulu; 429 Togerao; 430 Molao; 431, 434 Buala; 432, 435, 438 Malaita; 433 Bougainville; 437 Takopekope). 428–435 aedeagus ventral (433–435 detail aedeagal teeth); 436, 438–440 ventral tergite 8 (Pattern 2 436; Pattern 3 438; Pattern 1 439; Pattern 4 440); 437 ventrolateral tergite 8. Scale lines are 1 mm except for Figs 433–435 where they are 0.25mm.



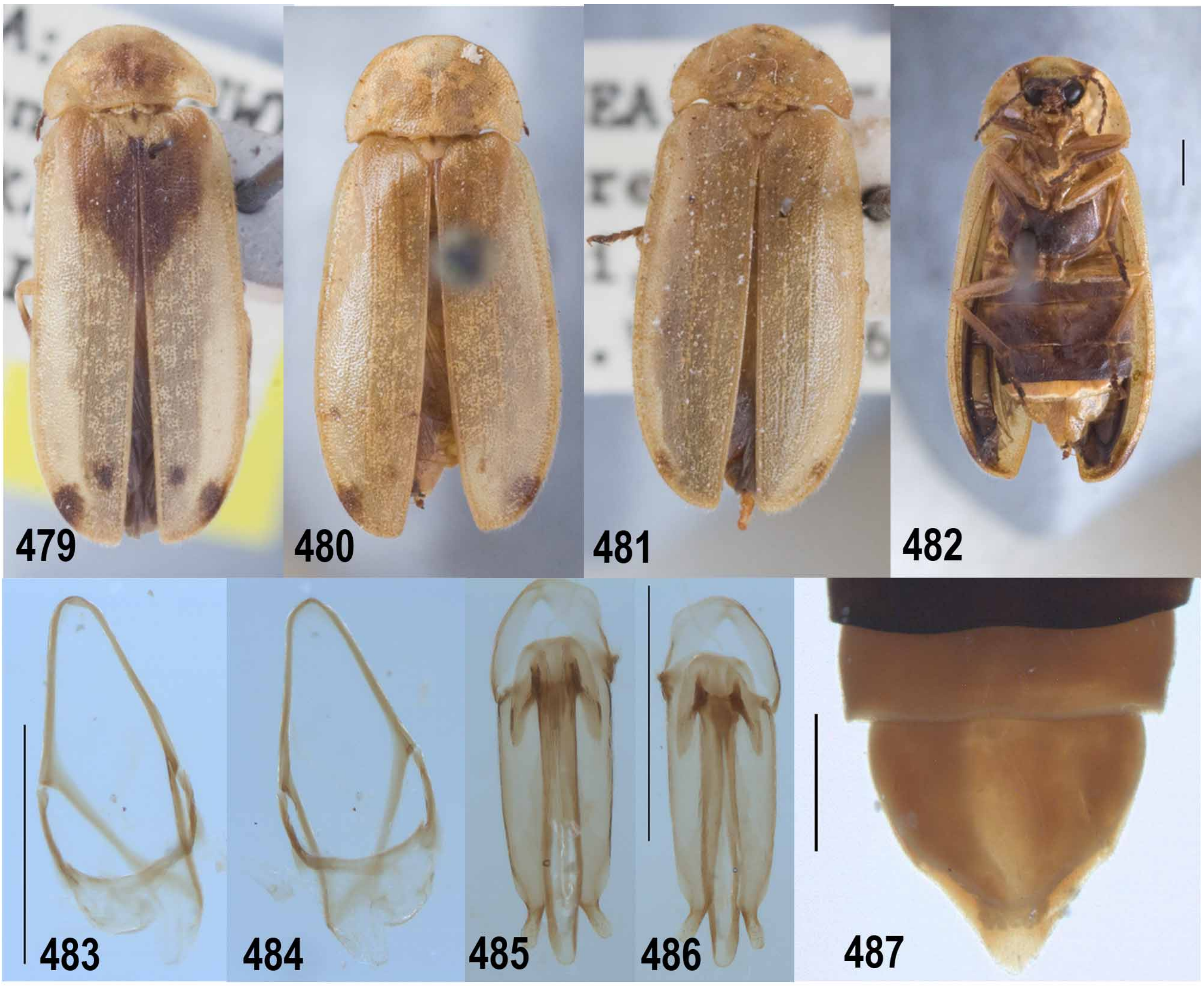

**FIGURES 441–455**. *Pygatyphella* spp. 441–444, 447, 448, 450, 451, 452–455 *Pygat. undulata* (males except for 443, 444 females); 445, 446, 449 *Pygat. tagensis* (449 paratype male). 441, 443, 445 dorsal; 442, 444 ventral; 446, 447 dorsal pronota; 448, 449 aedeagi (448 dorsal L and ventral, R; 449 ventral L and dorsal, R); 450, 451 aedeagal sheath dorsal and ventral; 452–454 abdomen male, dorsal, left lateral and ventral; 455 ventral tergite 8 (arrows indicate vertical expansion of anterolateral arms).



