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Systematics and Phylogenetics of Indo-Pacific Luciolinae Fireflies (Coleoptera: Lampyridae) and the Description of new Genera

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Abstract

This revision completes a taxonomic survey of fireflies (Coleoptera: Lampyridae) in the area encompassed by Australia, the Republic of Palau, Federated States of Micronesia, Papua New Guinea, Indonesia (West Irian/Papua), Solomon Islands, New Caledonia, Vanuatu and Fiji. It finalises the taxonomic issues arising from the 1969–70 voyage of the scientific vessel Alpha Helix to New Guinea. The firefly fauna of this area is exclusively Luciolinae. The scope of the revision was extended to include all known Luciolinae genera and certain species from SE Asia, and a phylogenetic analysis of 436 morphological characters of males, females, and associated larvae includes 142 Luciolinae species (Ballantyne & Lambkin 2009, and Fu *et al.* 2012a). The phylogenetic analyses infer four major groups within the Luciolinae. The monotypic *Missimia* Ballantyne is sister to all remaining Luciolinae and forms a grade to *Aquatica* Fu *et* Ballantyne. The large clade of *Curtos* Motschulsky, *Photuroluciola* Pic, *Colophotia* Motschulsky, *Poluninius* **gen. nov.**, *Pyrophanes* Olivier, *Pteroptyx* **s. str.** Olivier, *Medeopteryx* **gen. nov.**, *Trisinuata* **gen. nov.**, and *Australoluciola* **gen. nov.** forms a grade to the clade of *Luciola* **s. str.** Laporte (including *Bourgeoisia* Olivier). The monotypic *Emeia* Fu *et al.* forms a grade with a clade of *Luciola* and *Pygoluciola* Wittmer, sister to a large clade of *Convexa* Ballantyne, *Pacifica* **gen. nov.**, *Magnalata* Ballantyne, *Lloydiella* Ballantyne, *Asymmetricata* Ballantyne, *Pygatyphella* **s. str.** Ballantyne, *Atyphella* Olliff, *Aquilonia* Ballantyne, and *Gilvainsula* Ballantyne. *Luciola* is paraphyletic, found in up to six clades across the tree. Together with *Luciola*, *Magnalata*, *Aquilonia*, and *Gilvainsula* render *Atyphella* paraphyletic. The new genera described here are all monophyletic and supported in the phylogenetic analyses that also provide evidence for the inclusion of taxa within them. Twenty-three genera including five new ones, and ten new species, are recognised and keys are presented for the males and females. Certain females are characterised by the nature of their bursa plates.

Australoluciola **gen. nov.** is proposed for ten species from Australia and New Guinea, seven transferred from *Luciola* and three new, with species keyed from males, all of which have an entire light organ in ventrite 7. *Aus. anthracina* (Olivier), *Aus. aspera* (Olivier), *Aus. australis* (F.), *Aus. flavicollis* (MacLeay), *Aus. foveicollis* (Olivier), *Aus. nigra* (Olivier) and *Aus. orapallida* (Ballantyne) are transferred from *Luciola* with males assigned to *Aus. aspera* (Olivier), and a lectotype designated for *Luciola foveicollis* Olivier; *Aus. baduria* **sp. nov.**, *Aus. fuscamagna* **sp. nov.**, *Aus. fuscaparva* **sp. nov.**, *Aus. japenensis* **sp. nov.** and *Aus. pharusaurea* **sp. nov.** are described. Females of *Aus. australis* and *Aus. flavicollis* have two pairs of wide bursa plates.

The bent-winged fireflies of New Guinea and Australia are removed from *Pteroptyx* Olivier and assigned to *Medeopteryx* **gen. nov.** and *Trisinuata* **gen. nov.** *Medeopteryx* **gen. nov.** is erected for 17 species including two new; all have ventrite 7 with an entire light organ, trisinuate posterior margin and short posterolateral projections; the following 14 species in which males have deflexed elytral apices are transferred from *Pteroptyx* Olivier: *M. amilae* (Satô), *M. antennata* (Olivier), *M. corusca* (Ballantyne), *M. cribellata* (Olivier), *M. effulgens* (Ballantyne), *M. elucens* (Ballantyne), *M. flagrans* (Ballantyne), *M. fulminea* (Ballantyne), *M. hanedai* (Ballantyne), *M. platygaster* (Lea), *M. similisantennata* (Ballantyne), *M. sublustris* (Ballantyne), *M. tarsalis* (Olivier), and *M. torricelliensis* (Ballantyne). *M. clipeata* **sp. nov**. is described. Two species without deflexed elytral apices include *M. pupilla* (Olivier) which is transferred from *Luciola*, and *M. similispupillae* **sp. nov.** A Lectotype is designated for *Luciola pupilla* (Olivier). Females of *M. corusca* (Ballantyne), *M. cribellata* (Olivier), *M. effulgens* (Ballantyne), and *M. similispupillae* **sp. nov.** have two pairs of wide bursa plates. The second genus including species in which the males have deflexed elytral apices is *Trisinuata* **gen. nov.**, where all males have light organ in ventrite 7 bipartite and posterolateral projections expanded; it is proposed for eight New Guinean species: *T. microthorax* (Olivier), *T. minor* (Ballantyne), *T. papuae* (McDermott) and *T. similispapuae* (Ballantyne) are transferred from *Pteroptyx* Olivier, *T. papuana* (Olivier) previously known only from a female, has males associated and is transferred from *Luciola*, and *T. caudabifurca* **sp. nov.**, *T. dimidiata* **sp. nov.** and *T. apicula* **sp. nov.** are described. Females of *T. similispapuae* (Ballantyne) have two pairs of wide bursa plates.

Luciola **s. str.** is defined by scoring the type species *L. italica* (L), *Bourgeoisia* Olivier and *Lampyroidea* (based on its type species *syriaca* Costa) both of which are submerged into *Luciola*; *Luciola* **s. str** is addressed here from four Pacific Island species: *L. hypocrita* Olivier, *L. antipodum* Bourgeois both transferred from *Bourgeoisia*; *L. aquilaclara* **sp. nov.** and *L. oculofissa* **sp. nov**. are described. *L. oculofissa* **sp. nov**. is the only Luciolinae male known to lack light organs. Females of *L. italica* and *L. hypocrita* lack bursa plates.

Pacifica **gen. nov.** is proposed for five species from the Solomon Islands transferred from *Pygatyphella* (Ballantyne), and which the phylogenetic analysis shows to be distinctive viz. *P. limbatifusca* (Ballantyne), *P. limbatipennis* (Pic), *P. plagiata* (Blanchard), *P. russellia* (Ballantyne), and *P. salomonis* (Olivier).

A monotypic genus *Poluninius* **gen. nov.** is proposed for *Pol. selangoriensis* **sp. nov.** from Selangor, Malaysia. The genera *Colophotia, Pteroptyx*, *Pyrophanes*, and *Pygoluciola* are treated in an abbreviated fashion with generic diagnoses, lists of, and keys to, species. *Pteroptyx bearni* Olivier and *P. tener* Olivier are characterised from type specimens and female bursae and *P. similis* Ballantyne is synonymised with *P. bearni. Luciola semilimbata* Olivier is transferred to *Pyrophanes*, and *Luciola cowleyi* Blackburn to *Pygoluciola.* The following species are treated as *species incertae sedis*: *L. melancholica* Olivier, *L. ruficollis* Guérin-Méneville. The New Guinean records of *Luciola tenuicornis* Olivier, *L. timida* Olivier and *Photinus cinctellus* Motschulsky are suspect. Fifteen of the species treated here are recognised by flashing patterns. The functions of the terminal abdominal modifications, origins of the Australopacific firefly fauna, and use of female and larval characters in interpretations of relationships are considered.

Key words: *Australoluciola* **gen. nov.,** *Medeopteryx* **gen. nov.,** *Pacifica* **gen. nov.,** *Poluninius* **gen. nov.**, *Trisinuata* **gen. nov.**, Australia, Republic of Palau, Federated States of Micronesia, Papua New Guinea, Indonesia, Solomon Islands, New Caledonia, Vanuatu, Fiji, taxonomy, new species, identification keys, morphological phylogenetic analysis, female bursa plates

Introduction

Ballantyne and Lambkin's (2009) major taxonomic review of the Luciolinae established seven new genera and 19 new species and concentrated primarily on the genera related to *Atyphella* Olliff. With two exceptions, these genera and species 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. Six of the species placed in this *Atyphella* "complex" had been collected during the 1969–70 voyage of the scientific vessel Alpha Helix to New Guinea and were characterised by flashing patterns (Lloyd 1973a).

The first aim of this study was to resolve the outstanding taxonomic issues posed by the Alpha Helix voyage. It includes species first characterised by their flashing patterns, and that were initially placed within the genus *Luciola* Laporte (Table 1; Lloyd, 1973a; Ballantyne in Lloyd 1973b). The scope of our revision was subsequently extended to encompass all known Luciolinae genera, including certain species from SE Asia, while concentrating primarily on species presently included within the genus *Luciola*. Genera from outside the study area, as defined above, are treated in an abbreviated fashion with diagnoses, and keys to species.

To date the Luciolinae have been subject to six phylogenetic analyses, with each successive one based on increasing numbers of species and characters. Therefore, due this improved level of accumulated evidence, further action to subdivide *Luciola sensu stricto* within this study area is now warranted (Ballantyne & Lambkin 2000, 2001, 2006, 2009; Fu *et al*. 2012a). Previously, *Aquatica*, was erected as a new genus of aquatic Chinese fireflies, based on the phylogenetic results, and included four species originally described as *Luciola* spp. (Fig. 1; Ballantyne & Lambkin, 2009; Fu *et al.*, 2010). Fu *et al.* (2012a) erected another new monotypic genus, *Emeia*, for *pseudosauteri* (Geisthardt), which they transferred from *Curtos*.

Here, we comprehensively address 23 genera of Luciolinae of SE Asia and the Australopacific region, adding five new genera and 11 new species (Table 5). The "*Luciola* complex" from the study area is considered in its entirety (Figs 3, 4, nodes 1–52). The "*Atyphella* complex" (Fig. 5, clade 55) is addressed only in the form covered by Ballantyne and Lambkin (2009) with the exception of a new genus *Pacifica* **gen. nov.** (Fig. 4, clade 53). Several New Guinean *Luciola* records are incorrect or highly unlikely, and two species are treated as *species incertae sedis*.

TABLE 1. Current species identifications.

Current species identification [a, d]	**Species identification**[b]	**Code name/number** [c]	**Reference name/number**[e]
Australoluciola pharusaurea **sp. nov. (12)**	*Luciola* (*Luciola*) sp.	*Luciola* Species 4	Species 6
Australoluciola fuscamagna **sp. nov. (13)**	*Luciola* (*Luciola*) sp.	*Luciola* species 7	Species 4
Australoluciola fuscaparva **sp. nov. (14)**	*Luciola* (*Luciola*) sp.	*Luciola* Species 8	Species 5
Australoluciola anthracina (Olivier)	*Luciola* (*Luciola*) sp.	*Luciola* species 10	N/A
Luciola aquilaclara sp. nov. **(17)**	N/A	N/A	New Caledonia 1
Luciola oculofissa sp. nov. **(18)**			New Caledonia 2
Medeopteryx similispupillae sp. nov. **(8)**	*Luciola pupilla* Olivier	*Luciola* species 11	Species 2
Trisinuata dimidiata **sp. nov. (9)**	*Luciola* (*Luciola*) *sp.*	*Luciola* species 13	Species 1
Trisinuata caudabifurca **sp. nov. (11)**	*Luciola (Luciola)* sp.	*Luciola* species 14	Species 3

Footnotes: a. species identification used in this paper; b. species identification used in Lloyd 1973a; c. code name/number used in Lloyd 1973a; d. Fu *et al*. (2012a Figures 7–9) identified undescribed species by blue identification numbers included here in ( ) after the species name; e.Fu *et al*. (2012a Figs 7, 8) indicated undescribed species by red species numbers or code names .

Materials and methods

Characters we use follow Fu *et al*. (2012a) and Ballantyne and Lambkin (2009), who gave an extensive overview of morphological considerations, and the details of these core characters are elaborated upon further where necessary (Appendix 1).

Methods of dissection of female bursa and genitalia follow Ballantyne and Lambkin (2009); dissections were attempted on both ethanol preserved and pinned specimens. Certain ethanol preserved specimens had only the bursa removed. Abdomens of certain dried pinned specimens were removed and soaked in 20% cold KOH, with hourly observation, until bursa plates could be seen through the transparent abdominal cuticle. This method did not reveal other plates in the female reproductive tract and only allowed identification of the size and number of bursa plates. It did not permit reliable determination of absence. The complete reproductive system, with ovaries intact, could only be seen in freshly eclosed specimens. Deflexed elytral apices are characterised by their lengths along the posterior margin (A), outer margin (B) and inner (sutural) margin (Ballantyne 1987a:118, Fig. 2).

Additional voucher specimens are listed in Table 2.

Species are redescribed if no subsequent treatment other than the original description is available. Redescribed species are given abbreviated treatment.

The following 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: Figures 9, 10, 13, 19, 20, 26, 27, 45, 46, 47, 56, 57, 66, 67, 72, 83, 92, 93, 99, 100, 101, 104, 105, 109, 168, 177, 183, 191, 208, 209, 210, 211, 223, 224, 225, 226, 227, 239, 242, 251, 262. Ballantyne used an Altra 20 camera mounted on an Olympus SZX12 stereo microscope. Xin Hua Fu took Figure 1 with a Nikon D700 camera; Jen-zon Ho took Figure 2 with a Canon EOS50D camera. Ballantyne drew all line figures which were then inked by Derek Trow formerly of Charles Sturt University.

By mutual agreement, Ballantyne is the sole author of all new taxa and has provided all descriptions, photographs and diagrams in the taxonomic section. Lambkin undertook the phylogenetic analysis based on information provided by Ballantyne, described the phylogenetic analyses, and interpreted phylogenetic relationships in the Luciolinae.

Although we have covered in detail species from the study area as defined previously, we have also scored the type species, and several others, of all Luciolinae genera, whether they are from the study area or not. In the case of those genera not from the study area, we present an abbreviated treatment, with diagnosis, list of species, key to those species we can identify, and certain other taxonomic considerations, including in some cases details of female bursa.

TABLE 2. Voucher specimens used for phylogenetic analysis and interpretation of morphology (additional to those listed in Ballantyne & Lambkin 2009 Table 6 and Fu *et al.* 2012a).

Genus/Species	Specimen [1]	Authority for identification	References	Collection
Aquatica Fu *et* Ballantyne				
-*ficta* (Olivier)	F			ANIC
-*lateralis* (Motsch.)	F	Fu, Ballantyne, Ho		ANIC
Aquilonia Ballantyne				
-*costata* (Lea)	L	Label data only		ANIC
Asymmetricata Ballantyne				
-*circumdata* (Motsch.)	F	Silalom		QSBG
-*ovalis* (Hope)	F	Silalom		QSBG
Emeia Fu *et al.*				
-*pseudosauteri* (Geisthardt)	M F L	Fu	Fu *et al*. 2012a	NHMHZU
Luciola **s. str.** Laporte				
-*hypocrita* (Olivier)	female	Ballantyne	Deheyn & Ballantyne 2009	ANIC

Footnote: 1. M = male, F = female, L = larva.

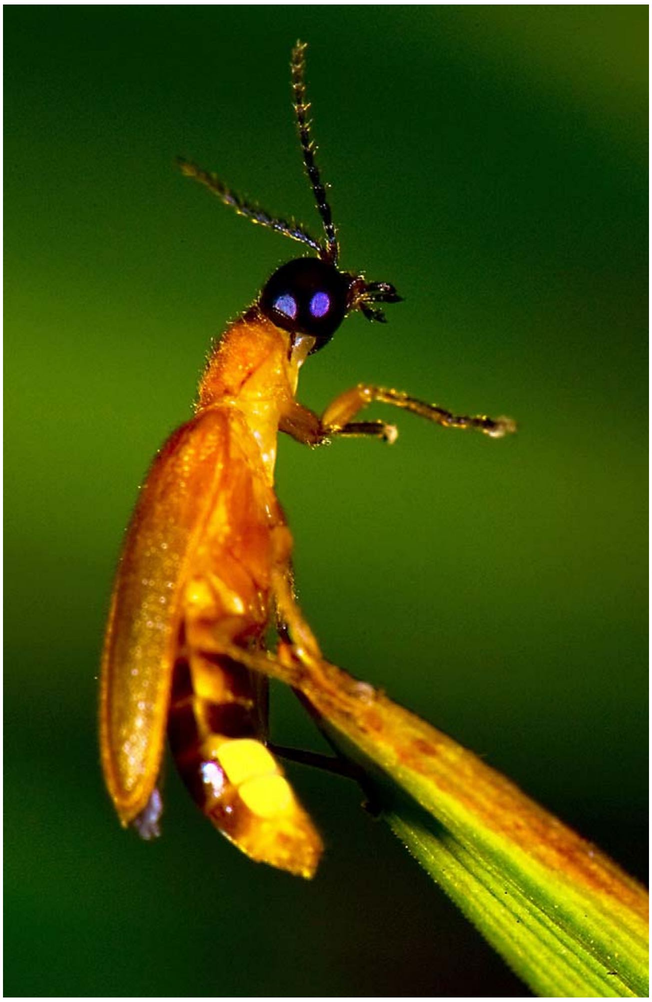


FIGURE 1. *Aquatica leii* (Fu *et* Ballantyne) male. Taken at 10.33 am 12.vii.2011 in Wuhan by X. H. Fu.

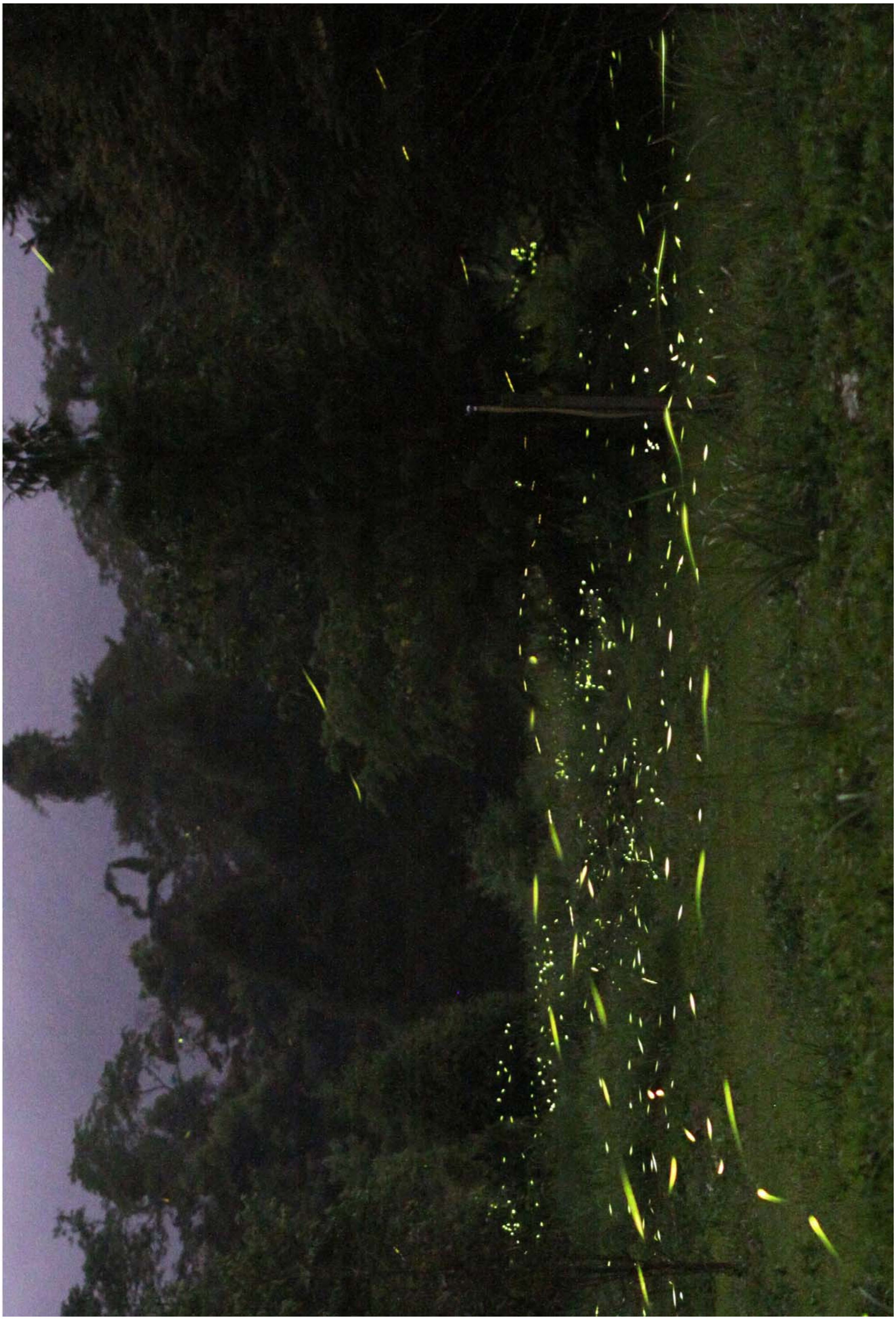
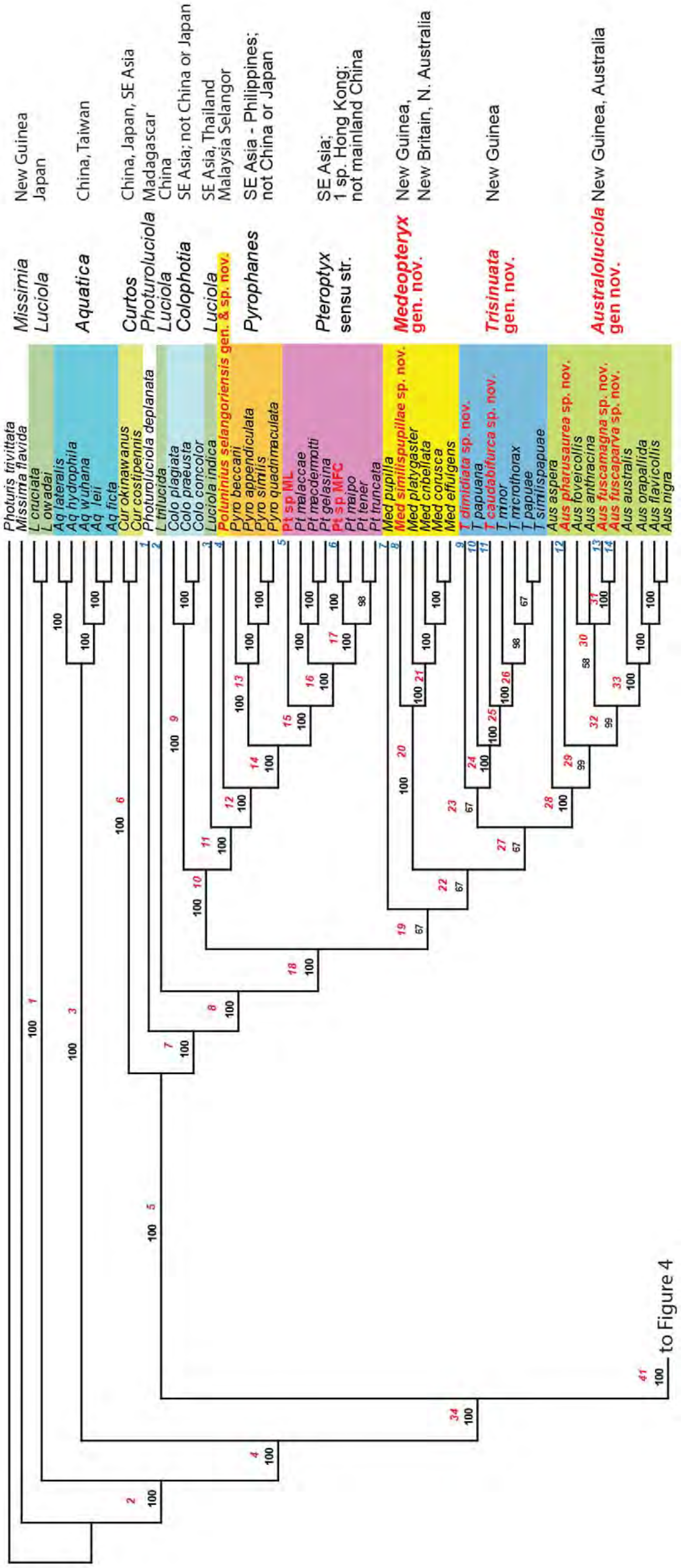
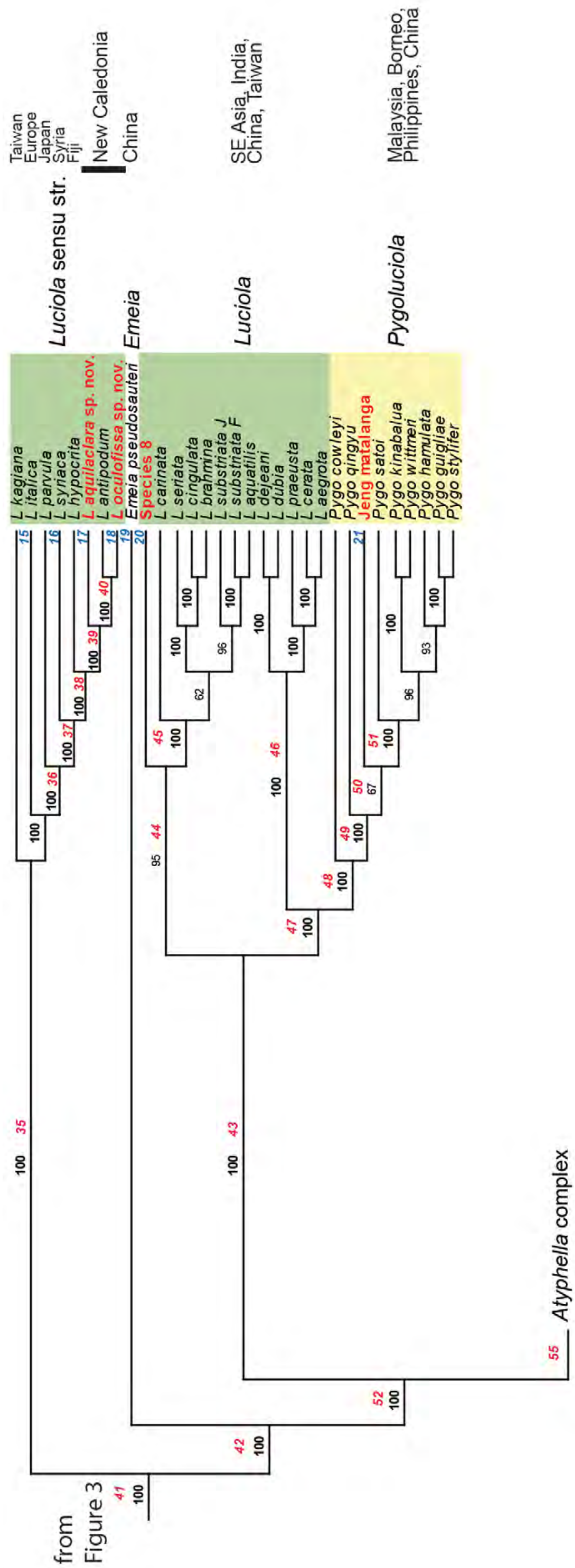
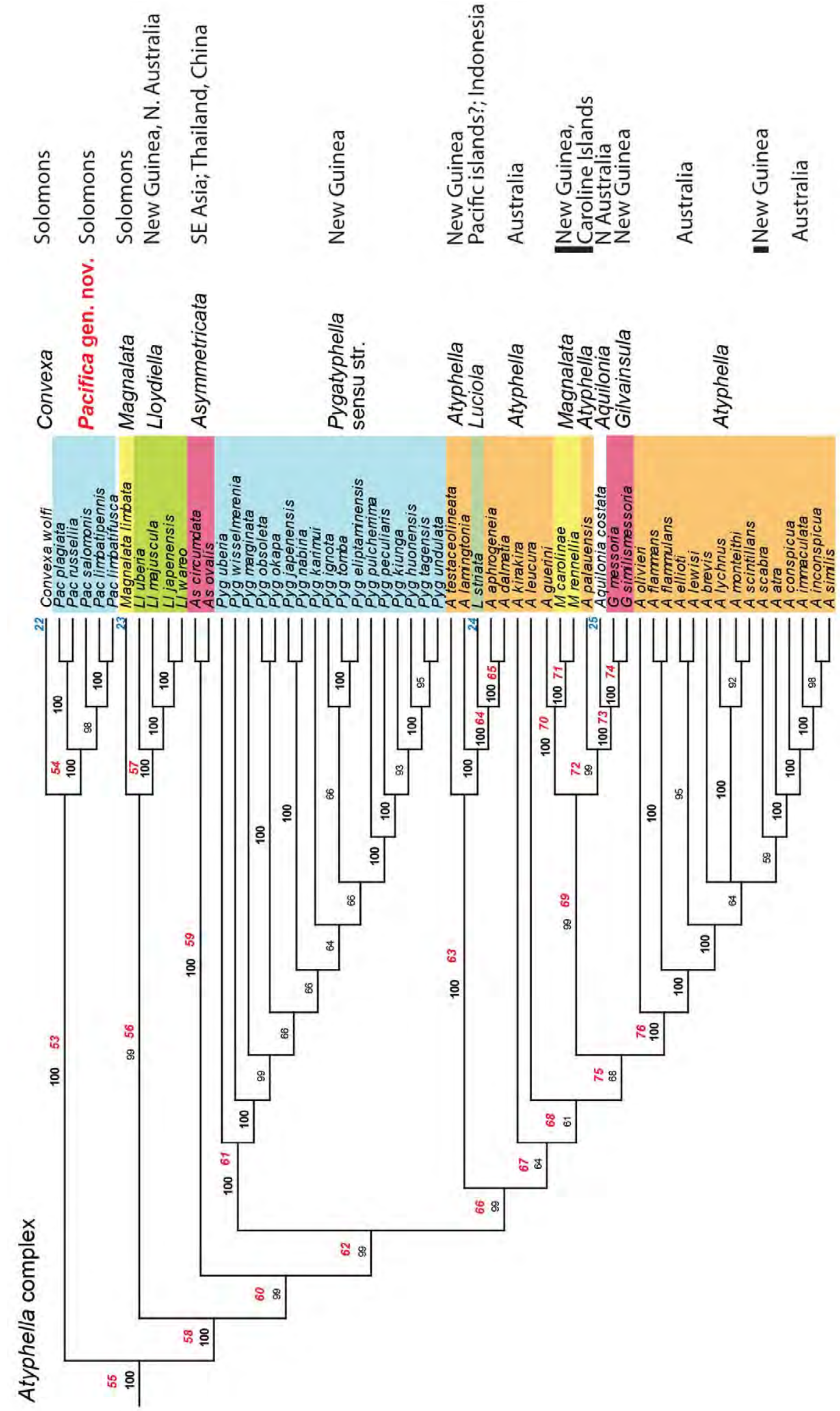


FIGURE 2. *Luciola cerata* Olivier flashing patterns taken at Wushikeng, Taichung county, Taiwan, 7.43pm 24.iii.2009 by Jen-zon Ho.


Photuris trivittata
Missimia flavida
L cruciata
L owadai
Aq lateralis
Aq hydrophila
Aq wuhana
Aq leii
Aq ficta
Cur okinawanus
Cur costipennis
Photuroluciola deplanata
L trilucida
Colo plagiata
Colo praeusta
Colo concolor
Luciola indica
Poluninius selangoriensis gen. & sp. nov.
Pyro beccarii
Pyro appendiculata
Pyro similis
Pyro quadrimaculata
Pt sp ML
Pt malaccae
Pt macdermotti
Pt gelasina
Pt sp MFC
Pt maipo
Pt tener
Pt truncata
Med pupilla
Med similispupilliae sp. nov.
Med platygaster
Med cnbeltata
Med corusca
Med effulgens
T dimidiata sp. nov.
T papuana
T caudabifurca sp. nov.
T minor
T microthorax
T papuae
T similispapuae
Aus aspera
Aus pharusaurea sp. nov.
Aus foveicollis
Aus anthracina
Aus fuscamagna sp. nov.
Aus fuscaparva sp. nov.
Aus australis
Aus orapallida
Aus flavicollis
Aus nigra
Missimia
Luciola
Aquatica
Curtos
Photuroluciola
Luciola
Colophotia
Luciola
Pyrophanes
Pteroptyx
sensu str.
Medeopteryx
gen. nov.
Trisinuata
gen. nov.
Australoluciola
gen nov.
New Guinea
Japan
China, Taiwan
China, Japan, SE Asia
Madagascar
China
SE Asia; not China or Japan
SE Asia, Thailand
Malaysia Selangor
SE Asia - Philippines;
not China or Japan
SE Asia;
1 sp. Hong Kong;
not mainland China
New Guinea,
New Britain, N. Australia
New Guinea
New Guinea, Australia
to Figure 4


L kagiana
L italica
L parvula
L syriaca
L hypocrita
L aquilaclara sp. nov.
L antipodum
L oculofissa sp. nov.
Emeia pseudosauteri
Species 8
L cannata
L seriata
L cingulata
L brahmina
L substriata J
L substriata F
L aquatilis
L dejeani
L dubia
L praeusta
L cerata
L aegrota
Pygo cowleyi
Pygo qingyu
Jeng matalanga
Pygo satoi
Pygo kinabalua
Pygo wittmeri
Pygo hamulata
Pygo guigliae
Pygo stylifer
Luciola sensu str.
Taiwan
Europe
Japan
Syria
Fiji
New Caledonia
China
Emeia
Luciola
SE Asia, India, China, Taiwan
Pygoluciola
Malaysia, Borneo, Philippines, China
Atyphella complex
from Figure 3



FIGURES 3–5. Majority rule tree for the complete analysis of the Luciolinae. Analysis consisted of consensus of 169 MPTs with a length of 5609 from a data set of 143 taxa and 436 morphological characters in (see Table 3). Figure 3, part 1: nodes 1–34; 4, part 2 Nodes 35–52; 5, part 3 nodes 55–76. Nodes (***red***). New genera, new species, and still undescribed species in **red** and **bold,** with identification numbers *blue*. Black values above branches show the % of MPTs over 50 % .