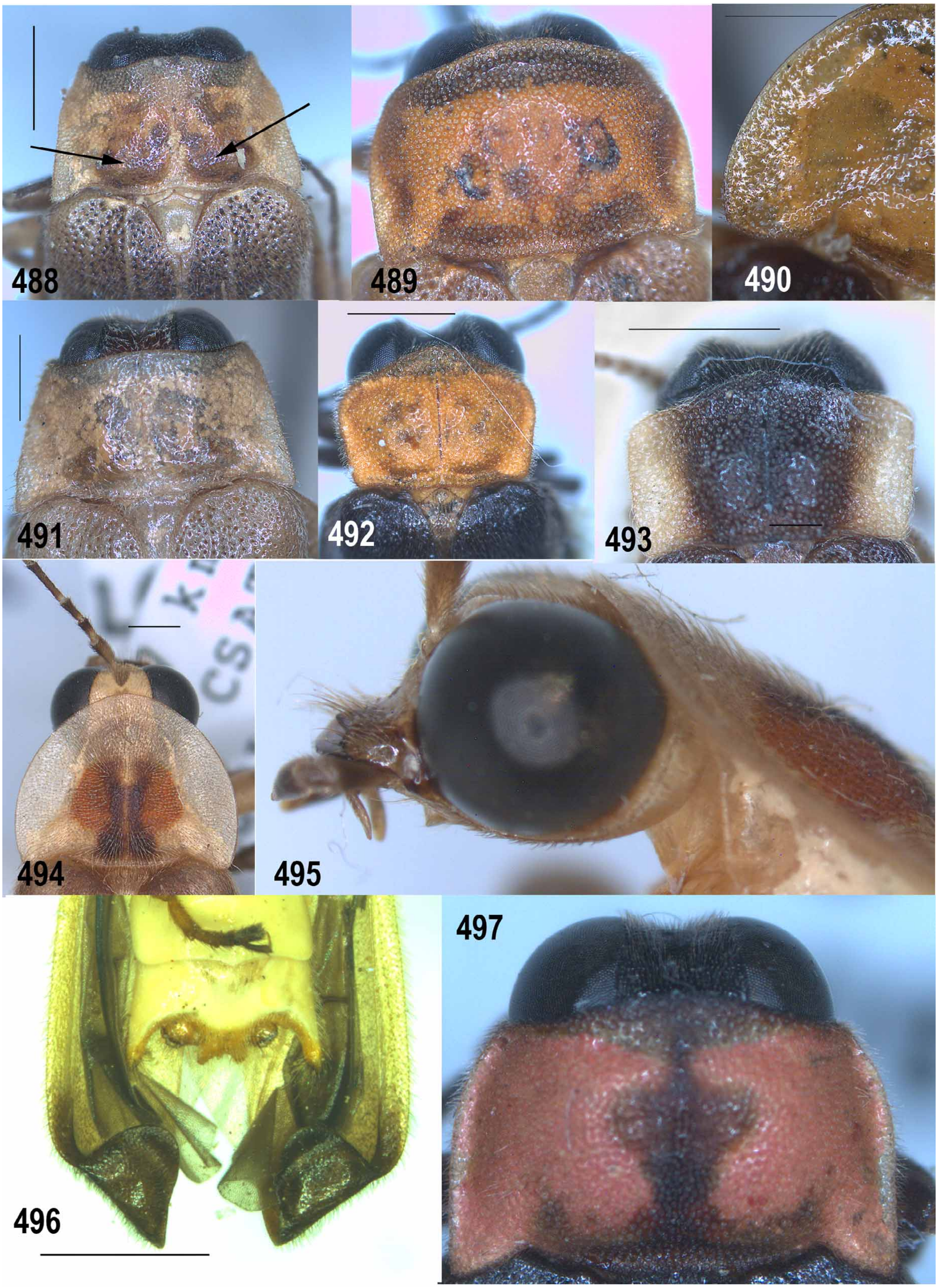

**FIGURES 456–466.** *Pygatyphella tomba* sp. n paratype males. 456, 458 dorsal; 457 ventral specimen 456; 459–461 diagrammatic representation of elytral colouration lateral margin to left; 462 pronotum dorsal; 463, 464 ventral terminal abdomen (463 with tergite 8; 464 after softening in hot water, tergite 8 removed); 465, 466 aedeagus, ventral, dorsal.