TABLE 3. Indo-Pacific Luciolinae data matrix 2013

```
                           111111111122222222223333333333444444444455555555556666666666777
Taxon/Node        123456789012345678901234567890123456789012345678901234567890123456789012
Photuris trivitta 00000000-10090-00000ca0110000001100000----0000000z-bc4a010a00-1000000111
                     1
Photuro deplanata 01000110a10210c10000-b0001110000100000a---01111210-0010001110-100000000a
Luciola italica   00002110-10080-00000d-0101011faab00000-a--01111110-004c001110-100000000-
L kagiana         00011110d100-0-00000--0111010000000000----01111110-0043000110-100000000-
L  parvula        00012110910070300000b-0001010000100000b---01111110-004-001110-100000000-
                                         1
L syriaca         00001110-1030b000000-e0001011mcch00000-b--01111110-004-001110-110000000b
L hypocrita       00010110-100-0-00000-d0001011gbba00000----01111110a004-0111211100000000-
                                         1
L antipodum       00013110-1030c00001b100101010000100000----01111110-004-0000211100000000-
L aquilaclara     00013110b10300400000a-0001010000100000----01111110c004e001020-0a0000000-
L oculofissa      00013110-1030300001a100101010000100000c---01111110-004-0000212100000000-
Aquatica leii     000011100000-5-00000--0001011ndde00000----01111210d004v001110-100000000c
                         1   1
Aq ficta          0000111001030-000000e-0001011pjed00000-c--01111210-004-001110-100000000-
                         1
Aq lateralis      00001110-1030-000001--0111010000000000----01111210-004m001110-100000000-
Aq hydrophila     00012110c10306000001--0111010000000000----01111110-004-000110-110000000-
Aq wuhana         00001110-1010-000000--0001010000000000----01111210-004-001110-110000000-
                             3
Luciola cruciata  00002110-1030-000001-g0211011qefk00000d---01100010e0020000110-100000000-
L owadai          00001110d10308000001--0111011rkgj00000----01100010-0010000110-110000000-
L cingulata       00002110-101---00000f-0211010000000100----01111210f004-000110-100000000d
L brahmina        00012110-100-0-00000--0211010000000100----01111210-0042000110-100000000-
L substriata J    00001110e101--w00000g-0111010000000100-d--01111210h004w000110-100000000-
                      2
L substriata F    00001110-101-7-00000-h0111010000000100f---01111210-004-000110-100000000-
                      2                  2
L aquatilis       00001110-101---00000h-0111010000000100----01111210-004-000110-100000000-
                      2
L. carinata       00001110-101---00000--0111010000000100----01111210-004-000110-100000000-
                      2
L. seriata        00001110-101---00000--0111010000000100----01111210-004-000110-100000000-
                      2
L dejeani         00013110-10060-00000-f0101011shhc00000----01111210b004d001110-100000000-
L dubia           00012110-1030-000001--0211010000000000----01111210-004-001110-100000000-
L cerata          00103110-10304000000--0211010000100000e---01111210-004-001010-100000000-
L praeusta        000031110abd5-200000--0111010000000000----01111210-0044001110-110000000e
L. aegrota        00003110-1030t-0001x110211010000100000----01111210-004n001010-100000000-
L striata         00020110-10200-00000--0211010000000000----01111210-0010010110-110000000-
Jeng matalanga    00000120-1030-00001-110211010000100000-e--01111210-004-000110-110000100-
                                                                                      2
Pyg cowleyi       000031111bac4d50001d000111000001100000-f--011112110101000102110b0000000f
                                                                        1
Pygo qingyu       00011120g1030-000001-j0211010000100000----01111210-004-001110-110000000-
Pygo guigliae     10011120-1030-100001k-0111010000100000----01111210-004-001110-110010100-
Pygo hamulata     10011120f1030g000001-k0211010000100000-g--01111210j0045001110-110010100-
Pygo kinabalua    10011120-1030f000001--0211010000100000g---01111210-004-001110-130010100-
Pygo stylifer     10011120-1030-000001j-0211010000100000----01111210-004f001110-110010100-
Pygo satoi        10011120-1030h00001f110111010000100000----01111210k004g001110-100010200g
Pygo wittmeri     10011120-1030-000001m-0211010000100000----01111210-004-001110-120010100-
Asymme circumdata 00020110-100-0-00000-n0111010000100000-h--01111210-0020001110-100000000-
As ovalis         00020110-10030600000n-0211010000100000j---01111210n0020001110-100000000-
Aquilonia costata 000111110cdb-j-00000--0111010000000000h---01111210m0020001110-1000000009
                                                  1                              1
Magnalata limbata 00010110-100-0-000008s0201010000000000m---01111210-0020001110-100000000h
                     2
M carolinae       00020110h10020-00000--0211010000100000-j--01111210p0000011110-100000000-
M rennellia       00020110-100z0-00000-r0211000001100000-k--01111210-0000001110-100000000-
                                                                       1
Gilvains messoria 000101108100-07000007-0211010000000000----01111210q0020011110-110000000j
G similismessoria 00010110-100-0-00000-u0211010000000000-n--01111210-0020011110-100000000-
                     2
Missimia flavida  00002110-1030e00001e121111010000100000----01100110r004b001100-140021ab10
Lloydie majuscula 00010110j100-0-0001-100111010000100000-m--01111210-0010011110-100000000-
Ll uberia         00010110-100-0800000-v0211010000100000n---01111210s0020011110-1000000008
Ll japenensis     00010110-1030900001h110211010000100000----01111210-0020011110-100000000-
Ll wareo          00010110-1000-00001j110211010000100000----01111210-0020011110-100000000k
                             3
Convexa wolfi     00120110k100-0-00000-t0211010000100000v---01111210t0020011110-100000000m
                                                                       4
Atyph aphrogeneia 00010110-1000u-000009c0001010000001000----0111121111110101110-100000000-
                      1      2                1   1
A atra            00020110-100-0d00000--0211000001100000-p--0111121101020001110-0c1000000-
A brevis          00020110-100x0-00000t-0211000001100000----0111121101010011110-101000000-
A conspicua       00020110m100-0e00000-x0111000001100000q---0111121101020001110-111100000-
A dalmatia        00020110-1020-000001--0211010000100000----0111121101010001110-100000000n
                             3
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......*continued on the next page*

TABLE 3. (Continued)

Taxon/Node	111111111122222222223333333333444444444455555555556666666666777 123456789012345678901234567890123456789012345678901234567890123456789012
A ellioti	00020110-100-0-00000u-0111000001100000----0111121101020001110-100000000-
A flammans	000201107100w0-00000-90211000001100000----0111121101020011110-0d0000000-
A flammulans	00020110-100-0-00000v-0211000001100000-q--0111121101020011110-0e1000000-
A guerini	00010110-100-0-00000s-0211010000100000----01111210-0020011110-100000000-
	2
A immaculata	0002111001010m000018100111000001100000----0111121101010001110-100000000p
	1 3
A inconspicua	000131111dce---0001-000111000001100000----0111121101020001110-101000000-
	1
A kirakira	00020110-100-0900000q-0211010000100000----01111210-0020011110-100000000-
A lamingtonia	00020110-100-0-00000-q0211010000100000k---01111210v000011110-100000000-
A leucura	00020110-100v0a00000p-0211010000100000----01111210-004h011110-100000000-
A lewisi	00010110-100-0-00000-w0111000001100000p---0111121101020011110-100000000q
A lychnus	00020110n100-0f000006-01110000011000003---0111121101000011210-100000000-
A monteithi	00020110-100u0-00000-y0111000001100000r---0111121101010011210-100000000-
A olivieri	00020110-100-0-00000--0211000001100000-3--0111121101010011110-100000000-
A palauensis	00020110p100-0-00000r-0211010000100000----01111210w0020011110-100000000-
A scabra	00020110-100-0g00000--0211000001100000----0111121100021011110-100000000r
A scintillans	00020110-100t0-00000w-0111000001100000-4--0111121101000001210-100000000-
A similis	00010110-1030k000019100111000001100000----0111121101010001110-101000000-
A testaceolineata	00020110-100-0b00000-p0211010000100000----01111210-0010011110-100000000-
Pac limbatipennis	00020110-100-0-001005701110100001000009---01111210-004-011110-100000000t
Pac limbatifusca	000201105100p0z00100-80111010000100000----01111210-004z011110-100000000-
Pac plagiata	00020110s100-0-00100450211010000100000-z--01111210-004-011110-100000000-
Pac russellia	00020110-100-0x00100--0211010000100000----01111210-004x001110-100000000-
Pac salomonis	00020110t100-0y00100-60211010000100000----01111210-004y011110-100000000-
Pyg tomba	00020110-100-0-0001g100211010000100000----01111210-004p001110-100000000-
	1
Py eliptaminensis	00020110q100-1h0101-100211010000100000----01111210x0020001210-100000000-
Pyg huonensis	00020110-100-1-0101m100211010000100000-r--01111210-0020001210-100000000s
Pyg ignota	000201106100s1-01016100211010000100000t---01111210-0020001210-100000000-
Pyg japenensis	00020110-100-0k0101-100211010000100000----01111210-0020001110-100000000-
	1
Pyg karimui	00020110-100-0-0101-100211010000100000u---01111210-0020001110-100000000-
	1 1
Pyg kiunga	00020110r100-1-0001n100211010000100000-s--01111210-0020001210-100000000-
	1
Pyg marginata	00020110-100-1j0101-1002110100001000004---01111210-0020001210-100000000-
Pyg nabiria	00020110-100q0-00015100111010000100000-5--01111210-0020001110-100000000-
	1 1
Pyg obsoleta	000201104100r0-00014110211010000100000-u--01111210y0020001110-100000000-
	1 1
Pyg okapa	00020110-100-0m0101q110211010000100000----01111210-0020001110-100000000-
	1
Pyg peculiaris	00020110-100-1-01017100211010000100000s---01111210-0020001210-100000000u
Pyg pulcherrima	00020110-100n1-0101p100211010000100000-t--01111210-0020001210-1000000007
Pyg tagensis	00020110-100m1-0101-100211010000100000----01111210-0020001210-100000000v
Pyg uberia	00010110u1030n00001r110111010000100000----01111210z0020001110-0f0000000-
	2 2
Pyg undulata	00020110-100k1-0101-100211010000100000----01111210-0020001210-1000000006
Pyg wisselmerenia	00020110v100-0-0101-1002110100001000005---01111210-0020001110-100000000-
Luciola indica	00003110-000---0001-000001010-10-00000----01111210-004-001110-100000000-
T dimidiata	00003110-000---0001-000001010-10-00000----01111210-004-001110-100000000-
L trilucida	00003110-100---0001-000001010-10m00000----11111210-004-001110-100000000-
T papuana	00003110w1030s00001-000001010-10t00000-2--011112103004-001110-100000000-
Aus foveicollis	000031110jkm---0001t000001010-10-000006---01111210-004-001110-110000000-
	2
Med pupilla	00003110-1010-00001k000001010-10u00000w---01111210-004-001110-110000000y
	3
M similispupillae	00003110-000-2-0001-000001010-10800000----01111210-004-001110-110000000-
T caudabifurca	000031110heg-w-0001c000001010-10-00000----011111102004-001110-110000000-
Aus anthracina	000031211ehf-a-0001-000001010110n00000-6--01111110-004-001110-110000000-
Aus aspera	00003120-1030-00001-000001010110p00000----01111210-004-001110-100000000w
Aus australis	000031111gfh-p-00000xz0001010110-00000----01111210-004q001110-110000000-
	11
Aus flavicollis	00003110121q--n0001-000001010110q00000----01111210-0046001110-110000000-
	1 1 2
Aus fuscamagna	000031211kmnh--0001-000001000110r00000----01111210-004-001110-110000000x
Aus fuscaparva	000031111mnp---0001-000001010110-00000----01111210-0047001110-110000000-
Aus nigra	00003110121r-q-0001s000001010110s00000-v--01111110-004-001110-110000000-
	1
Aus orapallida	000031111nps-r-0001-000001010110-00000-w--01111110-004-001110-110000000-
Aus pharusaurea	000031211pqtg--0001-000001010110900000----01111210-0048001110-100000000-
Pyr appendiculata	00003110-000---00000-20001010110-00000----011112104004s001110-100000000-
Pyro beccarii	00003110w000---0001-000001010110v00000x---01111210-004-001100-100000000-
	1
Pyro similis	000031103000f-p00000y-0001010110w000007---01111210-004-001110-100000000-
Py quadrimaculata	00003110-000---00000-40001010110700000-x--011112109004r001110-100000000z
Med platygaster	000031101000---0001-000001010-10x000021100-111121a-k04-001110-120000000-
	1

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TABLE 3. (Continued)

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                           111111111122222222223333333333444444444455555555556666666666777
Taxon/Node        123456789012345678901234567890123456789012345678901234567890123456789012
Med cribellata    00003110-000e--00000000001010-10-000020----111111b-m049001110-130000000-
                                    1
Med corusca       00003110-000---0001-000001010-10y0000207---111111c5n04-001110-130000000-
Med effulgens     00003110x000---00013000001010-106000022----111121d-p04-001110-130000000-
T minor           000031110------0001-000001010-10-000010----111121---04-001110-100000000-
T papuae          000031110------0001-100101010-10-000020----111111---04-001110-100000000-
T microthorax     000031111------0001-000101010-10-000020----111111---04-001110-100000000-
T similispapuae   00003120-100-0-0001-000101010-10-000020----111121---04-001110-100000000-
Pt macdermotti    00103110-000-0-00000z-0001010-10z000020----111121e-q04-000110-100000000-
                           1
Pt sp ML          00003110-100c0-00012000001010-103000020----111121k-a04-001110-1000000003
Pt sp MFC         000031110trv-x-000002-0001010-102000008---011112107004-001010-100000000-
Po selangoriensis 00003111-------0001-110001010-10-00000----01111210-004-001110-110000000-
Pt gelasina       00003110-000d-q0001y000001010-10-000120----111121f-r04k001110-1100000002
Pt malaccae       000031102000---0001-000001010-105000020y---111121g6s04-001100-100000000-
Pt tener          00003110-000--r0001z000001010-104000021011-111121h-t04-001110-100000000-
Pt maipo          00003110-000---00000--0101010-10-000021100-111121---04-001110-100000000-
Pt truncata       00003110y000---0001-000001010-10-000021100-111121j-u04t000110-100000000-
Colo praeusta     00001110-100b0s0001-000001010-10g00000y---01111210-004-001110-1200000004
                                                                                 3
Colo concolor     00001110-100-0-0001u000001010-10-00000-8--01111210-004-001110-130000000-
Colo plagiata     00001110z100a0-0001v000001010-10f00000----011112108004u001110-120000000-
Cur okinawanus    000131100000-0t000003m0011000000110000z---0111121101030001110-1100000005
                         1 1 1
Cur costipennis   000131110uvwjyu0001w000011010000110000-9--0111121101030001110-100000000-
Eme pseudosauteri 000011110vuayvv00001--0211000001100000----01111210g004j011110-100000000-
Species 8         00011110-1030-000000--0111010100000000----01111210-004-000110-100000000-
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TABLE 3. (Continued)

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                                             111111111111111111111111111111111111111111111
                  777777788888888889999999999000000000011111111112222222222333333333344444
Taxon/Character   345678901234567890123456789012345678901234567890123456789012345678901234
Photuris trivitta 1100893276540000000001000000000000000--a-0930002b8a-b-a0000000000-00a--0
Photuro deplanata 010110200a2-01000000000000000000100002-ca079000-2-8---b0000000000-00-6-0
Luciola italica   110111-012-a1100000000000000000010000--d-0640003-a----c0000000000-006--0
L kagiana         100111-012-f1100000000000000000010000----0--000-6---8--0000000000-00-a-0
L  parvula        100111-012-b11000000000000000000100003-e-0--000-----a-20000000000-00---0
L syriaca         11010b-zad011100000001000000000010000---c0-6000---b----0000000000-00b--1
L hypocrita       10010a4ybc01110000000000000000000010000-2-b0--000--9-----00000001---00---a
L antipodum       10010e-xfb01210000000000000000000010000-4--0--000--b-----0000000000-00---1
L aquilaclara     10110c-wd-0121000000000000000000100004-f-05-000n--9----0000000000-00-b-0
L oculofissa      10110d-veg012100000010000000000010000---e0--000--------00000001--------c
Aquatica leii     1001116012d-1100000000000000000010000--x-0ar0004--c----0000000000-00---0
Aq ficta          100111-012-d1100000000000000000010000-x--0--000-3-----d0000000000-00c--0
Aq lateralis      110111-012--1100000000000000000010000----0--000--c--9--0000000000-00---1
Aq hydrophila     110111f012f-1100000000000000000010000--3-0--000-------30000000000-00---1
Aq wuhana         110111-012--1100000000000000000010000----0--000--------0000000000-00---0
Luciola cruciata  100111d012--1100000000000000000010000w--f0--000-w-----e0000000000-00-c-0
L owadai          100111e012--1100000000000000000010000xy2-0bs0005----c--0000000000-007--0
L cingulata       100111-012e-1100000000000000000010000----0c-000---d---u0001101000-01d--1
L brahmina        100111-012-e1100000000000000000010000----0--000-4------0001101000-01---0
L substriata J    100111-012g-1100000000000000000010000--y-0-y000-------f0001101000-01---0
L substriata F    100111-012-h1100000000000000000010000yz-g0--0008-d-----0001101000-01-d-0
L aquatilis       100111h012--1100000000000000000010000--z-0e-000-5---d--0001101000-01-7-0
L. carinata       110111-012--1100000000000000000010000----0--000--------0001101000-01---0
L. seriata        100111-012--0100000000000000000010000----0--000--------0001101000-01---0
L dejeani         1101115012-c1100000000000000000010000-3-d0--000-------40000000000-00e--1
L dubia           110111-012--1100000000000000000010000----0--000---e----0000000000-00---1
L cerata          100111g012--1100000000000000000010000----0d-0106x-----g0000000000-00---1
L praeusta        100111-012-g1100000000000000000010000--4-0--010--e-----0000000000-00-e-0
L. aegrota        110111-012--0100000000000000000010000----0--010-----e--0000000000-00---0
L striata         110111-012--1100000000000000000010000----0--000--------0000000000-00---0
Jeng matalanga    110111-012--1100000000000000000010000----0--010---7---50010000000-00---0
Pyg cowleyi       10010f-ugj012100000000000000000000100005---0f-0006--7---h0000000000-00f--1
Pygo qingyu       0101101012--1100000000000000000010000---h0--010--f-----0000000000-00---0
                       1
Pygo guigliae     120111-012h-0100000000000000011110000--g-0--000-----7--0000010000-00---1
Pygo hamulata     110111-012-j01000000000000000000100007--k0-70009y-f----0000010000-00-f-1
Pygo kinabalua    120111j012--0100000000000000000010000-6-j0-5000-----f--0000010000-00---1
Pygo stylifer     ?10111-012j-0100000000000000011110000-5--04-000-------60000010000-00---1
Pygo satoi        110111-012-k0100000000000000000010000--h-03-000--g-----0000010000-00g--1
Pygo wittmeri     110111-012k-0100000000000000000010000-7--0--000---g----0000010000-00---1
Asymme circumdata 100111-012m211000000000000000000100008--p0--000-z---g--00000ab000-00-g-0
                   1
As ovalis         1001117012--1100000000000000000010000-85-0g-100b------j00000cd01--000-0d
                                                                                        1
Aquilonia costata 110111k011--1100000000000000000010000--j-02-000a------70000000000-00-8-0
Magnalata limbata 100111-010-m1100000000000000000010000-9-q0--000-----h--0000000000-00h--0
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TABLE 3. (Continued)

	1111111111111111111111111111111111
	77777778888888888999999999900000000001111111111222222222233333333334444
Taxon/Character	34567890123456789012345678901234567890123456789012345678901234
M carolinae	1001101010--2100000000000000000000010000-d-u0-e000-7-----k0000000000-00---0
	1
M rennellia	1001101010--1100000000000000000000010000-c--0-m000c--h----0000000000-00---0
Gilvains messoria	110111-010-n1100000000000000000000010000--n-0--000-8-----m0000000000-00-h-0
G similismessoria	1101119010n-1100000000000000000000010000-g-t0-k000d-h----0000000000-00---0
Missimia flavida	12007gnthk--0100010000000000000000100006-b-082000e-----80000000000-00j--1
Lloydie majuscula	100111-011--1100000000000000000000010000--p-0--000--j----0000000000-00---0
Ll uberia	100111w011p-1100000000000000000000100009--r0h-000f-----n0000000000-00---0
Ll japenensis	100111-011-p1100000000000000000000010000-a--0--000---j----0000000000-00---0
	2
Ll wareo	100111-011--1100000000000000000000010000-b-s0--0008-6--j--0000000000-00-j-0
Convexa wolfi	100111p011--1100000000000000000000010000--m-0--000gp----v0000000000-00---0
Atyph aphrogeneia	10010h-sjm0011000000000000000000010000a--m0j-000-----k--0000000000-00k--0
A atra	10110j-rk-0121000000000000000000010000h--y0--000-9-k---0000000000-00---0
A brevis	10?10kqqm-0121000000000000000000010000-j-z0--000--k----0000000000-00---0
A conspicua	10010m-pnp0111000000000000000000010000j--20--000h--6---0000000000-00---0
	2
A dalmatia	10010n-np-0111000000000000000000010000--q-0k-000--m----0000000000-00-k-0
	1
A ellioti	10?10p-mqr0121000001000000000000010000--k-0--000------90000000000-00---0
A flammans	10?111z012-q2100000000000000000000010000-k--0-b000---m---0000000000-00m--0
A flammulans	10?111-012--2100000000000000000000010000---30--000z----m--0000000000-00---0
A guerini	100111-010q-1100000000000000000000010000f--n0--000-n-----0000000000-00---0
A immaculata	10010q-kr-0121000000000000000000010000k---0-c000--n---s0000000000-00-m-0
A inconspicua	10010r-jsq0021000000000000000000010000-h--0-a000---n---0000000000-00n--0
A kirakira	1001101011--1100000000000000000000010000b--w0m-000-------000000001--000-00
A lamingtonia	100111-012-r1100000000000000000000010000e-r-0-n000jm-----0000000000-00-n-0
A leucura	100111-012--1100000000000000000000010000c---0--000--p----0000000000-00---0
A lewisi	10110sygtu0121000000000000000000010000g---0-8000---p---000000001----1-0f
A lychnus	10110t-fut0121000000000000000000010000-m--0--000------p0000000000-00p--0
A monteithi	10010u-ev-0121000000000000000000010000m-6-0-d000-------0000000000-00---0
A olivieri	10?1101012--1100000000000000000000010000-f--0n-000--5----0000000000-00---0
A palauensis	100111-010r-1100000000000000000000010000-e--0--000-k-5---0000000000-00-p-0
	1
A scabra	10010v-cw-0121000000000000000000010000n---0-j000k-----t000000001----100g
A scintillans	10010w-bxw0121000001000000000000010000---40--000--q----0000000000-00q--0
A similis	10010x-ay-0121000000000000000000010000---x0--000-------0000000000-00---0
A testaceolineata	100111-012--1100000000000000000000010000---v0p-000---q---0000000000-00---0
Pac limbatipennis	1001118012--110000000000000000000010001010-0--000------q000000000-00-r-1
Pac limbatifusca	100111-012--11000000000000000000001000101080--000---r---0000000000-009--1
Pac plagiata	100111-012--110000000000000000000010001010-0--000---s---0000000000-00-s-0
Pac russellia	100111-012--110000000000000000000010001010-0-z000w------0000000000-00---1
Pac salomonis	100111-012-u110000000000000000000010001010-0--000--s----0000000000-00t--0
	1
Pyg tomba	100111u012--110000000000000000000010001000-0t-000v-3--s--0000000000-00-t-1
Py eliptaminensis	100111r012--110000000000000000000010001010-0q-000mj-----w000000001000---1
Pyg huonensis	100111-012--1100000000000000000000100021-110-f000-------r000000001100-q-0
Pyg ignota	100111s012--110000000000000000000010001010-0--000-----q--0000000000-00---0
Pyg japenensis	100111-012--110000000000000000000010001010-0--000--------0000000000-00r--0
Pyg karimui	100111-012--11000000000000000000001000101060r-000-h-----0000000000-00---0
Pyg kiunga	100111-012-s1100000000000000000000100021q100--000y-r-----000000001000---0
Pyg marginata	100111-012s-11000000000000000000001000101050--000--------0000000000-00---0
Pyg nabiria	100111-012-9110000000000000000000010001000-0-p000m-4--r--0000000000-00s--0
Pyg obsoleta	100111-012t-110000000000000000000010001010-0-q000-g-4---x0000000000-00-9-0
	1
Pyg okapa	100111-012--110000000000000000000010001010-0s-000-----4--0000000000-00---0
Pyg peculiaris	100111-012-t1100000000000000000000100021p100-g000x-------0100000001000---0
Pyg pulcherrima	110111t012--110000000000000000000010001010-0-h000--------0000000000-00---0
Pyg tagensis	100111-012u-1100000000000000000000100021-110--000--------000000001100---0
Pyg uberia	100111-012-811000000000000000000001000100070--000---3----000000001----0-1j
	1
Pyg undulata	100111-012--1100000000000000000000100021n110--000-f---3--000010001100u--0
Pyg wisselmerenia	100111v012--1100000000000000000000010000-rs-0--000u-t-----0000000000-00-u-0
Luciola indica	?10110100---110000000000000000000001???0----0--0010-------0000000000-00---0
T dimidiata	010111-10e--1100000000000000000000010000----0--0010s------000000001----010m
L trilucida	110110100h8-1100000000000000000000010000----0--0007e-t----0000000000-00---0
	1
T papuana	110110100--x1100000000000000000000010000----0--0010q---t--000000001----010p
Aus foveicollis	010110100f--1100000000000000000000010000---90v-0010t------0000000000-00v--0
Med pupilla	010110100s--1100000000000000000000010000--8-0--0010c---u--0000000000-00-v-0
M similispupillae	010110100--61100000000000000000000010000----0--0010-------0000000000-00---0
T caudabifurca	110110100--w1100000000000000000000010000----0--0010-------000000001----010n
	1 1
Aus anthracina	0101101003-v1100000000000000000000010000----0--0010--u----0000000000-00w--0
Aus aspera	010110100-v-1100000000000000000000011110----0u-0010-------0000000000-00---0
Aus australis	010110100-7-1100000000000000000000010000--t-0--000p-u-----0000000000-00-8-0
	1
Aus flavicollis	010110100-w-1100000000000000000000010000p---0--000q-------0000000000-00-w-1
Aus fuscamagna	0101101003--1100000000000000000000010000----0--0010--v----0000000000-00x--0

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TABLE 3. (Continued)

Taxon/Character	
	111111111111111111111111111111111111111111111
	777777788888888889999999999000000000011111111112222222222333333333344444
Taxon/Character	345678901234567890123456789012345678901234567890123456789012345678901234
Aus fuscaparva	010110100-x-11000000000000000000010000--7-0--0010-------0000000000-00---0
Aus nigra	0101101004-711000000000000000000010000-s--0--000sd------0000000000-008--1
Aus orapallida	010110100n--11000000000000000000010000----0--000t-v-----0000000000-00---1
Aus pharusaurea	010110100-6-11000000000000000000010000----0--000-----v--0000000000-00-x-0
Pyr appendiculata	010111-105--1110000000001111010001000q---0--10111110101000000001----000q
Pyro beccarii	010111-10--y111000000000111101000100000----0w-10111110101000000001----0003
Pyro similis	010111x10z--11111000000011110100010000--9-0-t10111110101000000001----0004
Py quadrimaculata	010111-10-y-11100000000011110100010000-t--0x-10111110101000000001----0002
Med platygaster	010110100y--11000000000000000000010100--v-0--0010u-w----1000000000-00y--0
Med cribellata	010110100--z1100000000000000000011110t---0-v0010----w--1000000000-00-y-0
Med corusca	010110100-5-110000000000000000000011010-w--0--0010-w-----1000000000-00z--0
Med effulgens	010110100--51100000000000000000011010----0-w0010-------1000000000-00-z-0
	1
T minor	010110100---1100000000000000000001???0----0--0010-------000000001----010-
T papuae	?00110100---1000000000000000000001???0----0--0010-------000000001----010-
T microthorax	?00110100---1000000000000000000001???0----0--0010-------000000001----010-
T similispapuae	110110100---11000000000000000000010000----0--0010-------000000001----010-
Pt macdermotti	020110100-z-1111100001010000000011110--u-0--00111110101000000001----100r
Pt sp ML	010111-10---1100000000010000000011110s---0--00111000000000000001----0005
Pt sp MFC	0101101108--1100000000010000000011010----0--0010--y----0000000000-0023-0
	1
Po selangoriensis	110110110---11000000000000000000010000----0--00111111011000000001----011-
Pt gelasina	010110100---1110000001010000000011110r---0y-0010-x-----000000001----0106
Pt malaccae	0101101007--1110000000001000010001l110-u--0--0010a-x----000000001----000s
	1
Pt tener	010110100v--1100000000010001000011110----0-u0010----x--000000001----0007
Pt maipo	110110010---1100000000010000000011010----0--0010-------000000001----011-
Pt truncata	000110100-4-1100000000010001000011110-v--0--0010-y-----000000001----000v
Colo praeusta	020110100--41100001000000000000000010000u---1110010----y--000000001----000t
Colo concolor	010110100x--11000010000000000000000010000----1000010rz-----000000001----0108
Colo plagiata	020110100-3-11000010000000000000000010000z---1110010--z----000000001----000u
	1
Cur okinawanus	01011010099-11000000000000000000010000--w-0-x000r-2--z-y0000000000-0032-1
Cur costipennis	010110100--311000000000000000000010000v---0z-000-v-2---0000000000-0045-1
Eme pseudosauteri	110111-012--01000000000000000000010000d---0--000va---2-z0000000000-0054-1
Species 8	100111-012--11000000000000000000010000----0--000--------0000000000-1----1

TABLE 3. (Continued)

Taxon/Character	
	1111111111111111111111111111111111111111111111111111111222222222222222222
	4444455555555555666666666677777777778888888888999999999900000000001111111
Taxon/Character	5678901234567890123456789012345678901234567890123456789012345678901234567890123456
Photuris trivitta	05a0-c-003000ba4a234-ab-bcde23aa053--2-00a--00022023-a----u4900081000aja
Photuro deplanata	01b0-d-0050010060102a-00000045b0045--3-00-a2000-3034---a----2000-1002020
Luciola italica	01c0---0060010070000-b--00005630034----00--a000--045----a----000-1002010
L kagiana	10-0---00-0010030000---a0000---00y-----00z--000--0---z-z----c000-1001310
L parvula	10-0---00-00100-0000--c-0000---00----5-00-2-000a-067-------a-000-1002010
	2 1
L syriaca	10-0---00-00100-0001-c--0000---006-----00--z000-a058--------a000-100????
L hypocrita	bcda-b-01-2a100-0000b-a-0000---00----4-002--000--056------a--000-1002010
L antipodum	10e0---00910100-0000d--c0000--500------00-b-000--0------b----000a1002010
L aquilaclara	11-0---0080010090000-d--00006--00----6-00---000--09--------b-000-1002010
L oculofissa	ba-b-a-1a-3y100-0000--d-0000-7-007-----00--b000--0-2------b--000-1002010
Aquatica leii	10f0-e-00w10100w0000---d0000x-w00----p-00b--000--0-u---bs----000-1001n00
Aq ficta	10-0---00-10100-0000-e--0000---00q-----00-c3000340u--b-----5-000-1001p00
Aq lateralis	00g0-f-00-10100s0000--e-0000---00------00---000--0----------d000-10007hb
Aq hydrophila	00-0---00-10100-0001---e0000---00------00-340005-0---------c-000610002ak
Aq wuhana	10-0---00-10100-0001----0000---00------00---000--0-----------000-1001-00
Luciola cruciata	10h0---00-0010020000e---0000-v-00-q----00--c000--0-v-c----z--000x1000qfh
L owadai	10-0-g-00-00100-0001---f0000n--00j-----003--000450v----cu--63000-1000rgj
L cingulata	11j112200-00100-0001--f-0000-2-00------004--110--0--------c--000-1003111
L brahmina	01-111100-00100-0001---g0000---00-a----00---110--0------c---v000-1003111
L substriata J	01k110000x00100x0000-9--0000z--00-r--s-00---100c-0w----d-----000z1003111
L substriata F	01-110000-00100-0000f-h-0000-x-00rs--t-00645110-c0---d--v-y8-000-1003111
L aquatilis	01-110000-00100-0000----0000--y00st--u-00---100-d0-x-e------4000-1003111
L. carinata	01-110000-00100-0000----0000---00------00---100--0-----------000-1003111
L. seriata	01-111100-00100-0000----0000---00------00---100--0-----------000-1003111
L dejeani	00-0-h-0070010080000c-c-0000--400-6----00---000b-089--------b00091002011
L dubia	00-0---00-00100-0000----0000---00------00---000--0-----------000-1003011
L cerata	00m0---00-00100-0000--g-00009--00-g----00---000--07m-------d-000-1203011
L praeusta	00n0---00-00100r0000----0000---00------005--0006-0--------d--000-1203011
L. aegrota	00-0-j-00-00100-0000-g--0000---00------00---000--0-----------000-1203011
L striata	01-0---00-00100-0001----0000---00------00---000--0-----------000-1002010
Jeng matalanga	10-0---00-00100-0000----0000---00------00---000--0-----------000-11c3011
Pyg cowleyi	10-0---00q0000000000-f--0000--r00----m-007--000d-0-t---e-----000-11d3011
	1 1
Pygo qingyu	10-0---00-00100-00009-j-0000---00------01000001100---------f-000-11e3011
Pygo guigliae	10-0---00-10100-0002--101000--6008-----021-d000-70ba-z--e----000b2213011
Pygo hamulata	10-0-k-00-10100-0002-g101000-9-00------0215-000--0--------e--000-201????

......*continued on the next page*

TABLE 3. (Continued)

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                  1111111111111111111111111111111111111111111111111111111222222222222222222
                  444445555555555666666666677777777778888888888999999999900000000001111111
Taxon/Character   567890123456789012345678901234567890123456789012345678901234567890123456
Pygo kinabalua    10-0---00-101010d002g-111000-8-00----7-021--000--0---------e-000-2013011
                                                                                    2
Pygo stylifer     10p0---00a10100a2002--1010007--00-8----021d-0007-0a--y------e000-221????
Pygo satoi        10-0---00b10100b0002h-101001001109---8-021--000--0c---------f000c2013011
                                                                                    2
Pygo wittmeri     10-0---00-101011e002--1110008-700------021--000-80-a------f--000-2213011
Asymme circumdata 00r100000-01100-0000j---c000-w-00----q-1a----00-e0-----f--9y-000y20a3011
As ovalis         ef-x---000yz11105001--k-d000y-x00r-----1b866-00f-0-w-f--w---5000-20b3011
Aquilonia costata 01q0-m-00c00100c0001-p-h0000a-800------00--e000890d--x--f-x3-000-1001800
Magnalata limbata 00-0---00-00100-0000-m-j0000-d-00------00---000--0nh-g-------000j1002010
M carolinae       00s0---00-00100q0000k---0000---00----d-0097-000-b0-g---g--896000-1002010
M rennellia       00-0-n-00j00100-0000m--k0000k--00------00--7000h-0r-----g----000r1001900
Gilvains messoria 00-0---00-00100g0000p-m-0000g--00z-----00c8-000-f0--------g--000-1002020
G similismessoria 00t0---00-00100-0000----0000j--00-j--x-00--8000g-0---w--x--g7000-1002020
Missimia flavida  00u0-p-004101005000222 0m000034201000-0-00d-9000-g1100v--y-7-g00071004020
Lloydie majuscula 00-0---00-00100h0000n---0000h--00----g-00-f-000-h1101-------h000-1003011
Ll uberia         00-0---00-00100-0001-nn-0000--k00----h-00f--000--0---u-----h-000q1003011
Ll japenensis     00v0---00-00100-0000---n0000-h-00g-----00-g-0009-0q-------h--000-1003011
Ll wareo          00-0---00-00100-0000-7--0000-j-00-h----00--g000--0-r----h---000-1003011
Convexa wolfi     10w0-q-00e00100-00008-pq0000--f00----d-00g-f000-k0-j-t-hz-6x8000-1003011
                            1
Atyph aphrogeneia 00-0---00-00100-0000----0000---00a-----00e--000--0-c-h-------000-1002010
A atra            00-0---00-00100-0000---p0000---00----9-00---000j-0f--j-------000e100????
A brevis          00-0---00-00100d0000--q-0000b--00b-----00-kr000--0g---j-----000-100????
A conspicua       00-0---00-00100-00006---0000--c00-b----00---000-n0-e---j----000-100????
A dalmatia        00-0---00-00100j0000-h--0000--m00h-----00-e-000--0--------j--000-1002010
A ellioti         00-0-r-00-00100-0000r---0000-b-00----b-00k--000--0h--------j-000f100????
A flammans        00-0---00-00100-0000--r-0000---00------00-m-000--0j--s------j000-1001f00
A flammulans      00-0---00d00100-0000-5--0000--d00------00--m000--0-f--------k000-1001g00
A guerini         00-0---00-00100-00007--r0000-g-00------00---000--0-q-------k-000-1001b00
A immaculata      00-0---00-00100-0000-r--0000---00------00---000-m0---9----k--000g1001h00
A inconspicua     00-0-s-00-00100-0000-6s-0000---00------00---000--0-d----k----000-1001e00
A kirakira        gh-e---001dc100-0000----0000-k-00------00-j-000--0-----k-----000-1001500
A lamingtonia     00-0---00-00100-0000-k--0000-m-00----k-00---000k-0s--k-------000s1002010
A leucura         00-0---00-00100-0000-j--0000d--00-d----00h--000--0---m-------000-1001c00
A lewisi          ed-3---0007b100-0000--t-0000-a-00-9----00--k000--0-----m-----000d1001s00
                           1
A lychnus         00x0---00-00100-0000----0000c--00c-----00---000m-0k-----m----000-1001j00
A monteithi       00-0-t-00-00100e00005--s0000---00-c----00-9-000n-0m--8----m--000-100????
A olivieri        01-0---00-00100-0000-q--0000-c-00----c-00j--000-j0---------m-000-1001600
A palauensis      00-0---00g00100-0000-8u-0000--j00f-----00---000e-0----------m000-1001t00
A scabra          jk-d---011cd100-00004---0000---00------00--h000--0----------n000p1000m0c
                                  1
A scintillans     00-0---00-00100-0000s--t0000--e00------00---000--0---7-----n-000h1001k00
A similis         00-0---00-00100-0000q-v-0000--900------00--j000--0e-------n--000-1001d00
A testaceolineata 00-0-u-00-00100k0000----0000m--00------00---000--0-s----n----000-1002010
Pac limbatipennis 10-0---00z10100z2001-zx-000111000wx--y-00r--000--0-z------p--00111003011
                               1  3
Pac limbatifusca  10-0---00-10100-2001---w000111000xy--z-00-s-000--0z--6-----p-00111003011
                               1  3
Pac plagiata      10-0---00-10100-0001---x000111000uv--w-00---000r-0-y---q-----00101003011
Pac russellia     10-0---00y10100y0001z---000111000tu--v-00---000--0x--q-----w-00111003011
Pac salomonis     10-0---00-10100-2001---y000110000vw--z-00---000-r0y--r-------00111003011
                               1  3            1
Pyg tomba         10-0---00k10100-0001----0000--n00-k----00-n-000--1100---r----000-1002010
                                  1
Py eliptaminensis 10-0---00-10100-0001---u0000-e-00------00m--000--1101--n---w-000-2003011
Pyg huonensis     10-0---00-10100-0001-s--0000---00-e----00--n000--1102--------000-1003011
Pyg ignota        10-0---00f10100-2001-tw-0000--g00----e-00---000pw0pn-n-------000-1003011
Pyg japenensis    10-0---00-10100-0001---v0000--p00------00-q-000--1001p-------000-1003011
Pyg karimui       10-0---00-10100m2001-u--000101000-m----00---000--1100--p-----000-1003011
Pyg kiunga        10-0---00h10100-0001t---0000---00g-----00--p000--1100---p----000-1003011
Pyg marginata     10-0---00-00100-00013---0000-f-00----f-00---000-p0p---------p000-2003011
Pyg nabiria       10-0---00-10100-2001-3--0000---00k-----00--q000--1101-------q000-2003011
Pyg obsoleta      10y0---00n10100q0001--y-0000---00------00q--000--11030-1---q-000-2003011
                                  1
Pyg okapa         10-0---00m10100-101122--0000-n-01000-0-00---000q-1110-----q--000-1003011
                                                      1
Pyg peculiaris    10-0---00-10100-0001-4--0000f--00e-----00nh-000--11005--q-5--000m2003011
Pyg pulcherrima   10-0-v-00-10100-1000u-z-0000---00-f----00p--000--11030-0-----000n1003011
Pyg tagensis      10-0---00-10100f0000--2-0000--h00------00-p-000--0-p---r--4--000-1003011
Pyg uberia        km-f---000e6100-0002-v0-0100---00m-----00-r-000--0--------r--010-1003011
Pyg undulata      10-0---00-10100-0001---z1000e--00----r-02011000--0-k-------r-000k1003011
Pyg wisselmerenia 10-0---00-00100-0000v-3-0000--q00------00---000-q0---4--9---r000-1003010
Luciola indica    0010---00-001010-00122--0000---01000-0-00---000--110310-00110000-1002020
T dimidiata       np-y---00054100-0001114-0000---01110-0-00---000z-110310t010000005 1002020