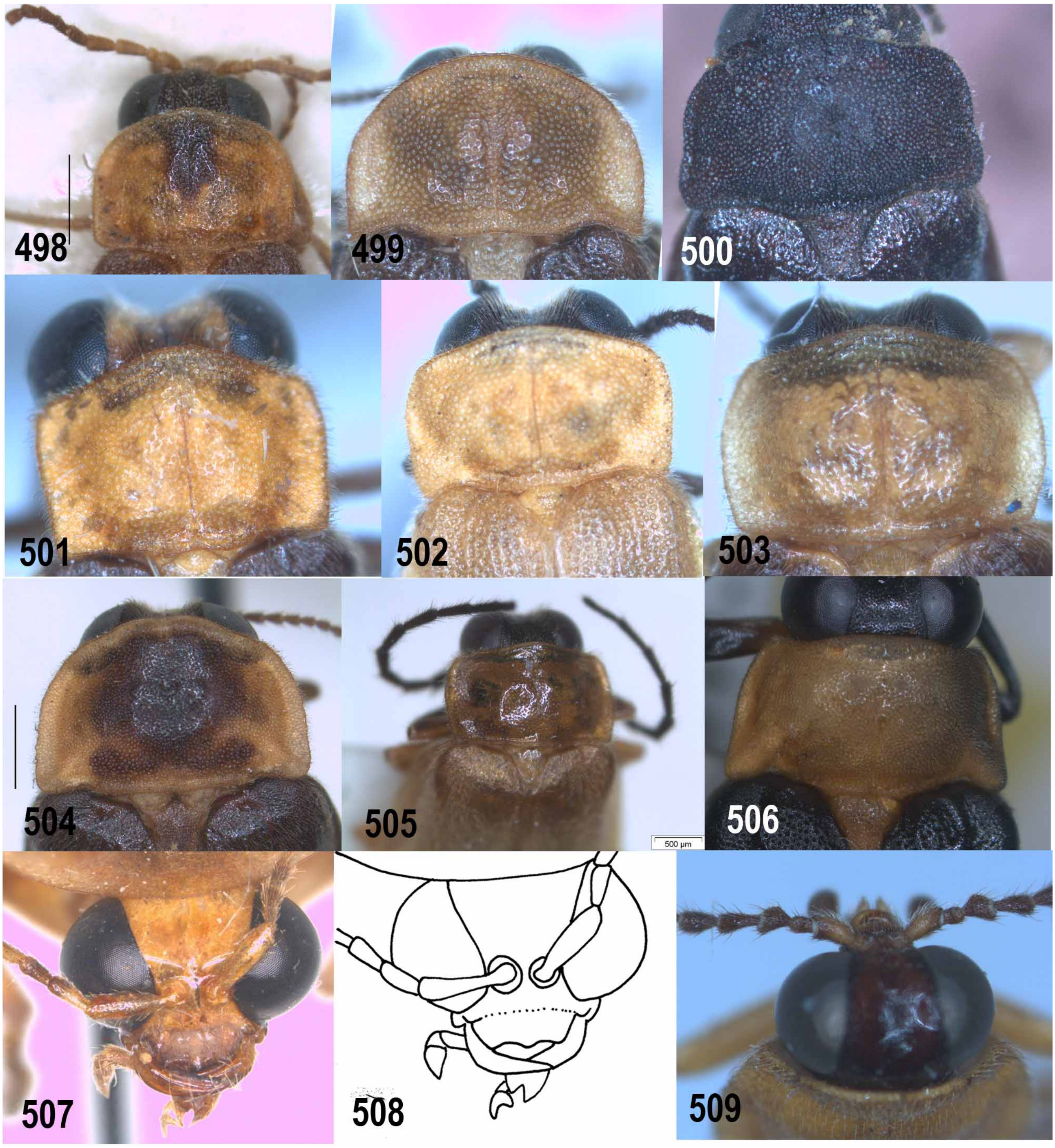

**FIGURES 467–478.** *Pygatyphella uberia* **sp. n.** paratype males. 467, 469 dorsal; 468 ventral; 470, 471 ventrites 6, 7 dorsal and ventral; 472, 473 tergite 8, tergites 7, 8 ventral; 474, 475 aedeagus ventral, dorsal; 476–478 aedeagal sheath dorsal, ventral and diagrammatic representation.




**FIGURES 479–487**. *Pygatyphella wisselmerenia* **sp. n.** paratype males and females (481, 482). 479–481, dorsal; 482 ventral; 484, 484 aedeagal sheath ventral, dorsal; 485, 486 aedeagus ventral, dorsal; 487 ventrites 6, 7 (tergite 8 removed).




**FIGURES 488–497.** Characters and states 1, Males. 488 *Pygoluciola satoi* paratype male pronotum (Philippines, ZRC) (arrow indicates pronotal tubercles); 489 *Luciola leii* male pronotum (China, ANIC); 490 *Convexa wolfi* (Kukugai, BPBM) detail left half pronotum; 491 *Pygoluciola hamulata* holotype male (Sarawak, MSNG) pronotum dorsal; 492 *Luciola nigra* (Kuranda, ANIC) dorsal pronotum; 493 *Luciola cowleyi* (Northern territory, ANIC) pronotum dorsal; 494, 495 *Photuris trivittata* paratype male (M8055, Lloyd) pronotum dorsal and head and pronotum left lateral; 496 *Pteroptyx malaccae* (ANIC) ventral terminal abdomen and elytral apices; 497 *Luciola cruciata* (Japan, ANIC) pronotum, dorsal.