L trilucida       01-0-w-00-0010002001---30000---00------00---000--0------d----000-1001u20
                                1
T papuana         mnz2-y-000431010800000 5-0000---0122010-00---000--110310-01000000-1002020
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......*continued on the next page*

TABLE 3. (Continued)

	1111111111111111111111111111111111111111111111111111112222222222222222
	4444455555555556666666666777777777788888888889999999999000000000011111111
Taxon/Character	5678901234567890123456789012345678901234567890123456789012345678901234567890123456
Aus foveicollis	0110-8-00-00100-0002210-0000---01110-0-00-t-000--11030-0--t--000-1002020
Med pupilla	0110---00-00100p000112-40000-z-01100-0-00s-z000--110310-10100000-1002020
M similispupillae	0110-x-00-00100-000111--0000---01110-0-00---000--110310v101000003100202O
T caudabifurca	p6-c---000651000100100-50000---0122110-00---000--110310s01000000-1002020
	1
Aus anthracina	0110---00-00100-000121--0000-p-01110-0-00---000-s11030-0----s000-1002020
Aus aspera	0110---00-00100-000021--0000---01110-0-00x--000--110310-01010000-1002020
Aus australis	0120---00-0010000000w--60000p--00------00--s000--11030-1--s-u000u1002010
	1
Aus flavicollis	10-0---00r1010000000----0000--z00nz--j-00---000--11030-0t--v-000-1003020
	1 1
Aus fuscamagna	0110---00-00100-000121--0000-y-01110-0-00---000--11030-0---t-000-1002020
Aus fuscaparva	0110---00-00100-000121--0000---01110-0-00y--000--11030-0---vt00041002020
Aus nigra	10-0-9-00s1010002000-w-20000---00-n----00---000s-11030-0----u000-1003020
	1 1
Aus orapallida	10-0---00t00100t2000x---0000--s00----n-00--t000--11030-0---u-000-1002020
Aus pharusaurea	01-0---00-0010002001----0000---00------00---000--110310-01010000-1002020
	1
Pyr appendiculata	43-j---000hm1010j00012--0000-q-01100-0-00--u000-z110310x00110100-1003020
Pyro beccarii	q23h-7-000gk1010h000126-0000q--01100-0-00-u-000--110310w00110100-1003020
Pyro similis	2q-k---000kg1010k00012--0000---01100-0-00---000--110310y00110100-1003020
Py quadrimaculata	34-m---000mh1010m00012-70000---01100-0-00---000u-110310200110100-1003020
Med platygaster	0110---00u001010u00011--0000--u01110-0-00---000--110310310110000-1002020
Med cribellata	0110-z-00-00100n200011--0000---01110-0-00-yx000t-110310410110000021002020
Med corusca	0110---00-001010w000117-0000t--01110-0-00---000-t110310510110000-1003020
Med effulgens	0110---00-001010x00012--0000-t-01100-0-00t--000--110310611100000-1003020
T minor	-------000--1010-001000-0000---01121-0-00---000--110310-11100000-1003020
T papuae	-------000--1010-001000-0000---0112110-00---000--110310-11100000-1003020
	2
T microthorax	-------000--100-2002000-0000---0112110-00---000--110310-10110000-1003020
	2
T similispapuae	-------000--1010-002100-0000---0121110-00---000--100311-00000000-1003020
	1111
Pt macdermotti	5-4n---002nt1011n00102--0000r--0120100-00---000-u11030-0---z-000-3003020
Pt sp ML	r75s---000tn1010t00010-80000s--01000-0-00v--000--110310701000000-1003020
Pt sp MFC	000t-5-00-00100u000102-90000-s-01000-0-00---000-v11030-06-w--000v1003020
Po selangoriensis	-------000--100-000022--0000---01000-0-00---000--11030-0-----000-1002020
Pt gelasina	ur-p---000ps1010p00002--0000-r-0120100-00ux-000v-11030-02---x000-1003020
Pt malaccae	68-z-6-000qr1010q000118-0000--t0110100-00---000--11030-03-v-y000t1002020
	2
Pt tener	s96q---000rq1010r00021--0000---00000-0-00--v000-y11030-04--2-000-1003020
	1
Pt maipo	-------000--100-200121--0000---01010-0-00---000--110310-00010000-1003020
Pt truncata	7s-r---001sp1010s00012--0000---01100-0-00-v-000y-11030-05---z000-1003020
Colo praeusta	vu-u---000vx1011y00121110010u-v2120102100--y000w-110310810101000-1004020
	2
Colo concolor	tb7v---000wv1011z00221110020---31100-1000---00101110310-10101000-1004020
	1
Colo plagiata	8t-w-4-000xw101140022111001 0v--2120102100-w-000--110310-10101000-1004020
Cur okinawanus	0080---00v10100v0000y-9-0000w--00p---a-00w--000xx0t--3-97--7w000w0002010
	1
Cur costipennis	00-0-3-00-10100-0000-y--0000-u-00-p----00--w000--0-b-2--8-2--000-0002010
	1
Eme pseudosauteri	1090-2-00p1010107001-x--0000---00d-----01-11000-60-2----z--s-000-1202011
Species 8	11-0---00-00100-0001----0000---00------01-01000--0-----------000-2103011

TABLE 3. (Continued)

	2222222222222222222222222222222222222222222222222222222222222222222222
	1112222222222333333333344444444445555555555666666666677777777778888888888
Taxon/Character	7890123456789012345678901234567890123456789012345678901234567890123456789012345678
Photuris trivitta	2060a-10--e-b20-00---a--20000?--0000-00000-0101080a-b-00290000100000a-0c
Photuro deplanata	00a0--000120101100-2--a-v000014-1001001000-02130a100110047000191-0a020a1
Luciola italica	00-06--1000-000a00-----a-000005-100--00000-10010-0--a-00561020100000--0-
L kagiana	00-0--00--a--c0-00---2---00000-81000-00000-1101090----00-j1020100000-a0-
L parvula	00b0--00--c-2a0-00-3--v-a00000-51000-10000-10010b0--c-00--1120100000--0-
L syriaca	?0-0--00------0-00-----v-000006-1000-10000-11010-0---b00-51120100000--0a
L hypocrita	00-0b--1000-000-00-4-v-2-00000-4100--?0000-10010-0b---00--1120100000b-0-
L antipodum	00z0c--1000-000b00---w--300000-6100--10000-10010-0--d-007-1120100000--0-
L aquilaclara	00-0---1000-000-00---bc--000007-100--?0000-10010-0---c006-1120100000-b0-
L oculofissa	00-0---1000-000-00-5---b-00000--100--?0000-10010-0---d00-41120100000--0-
Aquatica leii	00c101-10101010-00----3-b011002-100--00000-00010c0----00w-1010100100--0b
Aq ficta	00-111-10101010c00-------01100--100--00000-00010-0d---00--1010100100c-0-
Aq lateralis	x0-110-10101010-01-0-0010b0000-3100--00000-00010-0----00--0000100000--0-
Aq hydrophila	30d100-10101010d00-6--9-c00000--100--00000-00010d0---800--0000100000--0-
Aq wuhana	00-101-10101010-00-------01100--100--00000-00010-0----00--1010100000--0-
Luciola cruciata	y0-0e--1000-000e00---c-3-00000-2100--00000-00010-0---e00-w1010100000-c06
L owadai	z0e0d--1000-000-00-7--bcd00000--100--00000-00010e0--e-00--1010100000--0-
L cingulata	0100---1000-000-01-1111--r0000-7100--00001110010-0----00--0000000000--0d

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TABLE 3. (Continued)

	222222222222222222222222222222222222222222222222222222222222222222222222
	111222222222233333333334444444444555555555566666666667777777777888888888
Taxon/Character	789012345678901234567890123456789012345678901234567890123456789012345678
L brahmina	0100---1000-000-01-1011--c0000--100--00001010010-0----00--0000000000d-0-
L substriata J	0100---1000-000-01-0-0001d0000r-100--00001110010-0----00xy0000000000--0-
L substriata F	010112-1000-000-01-0-0110e0000s9100--00000-10010-0---f00yz0000000000--0f
L aquatilis	010112-1000-000-01-0-0110f0000t-100--00000-10010f0----00z-0000000000--0-
L. carinata	010111-1000-000-0101110---0000--100--00000-10010-0----00--0000000000--0-
L. seriata	0100---1000-000-01-0-10-0-0000--100--00000-10010-0----00--0000000000--0-
L dejeani	00-??????????????????????0????????????????10010-0c---00--0000100021--0-
L dubia	00f0--10-----e0-1110-0000g001a001001000?0-10010-0--9-00--0000100021-d0-
L cerata	00-0g-10----3-0f2110-0000h001b001001000010-10010g0----00--0000100021--0e
L praeusta	00g0--10----4-0-2110-0000j001c001001000010-10010-0----00--0000100021e-0-
L. aegrota	00-0--10--4--30g2110-0000k001d001001000000-11010h0----00--0000100021--0-
L striata	00-?--10------0-00-------0001-001001000000-10010-0----00--0000000000--0-
Jeng matalanga	00h0--10----540-00-8-d-2-0001e001001100010-01020-0----00--0000100020--0-
Pyg cowleyi	00-0h-10--5---0h00-9--d--0001f101001100000-10020j0e---00--0000000000--0-
Pygo qingyu	0070--10-----50-2110-0000m001g111001100000-11010-0----00--0000000010--0-
Pygo guigliae	00j0--10----d-0-00-------n001h111001100000-01020-0---g00-30000000000--07
Pygo hamulata	?0-??01020-09---00--0000000000--0-
Pygo kinabalua	00-0j-10------0-0100-0000p001j111001100000-0102070f---00--0000000000--0g
Pygo stylifer	?10???????????????????????????????????????01020-0--f-008-0000000000--0-
Pygo satoi	00-0--10------0-0100-10-0q001k111001000010-01020-0----009-0000000000--0-
Pygo wittmeri	0100k-10--z-e-0j??????????001m111001100000-01020-0--g-00-20000000000--0-
Asymme circumdata	00m0--10d----z120100-11-0s0001--1001000100-00010-0----00-x0000000000-f0-
As ovalis	00-07-10z-d---120100-11-0t0001-a1001000100-00010m08---00--0000000000--08
Aquilonia costata	00k0m--1000-000-00-z--e4-000008-100--00000-00010k0----00--0000000000f-0h
	11
Magnalata limbata	00-0---1000-000-00-y---d-00000f-100--00000-01010-0---900e-0000000000g-0-
M carolinae	00n0---1000-000m00---g---00000e-100--00000-01010n0h---00--0000000000--0-
M rennellia	00-0n--1000-000-00----f--00000--100--00000-01010-0----00-n0000000000--0j
Gilvains messoria	00p0---1000-000n00-x-f---00000k-100--00000-01010p0k---00h-0000000000-g0-
G similismessoria	00-0p--1000-000-00---x---00000-d100--00000-01010-0----00k-0000000000--0-
Missimia flavida	10q0---1000-000p00-w--g-f000003-100--00000-00010q0----00381010100000h-0-
Lloydie majuscula	00-0q--1000-000-00---e---00000m-100--00000-00010-0----00--0000000000-h0k
Ll uberia	00r0---1000-000-00-v---e-00000--100--00000-00010-0----00-m0000000000--0-
Ll japenensis	00-0---1000-000q00------e00000-c100--00000-00010r0--j-00--0000000000j-0-
Ll wareo	00-0r--1000-000-00----h--00000--100--00000-00010-0---k00--0000000000-j0-
Convexa wolfi	00x0---1000-000r00-u--j-x00000-b100--00000-10010s0j---00--00000-1000k-0-
Atyph aphrogeneia	00s0---1000-000-00-----x-00000--100--00001211010-0---a00a-0000000000--0m
A atra	?0-0---1000-000-00-------000009-100--00000-11010-0--m-00--0000000000--0-
A brevis	?0-0s--1000-000-00-----f-00000-g100--00000-11010-0---m00b-0000000000-k0-
A conspicua	?080---1000-000-00----k--00000--100--00000-11010-0---n00-b0000000000--0-
A dalmatia	00-0---1000-000-00-----g-00000--100--00000-1101060g---00--0000000000--0-
A ellioti	?0-08--1000-000s00---y---00000a-100--00000-01010-0n---00--0000000000--0-
A flammans	00-0---1000-000-00------g00000-h100--00000-01010-0----00c-0000000000--0n
A flammulans	00-05--1000-000-00-t--8--00000b-100--00000-01010-0--n-00--0000000000--0-
A guerini	0050---1000-000-00-------00000--100--00000-01010-0--k-00--0000000000--0-
A immaculata	00-0---1000-000-00---h---00000--100--00000-11010t0----00-c0000000000--0-
A inconspicua	00-0---1000-000-00----m-y00000--100--00000-11010-0----00--0000000000--0-
A kirakira	00-0---1000-000-00-----h-00000--100--00000-11010-0----00m-0000000000--0-
A lamingtonia	00-04--1000-000900----7--00000n-100--00000-11010-0----00-p0000000000--0-
A leucura	00-0---1000-000-00------h00000--100--00000-1101050---h00-e0000000000--0-
A lewisi	00-0---1000-000-00-----y-00000-f100--00000-11010-0m---00--0000000000--0p
A lychnus	0040---1000-000-00---j---00000c-100--00000-11010-0---p00-d0000000000m-0-
A monteithi	?0-0---1000-000-00-----j-00000--100--00000-11010-0--p-00--0000000000--0-
A olivieri	00-09--1000-000-00------j00000d-100--00000-01010-0----00d-0000000000--0-
A palauensis	00-0---1000-000-00----6--00000--100--00000-01010u0---j00-k0000000000-m0-
A scabra	b090---1000-000-00---z---00000-e100--00000-11010-0--q-00--0000000000--0-
A scintillans	00-0---1000-000t00---k---00000-j100--00000-11010-0p---00--0000000000--0-
A similis	00-0t--1000-000-00-----k-00000--100--00000-11010-0----00-a0000000000--0-
A testaceolineata	00t0---1000-000-00-s----k00000--100--00000-11010-0--h-00--0000000000-n0q
Pac limbatipennis	00-0---1001-001000-------00000x-100--00000-10010-06-3201000000000000-p0-
Pac limbatifusca	00-0---1001-001000-----5-00000y-100--00000-10010-07-2301000000000000--0-
Pac plagiata	00-0---1001-001000----p--00000v-100--00000-10010-04-5601110000000000--0t
Pac russellia	00-0---1001-001000-p-----00000u-100--00000-10010-03-6501000000000000-q0-
Pac salomonis	00-02--1001-001000----4--00000wq100--00000-10010w05-4701000000000000--0-
	11
Pyg tomba	0020---1000-000-00---p---00000--100--00000-01010-0--8-00--0000000000--0u
Py eliptaminensis	00-0---10100000u00-----z-00000h-100--00000-11010-0---r00f-0000000000--0-
Pyg huonensis	00-0---1000-000-00------z00000g-100--00000-0101040----00-f0000000000n-0-
Pyg ignota	00-0u--1000-000-00------m-00000-m100--00000-01010-0----00-g0000000000--0-
Pyg japenensis	00u0---1000-000-00----n--00000--100--00000-01010-1100000n-0000000000--f0
Pyg karimui	00-0---1000-000-00------m00000-n100--00000-01010-0s---00--0000000000--0r
Pyg kiunga	00-0---1000-000-00-r----400000--100--00000-01010v0----00j-0000000000--0-
Pyg marginata	00-03--1000-000-00---n---00000--100--00000-00010-0--r-00--0000000000--0s
Pyg nabiria	00-0---1000-000-00---4---00000--100--00000-01010-1100000--0000000000--g0
Pyg obsoleta	0030---1000-000v00-q---n-00000p-100--00000-01010-0--t-00p-0000000000p-0-
Pyg okapa	00-0---1000-000-00----5--00000--100--00000-0101030--s-00-q0000000000--0-
Pyg peculiaris	00-0---1000-000-00------n00000-k100--00000-11010-0----00g-0000000000--0-
Pyg pulcherrima	00-???????????????????????????????????????11010-0r---00--0000000000--0-
Pyg tagensis	00-???????????????????????????????????????11010-0---q00-h0000000000--0-

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TABLE 3. (Continued)

	2222222222222222222222222222222222222222222222222222222222222222222222222
	1112222222222333333333344444444445555555555666666666677777777778888888888
Taxon/Character	789012345678901234567890123456789012345678901234567890123456789012345678
Pyg uberia	00-0---1003-0-0-00---m---0001---100--00000-01000-1100000--0000-00000--h1
Pyg undulata	00v0---1000-000-00-----p-00000--100--00000-01010-0q---00--0000000000--0-
Pyg wisselmerenia	00-0v--1000-000w00----q--00000--100--00000-01010x0t--s00--000000000q-0-
Luciola indica	0100--00--------00-------00000--1100-00000-021-010----10--0000000--00-1-
T dimidiata	0100--00--v-78-800---5---00000--1000-00000-021-000----00--00000000500r1s
L trilucida	0100--00e-y-----00-n-3---00000--1000-00000-021-000----00--00000000300-1-
T papuana	0100--00--u--h-y00-----9-00000--1000-00000-021-000----00--00000000j00-1-
Aus foveicollis	0100--00f-w-g---00-----q-00000e-1000-00000-021j000--v-00--00000000-00-1-
Med pupilla	0100--008-7--v--00---6---00000ds1000-00000-021-000---u00--00000000900-1-
M similispupillae	0100--00v---h7--00------600000--1000-00000-0216000----00--00000000-00-1-
T caudabifurca	0100--007-h-u---00-k--s-500000--1000-00000-0219000----00--00000000-00s1v
Aus anthracina	0100--00----8w--00-m-q---00000c-1000-00000-0214000u---00--00000000400t1-
Aus aspera	0100--00w-8-v---00----2--00000--1000-00000-021-000----00--00000000-00-1-
Aus australis	0100--006---xy--00------p00000qr1000-00000-021a000---t00q-00000000b00-1-
Aus flavicollis	0100--00y-x-----00----36-00000a-1000-00000-021b000--u-00-r00000000c00-1-
Aus fuscamagna	0100--00h---ju--00---9---00000-p1000-00000-0217000----00--00000000700-1-
Aus fuscaparva	0100--00u-j-----00-----7-00000--1000-00000-0218000----00--00000000800-1w
Aus nigra	0100--00----fx--00-j-----00000b-1000-00000-021c000----00--00000000d00u1-
Aus orapallida	0100--00x-f-----00----r--00000f-1000-00000-021d000----00--00000000e00-1-
Aus pharusaurea	0100--00----wf-x00-------00000--1000-00000-0215000----00--00000000600-1x
Pyr appendiculata	0100--00----tj--00-----r-00000n-1100-00000-021f011110000--00007000g020c2
Pyro beccarii	0100y-00j-t----z00-h-r---00000m-1100-00000-021e011110000-s00008000f020b2
Pyro similis	0100--00----kt--00----t-r00000pu1100-00000-021g011110000r-00006000h020d2
Py quadrimaculata	0100--00t-k-9---00-------00000q-1100-00000-021h011110000--00005000k020e2
Med platygaster	0100--00--9--k-300------q00000g-1000-00000-021t000v---00--00000000u00-1-
Med cribellata	0100--00k---m9--00-g--u-700000ht1000-00000-021u000--w-00--00000000v00v1y
Med corusca	0100--009-m-----00---7---00000j-1000-00000-021v000w---00--00000000w00-1-
Med effulgens	0100--00----sm--00-----8-00000k-1000-00000-021w000---v00-v00000000x00-1-
T minor	0100--00--------00-------00000--1000-00000-021-000----00--00000000-00-1-
T papuae	0100--00--------00-------00000--1000-00000-??1-000----00--00000000-00-1-
T microthorax	0100--00--------00-------00000--1000-00000-??1-000----00--00000000-00-1-
T similispapuae	0100--00--------00-------00000--1000-00000-021-000----00--00000000-00-1-
Pt macdermotti	0100--00m-s-r---00---s---00000z-1100-00000-021k000---w00-t00000000m0201z
Pt sp ML	0100--00n-p-----00-e---t-00000tw1100-00000-021r000----00t-00000000s01w1-
Pt sp MFC	0100--00----qp--00-f--z-t00000--1100-00000-021s000--y-00--00000000t01x14
Po selangoriensis	0100--00--------00-------00000--1100-00000-021-000----00--00000000-0201-
Pt gelasina	0100x-00--r--s--00-----s-00000r-1100-00000-021m000x---00--00000000n0201-
Pt malaccae	0100--00s---nr-400----v-s00000yv1100-00000-021n000--x-00s-00000000p01-13
Pt tener	0110--00r-n-----00-d----900000s-1100-00000-021p000y---00--00000000q01-1-
Pt maipo	0100--00--------00-------00000--1100-00000-021-000----00--00000000-0201-
Pt truncata	0100--00----pn--00---t---00000--1100-00000-021q000---x00-u00000000r0201-
Colo praeusta	0100w-00p-q----500-c----800000u-1010-00000-021x010---y00u-00000000y0211-
Colo concolor	0100--00--6-zq--00---uw--00000-x1010-00000-021y010--z-00--00000000z0211-
Colo plagiata	0100--00q----g--00-----u-00000v-1010-00000-021z010z---00--00000000900y15
Cur okinawanus	00w0---1000-000600-b--x-u00000wy100--01000-11011y0---z00v-0000000000--0-
Cur costipennis	00-0z--1000-000-00---8---00000xz100--01000-11011z02-7400--0000000000--0-
Eme pseudosauteri	00y0---1000-000700-a--y--000003-100--00000-0001020----00--0000000000-z09
Species 8	00-0---1000-000-00-------00000--100--00000-10010-1110000--0000-00000---0

TABLE 3. (Continued)

	2222222222223333333333333333333333333333333333333333333333333333333333333
	8999999999900000000001111111111222222222233333333334444444444555555555556
Taxon/Character	901234567890123456789012345678901234567890123456789012345678901234567890
Photuris trivitta	-001a10---10-0-0010a0--0d0-00-00001010003100000004000010000000000????????
Photuro deplanata	0002--0---00-1a000080a-0-0200a10000000??????????????????????????????????
Luciola italica	-000-009--00-0-0100-0-a0-0-00-0000000000220000112000000001000000----?00?
L kagiana	-000b00---00-0-0100-0--0-0-00-000000000021000000400000000100000????????
L parvula	-000-00---00-0-0100b0--0-0-00-000000000122000012201220000100000????????1
L syriaca	-000c00---00-0-0100-0b-0-0-00-00000000000000000224012200001?0000????????
L hypocrita	-000-00--900-0-0000-0--0c0a00b00000000000220000122012200001000000----???1
L antipodum	-021-00---00-0-0000-0c-0a0-1c-01000001??????????????????????????????????
L aquilaclara	-021-00---00-0-0000-0--0-0b1a-01000001?????????????????????????????????1
L oculofissa	-021d008--00-0-0000c0--0-0-1b-01000001?????????????????????????????????1
Aquatica leii	-011e00--800-0g0000-0-c0-0-0110000000000020000000400000000100000101-02000 2
Aq ficta	-011-00---00-0-0000-0t-0-0c0110000000000020000000400000000100000101-02000
Aq lateralis	b010-00---00-0-0000-0--0-0-0100101000????????????????????????101f02000
Aq hydrophila	-010f10---00-0-000090t-0-0-00c00000000????????????????????????????????0
Aq wuhana	-010-00---00-0-0000-0--0-0-00-000000000020000000400000000100000????????0 2
Luciola cruciata	-001-107--00-0h0000d0--0-0-00-000000100020000000200000000100000-abc1000
L owadai	-001g10---00-0-0000-0d-0g0-00d00000010????????????????????????????????0
L cingulata	-000-10--7010-00000-0--0-0-00-000000000021000000400000000100001????????
L brahmina	c000-10---010-10000-0--110-00-00000000?????????????????????????????????
L substriata J	-000-10---010-00000-0-d0-0-00e0000000000020000000400000000100000-cab0010
L substriata F	-000h10---010-00000-0v-0h0d00-0000000000020000000400000000100000----0010
L aquatilis	-000-106--010-00000e0--0-0-00-0000000000020000000400000000100000-bca0010
L. carinata	-020-10---010-00000-0--0-0-00-00000000??????????????????????????????????

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TABLE 3. (Continued)

	222222222223333333333333333333333333333333333333333333333333333333333333
	899999999990000000000111111111122222222223333333333444444444455555555556
Taxon/Character	901234567890123456789012345678901234567890123456789012345678901234567890
L. seriata	-000-10---010-00000-0--0-0-00-00000000??????????????????????????????????
L dejeani	-030-01010011-01000-0-b0b0-00-000a0000??????????????????????????????????
L dubia	-020-01010011201000-0--0-0-00-000b0000??????????????????????????????????
L cerata	-050j01010011j01000-0--0-0-00f000c000000210000004000000000010000010-1-?000
L praeusta	d040-01010011m01000-0--0-0-00-000d0000002?000000400000000010000010-1-?000
L. aegrota	-070j01010011301000-0--0-0-00g000e000000200000004000100001000001 0-1-????
L striata	-021-1110100-1-0000-0--0-0-00-000000000002200000000000000001000000????????
Jeng matalanga	-020-11101011-01000-0--0-0-00-000-000000200000000200010000100100????????
Pyg cowleyi	e022-11101011y00000-0e-0-0-0dh00000000?????????????????????????????????0
	1
Pygo qingyu	-022-11101011-00000-0-e0-0-00-000101000200000004000000000010000010-1-???0
Pygo guigliae	-021-11101011c00000-0-f0j0-00-000000001020000000400110111100 01110-1-????
Pygo hamulata	-021-111010??d?0000-0--0-0f00-00000000??????????????????????????????????
Pygo kinabalua	-021m11101011b00000-0f-0-0-00j000000001020000000400110000101110?????????
Pygo stylifer	-021-11101011a00000f0--0-0-00-00000000??????????????????????????????????
Pygo satoi	-021-11101011f00000-0g-0k0-00-0000000000200000004000100001 0001010-1-????
Pygo wittmeri	-021-11101011e00000g0--0-0-1e-000000001020000000400110000100 00010-1-????
Asymme circumdata	-021-00---011h00000-0-g0-0-00-00000100?????????????????????????0----2101
As ovalis	-021p00---011g00000-0--0m0g00m0000010000220000002000000000 1000000----210?
Aquilonia costata	-002n00--600-0-0000-0--100n00k00000000000010000002000000000100000????????1
Magnalata limbata	f001-00---010-20000-0h-0-0-00-000000000002200000020000000001000000????????1
M carolinae	-021q005--010-00000-0-m0-10bf-00000000??????????????????????????????????
M rennellia	g001-00---010-00000m0--110-00-00000000??????????????????????????????????
Gilvains messoria	-002r00--5010-20000-0--100j00n00000000??????????????????????????????????
G similismessoria	-002-00---010-20000k0--100-00-00000000000220000002000000000100000????????
Missimia flavida	-021s00---010-20000-0--0n0e00p00100100002000000002002120001 00001????????
Lloydie majuscula	-002-00---010-20000-0--100h00-0000010000210000000100000000010 0000????????1
Ll uberia	-002t004--010-20000-0j-100-00-00000100??????????????????????????????????
Ll japenensis	-002-00---010-20000j0--100-00q000001000021000000200000000010 0000????????
Ll wareo	-002-00---010-20000-0-j100-00-000001000021000000200000000010 0000????????
Convexa wolfi	-021u00--4010-00000-0-h100-00-00000000012200000020000000001 00000????????
	4
Atyph aphrogeneia	-021-00---010-00000h0--0p0-00-00000000002200000000000000000100000????????1
A atra	-021-00---010-00000-0--0-0p00-00000000002200000210122000010 0000????????1
A brevis	h021-00---010-00000-0q-0-0-00-00000000??????????????????????????????????
A conspicua	-021-003--010-00000-0-q0-0-00r000000000102000132201220000100000????????
A dalmatia	-001v00---010-00000-0-k0-0-00-00000000??????????????????????????????????
A ellioti	-021-00--3010-00000-0--0-0q00-00000000??????????????????????????????????
A flammans	-001-00---010-00000r0--0q10cg-000000000022000001001220000100 0000----??01
A flammulans	-001800---010-00000-0r-0-10dh-00000000??????????????????????????????????
A guerini	-001-00---010-00000-0k-0-10aj-00000000?????????????????????????????????1
A immaculata	j021-002--010-00000-0-r0-0-00-00000000??????????????????????????????????
A inconspicua	-021-00---010-00000-0-p0-0-00-00000000004200003210122000010 0000????????
A kirakira	-022-00--2010-10000-0m-0r0-00s00000000??????????????????????????????????
A lamingtonia	-011700---010-00000n0--0-0-00-00000000??????????????????????????????????
A leucura	-022-00---010-20000-0--0-10fk-000000000022000000400000000010 0000????????
	3
A lewisi	-021-00---010-00000p0--0-0-00-00000000011200014200122000010 0000????????
A lychnus	-021-00a--010-00000-0--0-0r00-00000000002200000200122000010 0000????????1
A monteithi	-021-00b--010-00000s0--0s0-00t00000000??????????????????????????????????
A olivieri	m001900--a010-00000q0--0-0-00-000000000022000001000000000010 0000????????0
A palauensis	-001-00--b010-00000-0n-1-10gm-00000000002200000120112000010 0001????????
A scabra	-022-00---010-00000-0-s0-0-0090000000??????????????????????????????????
A scintillans	-021w00---010-00000-0s-0t0-00-00000000002200002240122000010 0000????????1
A similis	-021-00c--010-00000y0p-0-0-00-00000000002200003240122000010 0000????????1
A testaceolineata	-022-00d--010-00000-0--0-0m00-00000000??????????????????????????????????
	1
Pac limbatipennis	-021500--e010-00000-07-0v0-00-000000000022010100400000000010 0000????????
Pac limbatifusca	-021-00--f010-00000-08-0-0-00-000000000022010100400000000010 0000????????
Pac plagiata	-021y00--h010-00000-0-40-0-00-00000000??????????????????????????????????
Pac russellia	-021-00---010-00000-06-0-0-00-00000000??????????????????????????????????
Pac salomonis	-021-00j--010-00000x0-50-0900-00000000??????????????????????????????????
Pyg tomba	-021-00--j011k0000101000-0-0070000000??????????????????????????????????
Py eliptaminensis	-021x00--c010-0000101000u0-00-000000000022100000200000000010 0001????????
Pyg huonensis	-021-00--d011n00000-0--100s00-000000000022000000200000000010 0001????????
	1
Pyg ignota	-021600---011z0000101010-0t00u00000000??????????????????????????????????
Pyg japenensis	-022-00---011s0000201010-0-00-000000000022100000200000000010 0000????????
Pyg karimui	-022-00e--011u0000101010-0-00-000000000022100000200000000010 0000????????
Pyg kiunga	k022-00f--011r00000v0-80-0-00-00000000??????????????????????????????????
Pyg marginata	-022-00---010-0000101010-0-00-00000000??????????????????????????????????
Pyg nabiria	-022-00---011t0000111010-0v00v00000000??????????????????????????????????
Pyg obsoleta	-022-00g--011x0000101010w0-00-000000000022000000200000000010 0000????????1
	1 1
Pyg okapa	-022-00h--011v0000111210-0-00-000000000022000000200000000010 0000????????
Pyg peculiaris	n021-00--g010-00000u0-90-11en-000000000022100000200000000010 0001????????
	1
Pyg pulcherrima	-022-00---0????0000-1110x1u0080000000??????????????????????????????????
Pyg tagensis	-022-00k--011q00000-0-u100-00-00000000??????????????????????????????????

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TABLE 3. (Continued)

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                  222222222222333333333333333333333333333333333333333333333333333333333333
                  899999999990000000000111111111122222222223333333333444444444455555555556
Taxon/Character   901234567890123456789012345678901234567890123456789012345678901234567890
Pyg uberia        -022-00--k010-00000-0--0y0w00-0000000000220000002000000000100001?????????
Pyg undulata      -022-00---011p00000t0--0-0-00-0000000000221000002000000000100010?????????
Pyg wisselmerenia p022z00---011w-000101010-0-00-0000000000220000002000000000100000?????????
Luciola indica    00220-----00-0-0000-0--0-0-00-0000000000100000004000000000100000?????????
                      1
T dimidiata       00020-----00-0-0000-0--0-0-00-00000000??????????????????????????????????
L trilucida       00020-----00-060000z0--0e0-00-0000000000200000004000000000100000?????????
T papuana         00020----p00-0-0000-0--0-0-00y0000000000200000004000000000100000?????????
Aus foveicollis   00020m----00-1-0000-0-70-0k00-00000000??????????????????????????????????
Med pupilla       00020k-p--00-0-0000-0--0-0y00-00000000??????????????????????????????????
M similispupillae 00020--q--00-0-0000-0--0-0-00-0000000000300000004000000000100000011--12?0?
T caudabifurca    00020-----00-0-000020--0-0-00-00000000??????????????????????????????????
Aus anthracina    00020j----00-0-0000-0-w0f0-00x00000000??????????????????????????????????
Aus aspera        00020-----00-0-0000-0--0-0-00-000000000000000000040?????????????????????
Aus australis     00020-----00-0r0000-0w-0z0-00w00000000000000000004000000000100000011--12?00
Aus flavicollis   00020--m--00-0-0000-0--0-0x00-0000000000400000004000000000100000011--12?00
Aus fuscamagna    000209---q00-090000w0--030-00-00000000??????????????????????????????????
Aus fuscaparva    00020-----00-0-0000-0--0-0-00-00000000??????????????????????????????????
Aus nigra         00020--n--00-0s000030x-0-0-00-0000000000000000004000000000100000????????0
Aus orapallida    00221n---m00-0-0000-0--0-0-00-0000000000000000004000000000100000????????0
Aus pharusaurea   00020----n00-0-0000-0--0-0-00-0000000000100000004000000000100000?????????
Pyr appendiculata 00020u----00-1t0000-0z-040-00-0000000000000000004000000000100000011--1100?
Pyro beccarii     00020t----00-1-000040-60-0-00z0000000000100000004000000000100000?????????
Pyro similis      00020v----00-1-0000-0-y0-0300-0000000000200000004000000000100000011--1100?
Py quadrimaculata 00020w-r--00-1-0000-0--0-0-00-00000000??????????????????????????????????
Med platygaster   00020p-s-r00-1w0000-0y-0-0-00-0000000000000000004000000000100000?????????
Med cribellata    00020q---s00-1-000050--0-0-00200000000000000000004000000000100000011--11?0?
Med corusca       00020r----00-1-0000-0-x0-0z00-0000000000000000004000000000100000011--12?0?
Med effulgens     00020s----00-1x0000-0--050-00-0000000000000000004000000000100000011--12?0?
T minor           00020-----010000000-0--0-0-00-00000000??????????????????????????????????
T papuae          00020-----00-1-0000-0--0-0-00-00000000??????????????????????????????????
T microthorax     00020-----010000000-0--0-0-00-00000000??????????????????????????????????
T similispapuae   00020-----00-0-0000-0--0-0-00-00000000???????????????????????????11--1????
Pt macdermotti    00020x---z00-1-0000-03-0-0-00-00000000004000000040100000010?001?????????
Pt sp ML          000204-v--00-1-0000-04-0-0-00-00000000??????????????????????????????????
Pt sp MFC         000205-w--00-1-0000-0--0-0600-0000000000400000004000000000100000010--1100?
Po selangoriensis 00020-----00-1-0000-0--0-0-00-00000000??????????????????????????????????
Pt gelasina       00020y-t--00-1u0000-0--0-0400300000000000100000004000000000100000011--11?0?
Pt malaccae       00020z-u--00-1-0000-0-z060-00-0000000000100000004000000000100000011--11?0?
Pt tener          000202---t00-1z000060--0-0500-0000000000000000004000000000100000011--11?00
Pt maipo          00020-----00-1-0000-0--0-0-00-0000000000100000004000000000100000010--12000
Pt truncata       000203---u00-1v0000-0-2090-00-0000000000100000004000000000100000011--11?0?
Colo praeusta     110206-z-v00-180000-09-070-0040000000000120000000400000000100000011--11?00
Colo concolor     110207---w00-1-0000-0-30-0-00-00000000??????????????????????????????????
Colo plagiata     000208----00-1y000070--0-0700-0000000000200000004000000000100000011--11?0?
Cur okinawanus    -021200y-x010-00000-05-080-0050000000000210010003100000000100000????????0
Cur costipennis   -021300x--010-00000-0--0-0800-0000000000210010003100000000100000????????0
Eme pseudosauteri -021400--y011-00000-0--0-11zp600000000000310000124011200001100000----0?01
Species 8         -011-00---010-00000-0--000-00-00000000002100000040000000001000000----????
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TABLE 3. (Continued)

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                  333333333333333333333333333333333333333444444444444444444444444444444444
                  666666666777777777788888888889999999999000000000011111111112222222222333
Taxon/Character   123456789012345678901234567890123456789012345678901234567890123456789012
Photuris trivitta ?????????????????????????????????????????????????1a1-1e0-11000----f1301110
Photuro deplanata ?????????????????????????????????????????????????1-0100aca6-----a-e5--1???
Luciola italica   ?????????????????????????????????????????????????1-0100b---a2--a----b-100z
L kagiana         ?????????????????????????????????????????????????1b0100c-----2-3------100x
L  parvula        -100---21?1000000ab0c100000-d000??00000b00000001-011f0-b---a----d---1010
L syriaca         ?????????????????????????????????????????????????1c001d0--b---------d1110
L hypocrita       -10111-210110001a10101001010011 0??11000a000011101----day--a--bc--6-a100y
L antipodum       ????????????????????????????????????????????????01------2c----db-----1???
L aquilaclara     -101101200111011-00101000011010 0??110?0-000021101----e----b--cd----b0???
L oculofissa      -1011001101100101--0-100010--100??11000-000021001-----bc---b-----bd-1???
Aquatica leii     0010---0011100000ba0g100000-f0000000002201000000 0----f---c-6----c---100w
Aq ficta          0010---0011100000cf0b100000-e00000000022010000 01d1-00--0--c------13-110u
                                                                    4
Aq lateralis      0010---0011100000--0-100000--0000000002201000001-011c0-z--------b---0???
Aq hydrophila     0010---0011100000ge0d000000-a000000000220100 0001-0100gd-------g---7-1???
Aq wuhana         0010---0011100000--0-100000--0000000002201000001-011-0--------------1010
Luciola cruciata  0010---0011100000dc0a100000-b000000000220100 0001-011-0f8---c-2---c-91010
L owadai          0010---0011100000ed0f100000-c000000000220?000001e0100h--d76---e-a-5-0???
L cingulata       ?????????????????????????????????????????????????1-1a00j-0--------10-0110t
L brahmina        ?????????????????????????????????????????????????000000--0--------0---100-
                                                                 1 1            1
L substriata J    0000---001110001d0111100001110001111112110 11???1-1-00--0--d-----1-j-110s
L substriata F    0000---001110001e0111100001110001111112110 11???1-1-00k-0-9-d----1---110-
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TABLE 3. (Continued)

	333333333333333333333333333333333333333444444444444444444444444444444444
	666666666777777777788888888889999999999000000000011111111112222222222333
Taxon/Character	123456789012345678901234567890123456789012345678901234567890123456789012
L aquatilis	0000---001110?01f011110000111000111111211011???1g1y00-00e---0--0g11c110r
	1 1
L. carinata	???1-1-1-00121110-0--13-1???
L. seriata	???1-1-00--0--------1---1???
L dejeani	???1-1-00--0-b------1-a-1???
L dubia	???1-1-00m-0--------1---1???
L cerata	1100---110000101b001111100110111011100100000???1-0100----8----g-h---100n
L praeusta	1100---110000101c001111100110111011100100000???1-1-00n-0--------1---110-
L. aegrota	???000000p--7-----------x00m
L striata	???1-1-1-0011011001--12-1110
Jeng matalanga	???1-1-1b0-0----0-0-j0--1110
Pyg cowleyi	1100---010010101g011101100111011?11100000000???1-1p12000-e-------10-1???
	1
Pygo qingyu	1100---010110101h001101110110012011100100001???1h01130g---e---k-ke--0010
Pygo guigliae	???1-1-1a0-0-f-90-0-112-1010
Pygo hamulata	???00----q----f---------1???
Pygo kinabalua	???1-001g0--f-----------1010
Pygo stylifer	???1-1500--0---e0-0-10--1???
Pygo satoi	???1-161h0-0g--------10-1110
Pygo wittmeri	???1-1-1j0-0---f-----1f-1010
Asymme circumdata	-100---2000000000--0-100110--0000111000-00000001j1-00s-0---g-----13-1???
As ovalis	??0??1-1x00--0h-------n13-110j
Aquilonia costata	-100---2000000000--0-000000--000??11000-00000001-1700r-08--m0-0-1---110p
Magnalata limbata	-100---2100000000hk0j100110-h010??11000m00000001-1-00t00--j------10e110-
M carolinae	???1k01000-n---h-mn-p--j1???
	11
M rennellia	???1-0100000-j-------11-1???
	1 1
Gilvains messoria	???1-0000vkkm-9---m-qfmg1???
G similismessoria	???1m1n00--0-m------1---110k
Missimia flavida	???1n0000wed9d------r---100h
Lloydie majuscula	-100---2100000001jh0p100110-j000??10000p00000001-0100--ek----jf---g-100-
Ll uberia	???1-0100-hg--k--h------1???
Ll japenensis	???1p0100x-f-k---g--sg-f100g
Ll wareo	???1-0100--h---k-f----h-100-
Convexa wolfi	???1q1-00-00---j----t118110f
Atyph aphrogeneia	-100---2000000000kp0h100010-k000??10000c00000001-01140-ja----e-----h1010
A atra	-100---10?0000000mj0s100000-m000??10000e00000001-011k0-4--n---p-----1000
	11
A brevis	??0??1-1-1-0p11000-----13-1???
	1
A conspicua	???1-011-0--p----------m1110
A dalmatia	???1-1b1z01--g----------1???
A ellioti	???1r1-1-09100000-q--14-1???
A flammans	-100---10?0000?00nr0u100010-n000??10000f00000001-1-1-0q121000s--u1351110
A flammulans	???1-1-1m0-101000-9--13n1???
	1
A guerini	-100---21?0000?00pw0k100000-p010??10000n00000001-0100y-q--m--p---an-1???
A immaculata	???1-0100--s-p----r-----1???
A inconspicua	???1-011-0-3-n--------p61110
A kirakira	???1-011-0-m--h--k---s--1???
A lamingtonia	???1-1d1-0-12011--s--13-1???
A leucura	???1-1-1n0-0-h--0000-0k01110
	1
A lewisi	???1s1-1-0n10100-r---13-100e
A lychnus	-100---11?0000000qx0n110010-q000??10000g00000001-181-0-02100-t---1341110
	1
A monteithi	???1-011y0-t--p---t---q-1???
A olivieri	1100---11?0010000rm0w110010-r010??11000h00000001-1-190m0---n-q---1371110
A palauensis	???1-1-000-0j---1-01-0-01110
	1
A scabra	???1-011-0r-q-7-------r-1???
A scintillans	-100---11?0010000sn0m110110-s000??10000k00000001-011-0-5---p--u-vh-p1010
A similis	-100---10?0000000ty0x100110-t000??10000d00000001t011p0-rn----------k1010
A testaceolineata	???1-1c1-0-111000-8--13-1???
Pac limbatipennis	???1-1-00z-05-8-07v-x11-110b
Pac limbatifusca	???1-1z1-040-6-708---11w1110
Pac plagiata	???1-011-0----4--5w--89-1???
Pac russellia	???1-001-020-4---4---76-1???
Pac salomonis	???1-010023----4-6---98v1???
Pyg tomba	???191-1-0-0--g-0-x-----1???
Py eliptaminensis	???1-1-150-0--r-011--0-01110
Pyg huonensis	???1-1-1-0-0-q--011-w0-01110
Pyg ignota	???1-1-1x0s0---r011--0s01???
Pyg japenensis	???1-1-1-0-0--s-011--0u01110
Pyg karimui	???1v1-180-0t---001--0-0110a
Pyg kiunga	???1-1g1q0-0-r--011--0-01???
Pyg marginata	???1-1-1w0-0s-5-0-0--11-1???
Pyg nabiria	???1-1-1-080---s0110-0-01???

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TABLE 3. (Continued)

	333333333333333333333333333333333333333444444444444444444444444444444444
	666666666777777777788888888889999999999000000000011111111112222222222333
Taxon/Character	123456789012345678901234567890123456789012345678901234567890123456789012
Pyg obsoleta	-100---20???00000--0-100100--0000110000-00000001-1k1r0u0-5-t0000-0-01110
	11
Pyg okapa	???1-1h1-0-0-t-50110-0v01110
Pyg peculiaris	???1-1f170-0---q0110-0-01110
Pyg pulcherrima	???1w1-1v0t0-s--0110-0t01???
Pyg tagensis	???1-1-1-0-0r---0110-0-01???
Pyg uberia	???1-001s000u---0-00y0-11100
	1 1
Pyg undulata	???1-1e1-0-0--q-0110-0-0110c
Pyg wisselmerenia	???1-1j160-0--t-0110-0-01110
Luciola indica	???1-1-00-00---------12-110-
T dimidiata	???180100-------0----k--1???
L trilucida	???1-0100--9------j-zd--100d
T papuana	???1y0100-j---------3r--1004
Aus foveicollis	???1-01004w----v--------1???
Med pupilla	???1-0100-----v--------r1???
M similispupillae	???1-0100------------q--0003
T caudabifurca	???1-01005--------------1???
Aus anthracina	???1x0100-7--v------2j-30???
Aus aspera	???1-011t0--------y-----1011