**FIGURES 498–509**. Characters and states 2, Males. 498 *Lampyroidea syriaca* male (NHML) head and pronotum; *Atyphella immaculata* paratype pronotum (ANIC); 500 *Luciola hypocrita* type (Fiji, MNHN) pronotum; *Pteroptyx efful-gens* pronotum (New Guinea, BPBM); *Curtos costipennis* (Japan, ANIC) pronotum; 503 *Pyrophanes appendiculata* (Indonesia, ANIC) pronotum; 504 *Atyphella aphrogeneia* pronotum (New Guinea, NHML); *Pteroptyx malaccae* prono-tum (ANIC); 506 *Luciola owadia* paratype pronotum (Japan, ANIC); 507, 508 *Photuris trivittata* paratype male head anterior (M8055, Lloyd); 509 *Pyrophanes similis* head and antennae (Philippines, USNM).


**FIGURES 510–518**. Characters and states 3, Males and larvae. 510, 511, 512 *Colophotia concolor* (USNM) terminal abdomen, 510 ventral ventrites 6, 7; 511 posterior view apex of abdomen with tergites uppermost; 512 dorsal tergites 7, 8; 513, 515 *Bourgeoisia antipoda* aedeagus dorsal, ventral (BPBM); 514 *Bourgeoisia hypocrita* aedeagus, median lobe left side (Fiji, ANIC); 516 "New Caledonia" sp. aedeagus ventral (QM); 517 *Colophotia praeusta* larva ventral (USNM); 518 *Luciola owadai* paratype aedeagus ventral (ANIC).