Aus australis	0010---0000000100uz0r10001110000??1??00q00000001-0100--u--u--u----wq100-
Aus flavicollis	0010---0000000100vq0y10001110000??1??00r00000001-1q003v----u--7--10-010-
Aus fuscamagna	???010100------------n--1???
Aus fuscaparva	???010100---------4-----1???
Aus nigra	0010---0000000100w20q10001110000??1??00s00000001f0100--vw--------m-2000-
Aus orapallida	0010---000?000100xs0z10001110000??1??00t00000001-1r00--0v----vz--12z1102
Aus pharusaurea	???1-0100---------------100-
Pyr appendiculata	???1z1-00--0--x--w---11y110-
Pyro beccarii	???1-01006-6-x----6-4-x-1005
	1
Pyro similis	???1-1-00-x----x----1t--1???
Py quadrimaculata	???1-1s00---y--------1-x1???
Med platygaster	???120100-6--w---x-----s0006
Med cribellata	???1-0100--p--w-------z-000-
Med corusca	???1-01007-----w--5-52--100-
Med effulgens	???1-0100---x----9-----t100-
T minor	???1-0100---------------1???
T papuae	???010101---------------????
T microthorax	???1-0100---------------1???
T similispapuae	???010101---------------0???
Pt macdermotti	???131-00----y------1u--110-
Pt sp ML	???1-1-00-----z-----1zy-1???
Pt sp MFC	???141u00------z----0100110-
Po selangoriensis	???1-1-00-----------10--1???
Pt gelasina	???1-1000-----y-----1v--1100
	1
Pt malaccae	???1-1t008-----y-z--1w--1109
Pt tener	0010---0000000100yu0v100001100000?10000u0000000171-00000z-------61001110
	1
Pt maipo	0010---0001100100--0-100001100000010000-00000001-1-00-----------1---010-
Pt truncata	???1-1000-y--z------0y--100-
Colo praeusta	0010---0000000100zt02100001100000?10000v0000000151-00---3-------1---1108
Colo concolor	???00000095--3----3--p--0???
Colo plagiata	???1-1v00--0--3-----7120110-
Cur okinawanus	0010---00?00000002v0t100100-u000??00000w00000001-0100-z----3-y2-8-3u100-
Cur costipennis	0010---1000000000--0-100100--0000100000-00000001-1w00--04-------13--1107
Eme pseudosauteri	-1011012101100001--0-100000--0010111000-00000001-011u0-----8-nh-94--0010
Species 8	???1-1-00--0--------1---110-

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TABLE 3. (Continued)

	4444		4444		4444
	3333		3333		3333
Taxon/Character	3456	Taxon/Character	3456	Taxon/Character	3456
Photuris trivitta	0000	Missimia flavida	0000	Pyg undulata	0101
Photuro deplanata	??1a	Lloydie majuscula	1e1h	Pyg wisselmerenia	0101
Luciola italica	1a1b	Ll uberia	??1m	Luciola indica	1?1?
L kagiana	191-	Ll japenensis	1f1k	T dimidiata	??1-
L parvula	1b1c	Ll wareo	1g1n	L trilucida	171-
L syriaca	0000	Convexa wolfi	1d1f	T papuana	0000
L hypocrita	0000	Atyph aphrogeneia	0000	Aus foveicollis	??1-
L antipodum	??00	A atra	0000	Med pupilla	??1-
L aquilaclara	??00	A brevis	??00	M similispupillae	1-1-
L oculofissa	??00	A conspicua	0000	T caudabifurca	??1-
Aquatica leii	0000	A dalmatia	??01	Aus anthracina	??1-
Aq ficta	0101	A ellioti	??01	Aus aspera	151-
Aq lateralis	??1-	A flammans	0101	Aus australis	1h1r
Aq hydrophila	??1-	A flammulans	??01	Aus flavicollis	1k1s
Aq wuhana	0101	A guerini	??1g	Aus fuscamagna	??00
Luciola cruciata	1z15	A immaculata	??1d	Aus fuscaparva	??00
L owadai	??1-	A inconspicua	0000	Aus nigra	1m1t
L cingulata	0000	A kirakira	??1q	Aus orapallida	1n1u
L brahmina	0000	A lamingtonia	??01	Aus pharusaurea	141-
L substriata J	0000	A leucura	0101	Pyr appendiculata	1q1w
L substriata F	0000	A lewisi	0001	Pyro beccarii	1p1v
L aquatilis	0000	A lychnus	0000	Pyro similis	??01
	1	A monteithi	??00	Py quadrimaculata	??01
L. carinata	??00	A olivieri	0101	Med platygaster	1r1y
L. seriata	??00	A palauensis	0100	Med cribellata	1s1z
L dejeani	??00	A scabra	??00	Med corusca	1t12
L dubia	??1-	A scintillans	0000	Med effulgens	1u13
L cerata	1j1-	A similis	0000	T minor	??1-
L praeusta	0000	A testaceolineata	??01	T papuae	??00
L. aegrota	0000	Pac limbatipennis	1318	T microthorax	??1-
L striata	0101	Pac limbatifusca	1619	T similispapuae	??00
Jeng matalanga	0000	Pac plagiata	??00	Pt macdermotti	0100
Pyg cowleyi	??00	Pac russellia	??00	Pt sp ML	??00
Pygo qingyu	121-	Pac salomonis	??17	Pt sp MFC	1w01
Pygo guigliae	0000	Pyg tomba	??00	Po selangoriensis	??1-
Pygo hamulata	??00	Py eliptaminensis	0101	Pt gelasina	0101
Pygo kinabalua	0000	Pyg huonensis	0101	Pt malaccae	0000
Pygo stylifer	??00	Pyg ignota	??01	Pt tener	0101
Pygo satoi	0000	Pyg japenensis	0101	Pt maipo	0101
Pygo wittmeri	0000	Pyg karimui	0101	Pt truncata	0001
Asymme circumdata	??16	Pyg kiunga	??01	Colo praeusta	0101
As ovalis	011-	Pyg marginata	??01	Colo concolor	??00
Aquilonia costata	0000	Pyg nabiria	??01	Colo plagiata	1v00
Magnalata limbata	1c1e	Pyg obsoleta	0101	Cur okinawanus	1x14
M carolinae	??01	Pyg okapa	0101	Cur costipennis	0000
	1	Pyg peculiaris	0101	Eme pseudosauteri	1-1-
M rennellia	??1p	Pyg pulcherrima	??01	Species 8	0000
Gilvains messoria	??00	Pyg tagensis	??01		
G similismessoria	0100	Pyg uberia	0101		

Abbreviations, taxonomic characters

A — aedeagus dimensions for certain *Pteroptyx* spp.; distance from dorsal base of lateral lobes to apex of median lobe (see also B); expressed as B/A (Figs 217–219)

ASD — distance between antennal sockets

ASW — antennal socket greatest diameter

B	aedeagus dimensions for certain *Pteroptyx* spp.; distance from dorsal base of lateral lobes to apex of lateral lobes (see also A); expressed as B/A (Figs 217–219)
FS	antennal flagellar segments
GHW	greatest head width (across eyes, measured parallel to ASD)
L	length
Legs 1, 2 etc	Legs and parts of legs are referred to by their segment number – e.g. legs 1 are prothoracic legs; tarsi 2 =mesothoracic tarsi; femora 3 = metathoracic femora.
LL	lateral lobes, aedeagus
LO	light organ
MFC	metafemoral comb
MS	mesoscutellum
SIW	smallest interocular width (measured horizontally, may be on the same level as ASD, ASW, 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
W	width
W/L	width/length
X	times

Depositories

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

AMSA	Australian Museum, Sydney, Australia (M. Moulds)
ANIC	Australian National Insect Collection, CSIRO Entomology, Canberra (T. Weir) including Department of Agriculture, Port Moresby collection
BPBM	Bernice P Bishop Museum, Honolulu (A. Ramsdale)
FRIM	Forest Research Institute Malaysia, Kuala Lumpur (N. Badruddin)
JELC	James E Lloyd, Gainesville, Florida
MAGNT	Museum and Art gallery of the Northern Territory (G. Daly)
MCSN	Museo Civico di Storia Naturale Genoa (R. Poggi)
MNHN	Natural History Museum, Paris (J. Menier)
NHML	Natural History Museum, London (M. Barclay)
NHMHZU	Natural History Museum, Huazhong University (X. H. Fu)
QMBA	Queensland Museum, Brisbane, including J. Sedlacek collection and from 2011 the University of Queensland Insect Collection (G. Monteith)
QSBG	Entomology collection Queen Sirikit Botanic Garden, Chiang Mai, Thailand (S. Silalom)
SAMA	South Australian Museum, Adelaide (P. Hudson)
UQIC	University of Queensland, Brisbane (G. Monteith) (In 2011 the UQIC was incorporated into that of QMBA in Brisbane).
USNM	United States National Museum, Washington

Specimen contributor abbreviations

Some names are abbreviated for the sake of brevity : WB=W Brandt; LEC=L E Cheesman; EF=E Ford; NK=N Krauss; COB=C W O'Brien; JS=Joe Sedlacek (JH, MS members of Sedlacek family); RS=R Straatman; JLG=J L Gressitt.

Phylogenetic analysis

The phylogenetic analysis of the Luciolinae is expanded both in number of species addressed and breadth of characters scored (Table 3, Appendix 1) and follows Fu *et al.* (2012a). The analysis addresses 143 species, including the type species of the 7 genera and 2 subgenera of the Luciolinae *sensu* McDermott (1966). Taxon sampling includes all the species scored in Ballantyne and Lambkin (2009) with the addition of more than 20 species. The additional species are listed in Fu *et al.* (2012a). The remaining undescribed specimens scored here are listed below in Table 4. An extensive character matrix is presented in Table 3, which includes 436 characters: 326 male, 33 female, 48 larval (see Fu *et al.* 2012a).

Our earlier phylogenetic analyses of the Lampyridae were expanded to include 143 Luciolinae species and the list of exemplar taxa and characters and states follows Fu *et al.* (2012a) and is repeated here as Appendix 1 (Ballantyne & Lambkin, 2000, 2001, 2006, 2009). 436 morphological characters of males, females and larvae were scored. The morphological matrix with the full list of exemplar taxa is given in Table 3 and is deposited along with phylogenetic results and consensus tree in Treebase (Treebase.org; http://purl.org/phylo/treebase/phylows/study/TB2:S13966). Most are binary, but 59 characters were coded as multistate characters, each with three states. Seven characters were coded with four states, five characters with five states, and one character with six states. 334 characters are informative and one is constant. The 29 characters (408–436) that describe colour, and four characters that describe mimicry or colour patterns (433–436) were included in the phylogenetic analysis as in our previous analyses (Ballantyne & Lambkin, 2009; Fu *et al.*, 2012a). Both a binary character, describing the absence or presence of a feature, and a fused multistate, describing the states of the feature, were included as in our previous analyses (Ballantyne & Lambkin, 2000, 2001, 2006, 2009; Fu *et al.*, 2012a) to avoid the use of 'missing' data, and decrease the loss of phylogenetic information. This was particularly important as some extremely complex derived structures involving many characters were not present in some taxa. We have also continued to use the option described in Ballantyne and Lambkin (2009) for dealing with inapplicables that includes a unique state for each taxon in each character that is inapplicable. With Mesquite (Maddison & Maddison, 2006), we have been able to use 33 states (0–9 plus the alphabetically coded characters with the exception of non-allowed i, j, and o) (Table 3). Where a character is inapplicable for more than 31 taxa, one taxon in a species group was scored with the unique state and the remainder scored '-'. This method prevents grouping based on inapplicable states, which overcomes the problems of missing data and primary homology assessment. We scored 204 of the characters with inapplicables.

TABLE 4. Undescribed species.

Species Number	Identification number Figures 3–4	Locality	Collection
8	20	Thailand	ANIC
Pt sp ML	5	Malaysia \Selangor	NHML
Pt sp MFC	6	Indonesia Surabaya	ANIC

Character analysis

Phylogenetic analyses presented here do not prejudge the relative informativeness of characters (Källersjö *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). Characters with more than one derived state were coded as multistate, and treated as unordered (i.e. non-additive)(Meier, 1994). Cladistic analyses completed a minimum of 1000 random step-wise addition heuristic searches, with each replicate restricted to 1 million rearrangements and 32,000 most parsimonious trees (MPT), TBR branch swapping, MULPARS, and branches having maximum length zero collapsed to yield polytomies using PAUP*4.0b10 (Swofford, 2002).

The 50% majority-rule consensus tree was computed using PAUP*. Groups are preserved in the majority rule consensus tree even if there are some MPT that support conflicting groups (Margush & McMorris, 1981). Unfortunately Bremer support values (Bremer, 1988, 1994; Källersjö *et al.*, 1992), that measure the support for each node of the tree could not be computed as the number of taxa exceeded the capacity of the TreeRot v.2 program (Bremer, 1988, 1994; Källersjö *et al.*, 1992, Sorenson, 1999) could cope with. Therefore the taxon sample was reduced to 61 taxa focussing on the Indo-Pacific study group, and the analyses repeated. Bremer support values were then calculated with TreeRot v.2 with 20 heuristic searches of the data to measure the strength of evidence for nodes on a MPT from the 61 taxa analysis. Two separate analyses of all characters were completed for all taxa that were scored firstly for female characters (88 taxa) and secondly for larval characters (42 taxa). Strict consensus was computed using PAUP* (Schuh & Farris, 1981).

Phylogenetic Results

Analysis of 436 characters of the 143 Luciolinae taxa (termed the complete analysis) in the data matrix in Table 3 produced 169 MPT of length 5609, consistency index (Kluge & Farris, 1969) 0.8089, consistency index without uninformative characters (Kluge & Farris, 1969) 0.7594, retention index (Farris, 1989) 0.7396, and rescaled consistency index (Farris, 1989) 0.5982. The 50% majority rule (Figs 3–5) consensus tree was calculated. As TreeRot v.2 was unable to cope with the large number of taxa in the matrix, the 50% majority rule consensus tree is presented (Figs 3–5) showing the % of MPT with nodes. For those nodes found in 100% of MPT, the % is shown in bold. Many nodes are numbered (1 to 76) in red, bold italics. A selection of terminal branches is numbered (1 to 23) in blue, bold italics.

Analysis of the reduced taxon sample focussing on the 61 Indo-Pacific study group taxa (termed the 61 IP analysis) produced 163 MPT of length 2615, consistency index 0.8470, consistency index without uninformative characters 0.7065, retention index 0.7076, and rescaled consistency index 0.5994. The strict consensus tree (Fig. 6) for the 61 Indo-Pacific study group taxa was calculated and Bremer supports shown above the nodes.

Analysis of the 88 taxa scored for female characters (termed the 88 female analysis) produced 1349 MPT of length 3892, consistency index 0.8109, consistency index without uninformative characters 0.7316, retention index 0.7204, and rescaled consistency index 0.5841. The 50% majority rule consensus tree (Fig. 7) for the 88 taxa scored for female characters was calculated.

Analysis of the 42 taxa scored for larval characters (termed the 42 larvae analysis) produced 4 MPT of length 2245, consistency index 0.8232, consistency index without uninformative characters 0.6595, retention index 0.6686, and rescaled consistency index 0.5504. The 50% majority rule consensus tree (Fig. 8) for the 42 taxa scored for larval characters was calculated.

The phylogenetic trees from the four analyses generally agree on the inferred relationships between the taxa with our previous analyses (Ballantyne & Lambkin 2000, 2001, 2006, 2009; Fu *et al*. 2012a) and also with each other. The genera *Aquatica*, *Curtos*, *Photuroluciola*, *Colophotia*, *Pyrophanes*, *Emeia*, *Pygoluciola* (95% MPT in 88 female analysis), *Convexa*, *Lloydiella*, *Assymetricata*, *Aquilonia*, and *Gilvainsula* are found in all MPT from all analyses as do *Pteroptyx* and *Pygatyphella* in the restricted sense presented here. As in all previous analyses *Luciola* is paraphyletic, and despite the recognition and description of many new genera here, remains so, found in up to six clades across the tree. Together with *Luciola*, *Magnalata*, *Aquilonia*, and *Gilvainsula* render *Atyphella* paraphyletic except in the 88 female analysis (Fig. 7) indicating that female characters may be significant in the definition of *Atyphella*.

Phylogenetic Relationships

The phylogenetic analyses provide support for the description of several new monophyletic genera in addition to evidence for the inclusion of taxa within them.

The separation of *Poluninius selangoriensis* **gen.** and **sp. nov**. from all other taxa is well supported: it is recovered in all MPTs for the complete analysis (Fig. 3, number 4 (blue bold italic)). Bremer support (BS) of 3 in the 61 IP analysis is consonant with the monophyly of this genus (Fig. 6). In both analyses, *Poluninius selangoriensis* gen. and sp. nov. is closely related to, but distinct from, *Luciola indica* (Fig. 3, number 3).

The main clade of *Medeopteryx* **gen. nov.** is well supported and found in all MPTs for the complete analysis (Fig. 3, clade 20 (red bold *italic*)) and the 88 female analysis (Fig. 7), and has a BS of 1 in the 61 IP analysis (Fig. 6). The inclusion of *Med. pupilla* in *Medeopteryx* **gen. nov.** is more problematic, as this taxon forms a grade to the main clade of *Medeopteryx* **gen. nov.** in only 67% of MPT for the complete analysis (Fig. 3, clade 19), although it is part of the genus in all MPTs for the 61 IP analysis (Fig. 6), albeit with a BS of 1.

The main clade of *Trisinuata* **gen. nov.** is well supported, found in all MPTs for the complete analysis (Fig. 3, clade 24) and with a BS of 2 in the 61 IP analysis (Fig. 6). The inclusion of *T. dimidiata* **sp. nov.** in *Trisinuata* **gen. nov.** is also problematic, as while this taxon is sister to the main clade of *Trisinuata* **gen. nov.** in 67% of MPT for the complete analysis (Fig. 3, clade 23), it is more closely related to *Medeopteryx* **gen. nov.** in all MPT for the 61 IP analysis (Fig. 6), with a BS of 1.

Australoluciola **gen. nov.** is well supported, found in all MPTs for the complete analysis (Fig. 3, clade 28) and the 42 larvae analysis (Fig. 8), with a BS of 1 in the 61 IP analysis (Fig. 6). However, *Australoluciola* **gen. nov.** is not well supported in the 88 female analysis (Fig. 7).

Pacifica **gen. nov.** is well supported and is recovered in all MPTs for the complete analysis (Fig. 5, clade 54) and the 88 female analysis (Fig. 7).

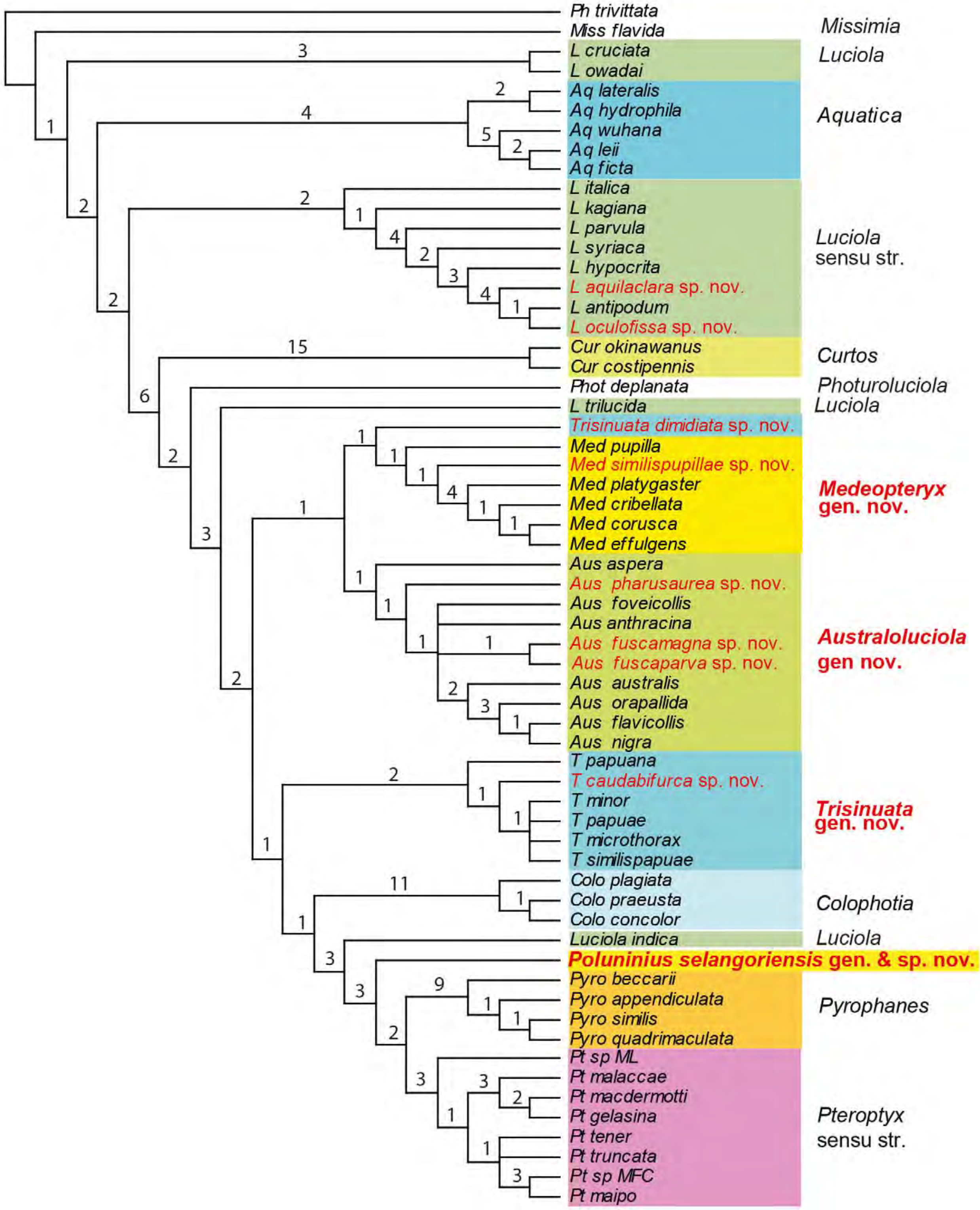


FIGURE 6. Strict consensus tree for 61 IP analysis; consensus of 163 MPT of length 2615 from phylogenetic analysis of 61 Indo-Pacific study group taxa. New genera, new species, and still undescribed species in red, bold. Bremer supports above branches.

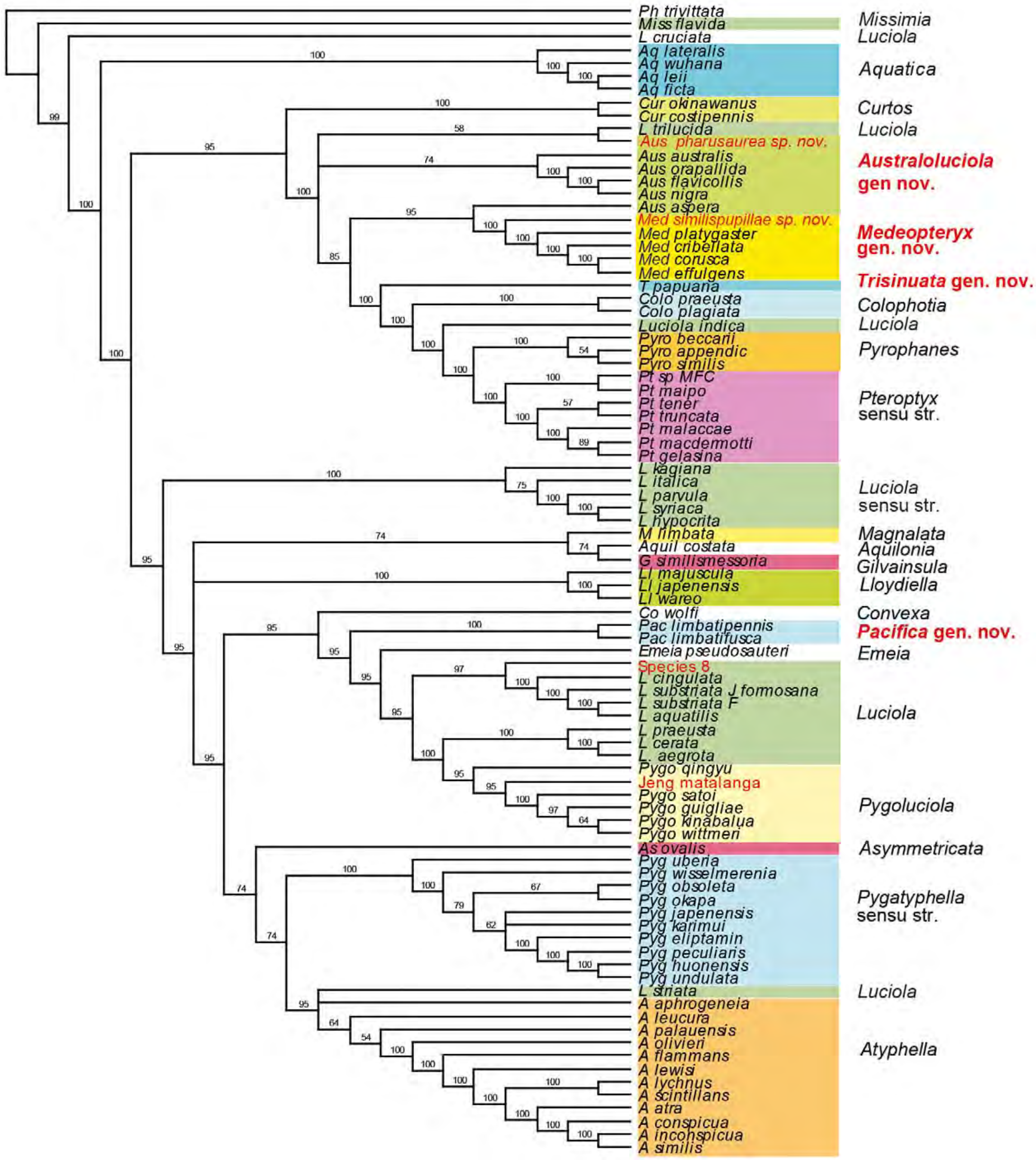


FIGURE 7. Majority rule tree for female analysis. Tree shows the consensus of 1349 MPTs of length 3892 from the analysis of all characters for the 88 taxa with female traits scored. New genera, new species, and still undescribed species in ***red***. Showing the % of MPT over 50 %, above branches.

Taxonomic Results

This work represents the most comprehensive attempt to date to resolve the genus *Luciola* Laporte. All the species originally described as *Luciola* from the Australopacific study area are considered here and almost all are accommodated in new genera (see Table 5). For example, *Trisinuata* **gen. nov.** and *Australoluciola* **gen. nov.** include species from both Australia and New Guinea without deflexed elytral apices. The bent-winged fireflies from New Guinea and Australia are assigned to two new genera *Medeopteryx* **gen. nov.** and *Trisinuata* **gen. nov.** *Bourgeoisia* Olivier is submerged in *Luciola* **s. str**. which is addressed from three Pacific Island species including two new, and a population of the type species *L. italica* from Pisa, Italy. Species from SE Asia were included and the analysis reveals indications for further subdivisions within *Luciola* (Fig. 3 Nodes 1, 8; Fig. 4 nodes 44, 46). These will be addressed elsewhere and several are already in preparation (Ballantyne *et al*. in prep.).

TABLE 5. Luciolinae genera recognised.

Genus	Number of species	Region	References
Aquatica Fu *et* Ballantyne	5	China	Fu *et al.* 2010
Aquilonia Ballantyne	1	N. Australia	Ballantyne & Lambkin 2009
Asymmetricata Ballantyne	2	S E Asia	Ballantyne & Lambkin 2009
Atyphella Olliff	23	Australia, New Guinea, Pacific Islands	Ballantyne & Lambkin 2009
Australoluciola **gen. nov.**	12	Australia, New Guinea	
Colophotia Motschulsky	3	S E Asia	Ballantyne & Lambkin 2009
Convexa Ballantyne	1	Solomon Islands	Ballantyne & Lambkin 2009
Curtos Motschulsky	19	S E Asia	Jeng *et al.* 1998*;* Chûjô & Satô 1970; Fu *et al.* 2012a
Emeia Fu *et al.*	1		Fu *et al*. 2012a
Gilvainsula Ballantyne	2	New Guinea	Ballantyne & Lambkin 2009
Lloydiella Ballantyne	4	New Guinea	Ballantyne & Lambkin 2009
Luciola **s. str.** Laporte including *Bourgeoisia* Olivier	Not determined; addressed here from 5 species	Europe, possibly Japan, Pacific Islands - New Caledonia and Fiji	Ballantyne & Lambkin 2009
Magnalata Ballantyne	3	Solomon Islands	Ballantyne & Lambkin 2009
Medeopteryx **gen. nov.**	17	New Guinea. Australia	
Missimia Ballantyne	1	New Guinea	Ballantyne & Lambkin 2009
Pacifica **gen. nov.**	5	New Guinea, Solomon Islands	Ballantyne & Lambkin 2009
Photuroluciola Pic	1	Madagascar	Ballantyne & Lambkin 2009
Poluninius **gen. nov.**	1	SE Asia	
Pteroptyx **s. str.**	12	SE Asia	Ballantyne *et al.* (2011); Ballantyne 2001, 1987a; Ballantyne & McLean 1970
Pygatyphella (Ballantyne)	17	New Guinea	Ballantyne & Lambkin 2009
Pygoluciola Wittmer	8	SE Asia	Ballantyne & Lambkin 2009 Fu & Ballantyne 2008
Pyrophanes Olivier	4	SE Asia, New Guinea, Australia	Ballantyne & Lambkin 2000, 2009
Trisinuata **gen. nov.**	8	New Guinea	

Characteristics of lucioline males, females and larvae

Males. Ballantyne (1987b) addressed male morphology in detail with suggested functions for many of the modifications observed. Certain of those interpretations are reassessed (see Discussion).

Females. (Tables 6, 7). Macropterous, or flightless due to shortened fore and/or hind wings. Macropterous females assumed capable of flight, and some were taken in flight. *Colour*: dorsal colouration of macropterous females, and those with little wing loss (e.g. *Luciola hypocrita, Atyphella olivieri, L. italica*) as for male; colour similarity may not allow a reasonable chance of identification especially among the many similarly coloured *Medeopteryx* **gen. nov.** species; dorsal colouration of flightless females usually very pale; ventral colouration of flighted females usually differing from male only in terminal abdomen where V7, 8 are often paler than ventrites preceding the LO; ventral colouration of flightless females very pale similar to most of dorsal surface. *Pronotum*: shaped like that of male in macropterous females, sometimes with very rounded anterolateral corners; smaller head of female can be retracted beneath and within prothoracic cavity; flattening of hypomeron following male pattern; pronotal outline of flightless females of *Atyphella inconspicua, A. lewisi, A. conspicua* differing from male in having subparallel sides and broadly rounded anterior margin. *Elytra*: of macropterous females assume same shape as that of males (either subparallel or convex-sided); without deflexed elytral apices; extent of wing development in flightless females summarised in Table 6. *Head*: eyes reduced compared to male; clypeolabral suture present, labrum soft and flexible except in *Missimia* where suture absent and labrum inflexible; macropterous females without an anterior head prolongation carrying antennae except for *Pygoluciola* spp. which have a short parallel-sided prolongation; wingless females with eyes considerably reduced and an anterior head "prolongation" with sides tapering towards the mouthparts, which are carried well in front of the anterior eye margins. *Mouthparts*: almost always well developed indicating the possibility of feeding; shape and dentition of apical labial and maxillary palpomeres as for male. *Antennae*: usually 11 segmented, without expansion of flagellomeres and segments longer than wide; shorter in some flightless females (7–8 segments in *A. inconspicua* and *A. scintillans*), where at least 4 or more flagellomeres are about as wide as long. *Legs*: simple, without MFC, swollen and curved femora/tibiae (except for curved tibiae of all legs in *Pygoluciola guigliae*), excavations of the inner margin of basitarsus 2. *Abdomen*: with 7 visible ventrites (actual segments 2–8); V1 often represented by small paired pale plates in intersegmental membrane, V2 often with larger paired, cuticularised lateral portions, and membranous central portion; LO beneath V6; V7 with posterior margin usually medianly emarginate and lateral margins tapering; V8 with strongly tapering margins, narrow posterior margin may be medianly emarginated; V8 with an anteromedian apodeme (projecting beneath the LO), onto which muscles from the valvifers attach; in dried specimens torsion in these muscles may produce possible artefacts in V7 in some *Pygoluciola* spp. where transverse ridges and swellings occur on dorsal or ventral surfaces (Ballantyne & Lambkin, 2001, 2006; Ballantyne 2008); ventrites posterior to LO often paler than those preceding it, underlying fat body particularly beneath V7 may suggest LO material (no evidence suggests LO extends into this segment)**.**

*Female genital tract***:** Ballantyne *et al.* (2011) on *Pteroptyx maipo* Ballantyne is followed and descriptions apply to *P. maipo* unless stated otherwise. *Vagina*: an elongate cylindrical tube leading anteriorly from vulva, just in front of styli, enlarging anterior to entry of common oviduct to form an elongate, blind ending muscular bursa copulatrix (Tandon 1970 differentiated the bursa from the vagina by the entry of the median oviduct). *Median oviduct*: arising from vagina, posterior to bursa, branching into two lateral oviducts, thence into numerous ovarioles; may contain plate at junction with vagina (point of origin of median oviduct delimits vagina from bursa). *Bursa*: without plates in certain *Luciola* and possibly other genera; with paired narrowed strips in *Aquatica* and certain *Luciola*; narrowed paired plates bearing internal hooks in *Pygoluciola*; with two sets of broad plates on each side in *Medeopteryx* **gen. nov**., some *Pteroptyx, Colophotia, Pyrophanes*, and certain New Guinean species, where the posterior pair incline transversely; inner surfaces of anterior plates densely rugulose; distance between anterior and posterior plates may reflect presence of a partially digested spermathophore or method of preservation; in ethanol preserved specimens of *Medeopteryx* **gen. nov.** the bursa assumes a kinked shape with a constriction between the anterior and posterior plates; with broad single plates on each side in *Pteroptyx maipo* and *P. valida* where shape of plates suggests that the anterior and posterior plates seen in other *Pteroptyx* species have fused. *Spermatheca*: small, stalked arising from posterior area of bursa; basal area raised, may be coloured more darkly than remainder and appear as a thin transverse plate between the posterior bursa plates. *Spermathecal digesting gland*: opening from anterior end of bursa (may not be expanded and often difficult to see unless immersed in water); thin walled in *P. maipo*; elongate, tubular with muscular walls in ethanol preserved females of *Asymmetricata ovalis* and *As. circumdata*. *Female genitalia*: with elongate laterally expanded coxites extending anteriorly into slender valvifers (baculi) lying beside the vagina. During egg laying the coxites and styli protrude from the end of the abdomen. Muscles from the valvifers attach onto the anterior apodeme of V8 and the sides of the vagina, and their contractions widen the vagina during egg laying (Ballantyne *et al.* 2011). *Spermatophores*. Few whole spermatophores were seen inside the bursa. In a single female of *P. maipo* the spermathophore appeared to be held in place by the anterior ends of the bursa plates, partially within the bursa and partially protruding into the spermathophore digesting gland (Ballantyne *et al.* 2011).

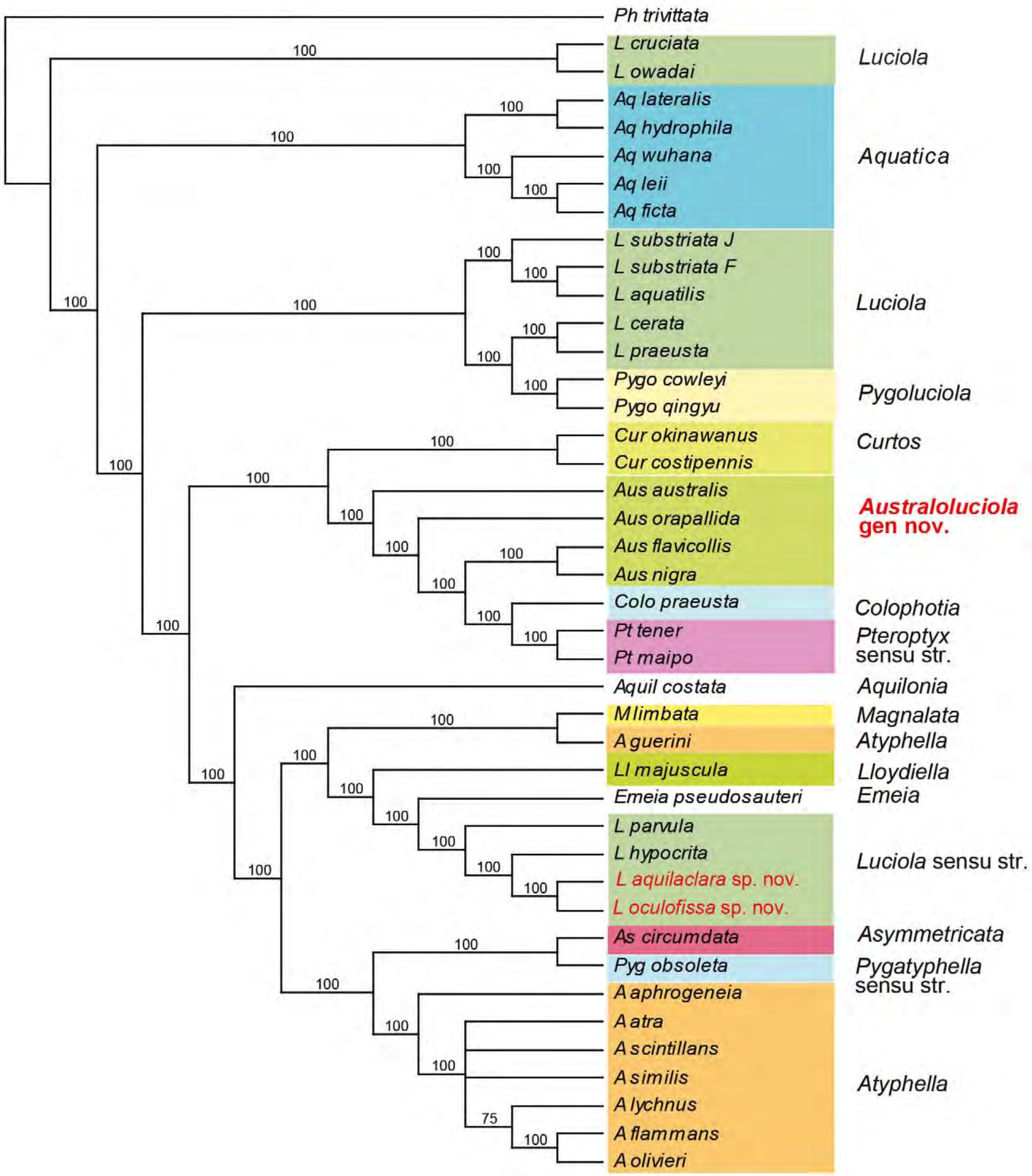


FIGURE 8. Majority rule tree for larvae analysis. Tree shows the consensus of 4 MPTs of length 2245 from phylogenetic analysis of all characters for the 42 taxa scored for larval characters. New genera, new species, and still undescribed species in **red**. Showing the % of MPT over 50 %, above branches.

Larvae (Table 6). Fu *et al.* (2012b) overviewed lucioline larvae, described general features including generic characteristics, and presented a key to genera, and some species, of aquatic and terrestrial larvae. They recognised 20 genera of which 13 had larval associations, and addressed 38 species. Here we recognise 42 species with larval associations (Fig. 8).

TABLE 6. Females and larvae.
** = only pinned females available; brackets indicate number of species examined

				Female			Larva [7]
Genus	**Fore Wings**[1]	**Hind wings**[2]	**Evidence for association** [3]	**Bursa plates** [4]	**Plate at base of oviduct**[5]	**Head type** [6]	
Aquatica Fu *et* Ballantyne (3)	M	F	IC	FS	L	WF	A, G
Aquilonia Ballantyne** (1)	M	F	IC	NI	NI	WF	T, LE
Asymmetricata Ballantyne (2)	M	F	LD	none	L	WF	T, LE
Atyphella Olliff (8)	M, B	F, S, V	LD, IC	None #	?	WF, wf	T, LE
Australoluciola **gen. nov.**	M	F	LD, IC	BP (2)	?	WF	T, NLE
Colophotia Motschulsky (2)	M	F	LD	BP (2)	S	WF	T, NLE
Convexa Ballantyne **(1)	M	F	LD	?	?	WF	?
Curtos Motschulsky	M	F	LD	?	?	WF	T, NLE
Emeia Fu Ballantyne & Lambkin	B	S	IC	none	absent	wf	T, LE
Gilvainsula Ballantyne**(1)	M	F	LD	NE	?	WF	?
Lloydiella Ballantyne **(1)	M		LD	NE		WF	T, LE
Luciola Laporte s str.[1] Clade 35 Fig. X	M, B	F, S	LD	none		WF, wf	? T, ? LE
Luciola two species Fig. 3 Node 1	M	F	Ohba	FS	?	WF	A, G
Luciola six species Fig. 4 Node 45	M	F	Thancharoen, Silalom	NE	?	WF	A, M
Luciola five species Fig. 4 Node 46	M	F	LD	H (1)	?	WF	T
Magnalata Ballantyne **(1)	M	F	LD	?	?	WF	?
Medeopteryx **gen. nov.**	M	F	Ballantyne, Lloyd, Buck	BP (2)	S	WF	T NLE
Missimia Ballantyne ** (1)	M	F	LD	NI	?	WF	?
Pacifica **gen. nov.****	M	F	LD	?	?	WF	?
Photuroluciola Pic	Not associated	?	**?**	**?**	**?**	**?**	?
Poluninius Ballantyne	Not associated	?	**?**	**?**	**?**	**?**	?
Pteroptyx Olivier s. str.	M	F	LD, R	BP (1, 2)	S	WF	T, NLE
Pygatyphella (Ballantyne) **	M	F	LD	?	?	WF	? T ? LE
Pygoluciola Wittmer	M	F	LD	H (1)	?	WF	?
Pyrophanes Olivier	M	F	LD	BP (2)	S	WF	? A G
Trisinuata Ballantyne	M	F	LD	BP (2)	?	WF	?

Footnotes: 1. Fore wings M = macropterous; B= brachelytral. 2. Hind wings F = fully developed; S = shortened; V= vestigial. 3. IC = in copulo; LD = label data; R = reared. 4. BP = broad plates (number of pairs); FS = fine strips; H = hooked; NE not examined; NI = no evidence; # = only *A. flammans* examined. 5. L = large; NI = not investigated; S = small. 6. WF =fully winged female; wf = brachelytral or wingless female. 7. A = aquatic; G = abdominal gills; LE = laterally explanate tergal margins; M = metapneustic; NLE = Tergal margins not laterally explanate, laterotergites usually visible from above.

TABLE 7. Flightless females.

Species	Fore wings	Hind wings	Flighted	Head type
Atyphella atra	Full	Absent	No	Wingless female
A. conspicua	brachelytral	Vestigial	No	Wingless female
A. flammans	Full	¾ elytral length	No	Wingless female
A inconspicua	Brachelytral	Absent	No	Wingless female
A lewisi	Brachelytral	Absent	No	Wingless female
A. lychnus	Full	Vestigial	No	Wingless female
A. olivieri[1]	Full	Slightly shortened	?capable of short flight	Winged female
A. palauensis	Full	shortened	No	Wingless female
A scintillans	Brachelytral	Vestigial	No	Wingless female
A. similis	Brachelytral	Absent	No	Wingless female
A. testaceolineata[2]	Full	Absent	No	?
Luciola hypocrita	Brachelytral	Absent	No	Wingless female
L. syriaca	Brachelytral	?	No	Wingless female
L. italica	Full or very slightly shortened	Slightly shortened	?capable of short flight	Winged female
L. parvula	Slightly shortened	Absent	No	Wingless female

Notes: 1. Ballantyne & Lambkin (2000) described this female as macropterous but modified their interpretation in Ballantyne & Lambkin (2009) to indicate that there was a possibility that this female could be capable of flight for only short distances as the hind wings are slightly reduced; 2. Ballantyne & Lambkin (2009) did not score this single female which is not reliably associated.

Key to genera and certain species groups of Luciolinae using males

This key reflects the results obtained in the phylogenetic analysis herein (Figs 3–5) and is an expansion of Ballantyne and Lambkin (2009). Genera related to *Atyphella* Olliff are treated in the form recognised by Ballantyne and Lambkin (2009).

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 (Ballantyne & Lambkin 2009 Figs 21, 22, 27, 29, 30, 32–34) . . . . *Missimia* Ballantyne
- Clypeolabral suture present (Ballantyne & Lambkin 2009 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 without 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 (Ballantyne & Lambkin 2009 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 without 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 (Ballantyne & Lambkin 2009 Figs 35, 36, 37). 3

3. LO absent, or present only in V6; eyes with strong posterior emargination; dark almost black dorsal colouration (Ballantyne & Lambkin 2009 Fig. 59) . . . . *Luciola* **s. str.** Partim[1;] **Fig. 4 Node 38**
- Eyes with or without 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 (Ballantyne & Lambkin 2009 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 (Ballantyne & Lambkin 2009 Figs 36, 75) 22
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 Ballantyne & Lambkin 2009 Fig. 514) (Ballantyne, 1968 Figs 162c, 169) . . . . *Luciola* **s. str.** Partim[2]; **Fig. 4 Node 35**
Elytral humeral carina present (Ballantyne & Lambkin 2009 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 (Ballantyne & Lambkin 2009 Figs 57, 58); MPP always obviously developed, sometimes L>W with apex inclined dorsally (Ballantyne & Lambkin 2009 Figs 60, 61); aedeagal LL always narrower at apices than at bases; LL without 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 (Ballantyne & Lambkin 2009 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. Pronotum subparallel-sided, with hypomeron widely flattened and surfaces closely adpressed along its length . . . . *Emeia* Fu *et al.* **Fig. 4 Number 19**
If pronotum subparallel-sided then hypomeron not widely flattened with surfaces closely adpressed along its length 8
8. Aedeagal sheath surrounded by a set of 3 sclerites (2 lateral and one ventral) (Jeng *et al.* 2003 Fig. 14) Fig. 43; at least some punctures in elytron in semiparallel rows; anterior margin of entire LO emarginated, often deeply (Fu *et al*. 2012a Figs 44, 45) . . . .
Fig. 4 Node 45 *Luciola carinata* Gorham**,** *L. substriata* Gorham**,** *L. aquatilis* Thancharoen, *L. seriata* Olivier, *L. cingulata* Olivier, *L. brahmina* Bourgeois
Aedeagal sheath without sclerites surrounding it; elytral punctation not in lines; anterior margin of entire LO not emarginated 9
9. LO triangular in outline, straight sides tapering posteriorly to a narrow rounded apex. (Fu *et al*. 2012a Fig. 46) . . . . .Undescribed species from Thailand **Fig. 4 Number 20**
LO not triangular in outline. 10
10. Posterior half of aedeagal sheath (posterior to tergite articulations at sides) irregularly emarginate along both sides (Jeng *et al.* 2003 Figs 29–31); aquatic species from China and Japan; Fu *et al.* 2010 Figs 5, 13, 14, 22–24, 36, 37) . . . .*Aquatica* Fu, Ballantyne & Lambkin
If posterior half of aedeagal sheath (posterior to tergite articulations at sides) emarginate this is evenly emarginate on one side only; posterior margin often not emarginate 11
11. 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; 2009 Fig. 60) . .*Pygoluciola* Wittmer Partim **Fig. 4 Node 51**
MPP developed, may be elongate (L>W), not inclining strongly dorsally; median posterior margin of T8 not narrowly produced and inclining ventrally 12
12. 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 (Fu & Ballantyne 2008 Figs 17, 19; Ballantyne 2008 Fig.9) 13
Aedeagal sheath sternite without 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 14
13. Basal section of LL of aedeagus fused for almost all of their length dorsally; inner ventral margins of LL with elongate cylindrical lobes (Jeng *et al*. 2003 Figs 27, 28; Fu & Ballantyne, 2008 Fig. 20); apical section of LL very short . . . .
Luciola dejeani Gemminger, *L. dubia* Olivier, *l. praeusta* Kiesenwetter, *L. cerata* Olivier, *L. aegrota* Olivier **Figure 3 Node 46**
Basal section of LL of aedeagus not fused; inner ventral margins of LL without elongate cylindrical lobes; apical section of LL always longer than ML, often very pale and membranous; aedeagus with strongly asymmetrical bilobed basal piece; MPP scarcely produced; V7 almost entirely occupied by LO; posterolateral corners of T8 either very narrowly pointed, and slightly down turned (Fu & Ballantyne 2008 Figs 17, 19; Ballantyne 2008 Fig. 9) or not . . .*Pygoluciola* Wittmer Partim **Fig. 4 Node 48**
14. Median lobe of aedeagus without lateral teeth 15
Median lobe of aedeagus with lateral teeth; Pacific Ocean species restricted to the Solomon Islands (Ballantyne & Lambkin 2009 Figs 364–376) . . . . *Pacifica* **gen. nov. Fig. 5 Node 54**
15. Pronotum wider than width across elytral humeri; often with small indentation along posterolateral margin, near corner (Ballantyne & Lambkin 2009 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 (Ballantyne & Lambkin 2009 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 sutural ridge only (Ballantyne & Lambkin 2009 Figs 64, 69–71); apical labial palpomere shaped like a wide flattened triangle with 3 or more teeth on inner margin; posterior half of V7 usually arched, sometimes swollen (Ballantyne & Lambkin 2009 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; T8 symmetri-

cal, not narrowed in posterior half, posterior margin thick and down turned and engulfing the MPP in *Pygat*. *undulata* only (Ballantyne & Lambkin 2009 Figs 504–506) . . . . *Pygatyphella* (Ballantyne)
Pronotum wider than, or subequal to, width across elytral humeri, lateral margin without 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 (Ballantyne & Lambkin 2009 Fig. 84); posterior area of hypomeron narrowly to widely flattened and often closely adpressed; elytra often with ridge continuing around apex (Ballantyne & Lambkin 2009 Fig. 83); dorsal colouration variable, rarely as described above; shape of apical labial palpomere variable, either a narrow to wide flattened triangle with 2 or more teeth on inner margin, or inner margin irregular not dentate, or ovoid, inner margin without 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; T8 usually symmetrical, may be asymmetrical and partially engulfing MPP from above (Ballantyne & Lambkin 2009 Figs 6, 7, 108–111) 16

16. T8 strongly asymmetrical; V7 LO bipartite, or entire with anterior median emargination (Ballantyne & Lambkin 2009 Figs 6, 7, 108–111) . . . . *Asymmetricata* Ballantyne
T8 symmetrical, not strongly emarginated on right side; LO bipartite or entire, if entire without anterior median emargination. 17

17. 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 (Ballantyne & Lambkin 2009 Figs 12, 13, 73, 74) . . . . *Convexa* Ballantyne
Pronotum wider than or subequal in width to width across elytral humeri (Ballantyne & Lambkin 2009 Figs 76, 77); pronotal punctation not small and sparse; elytral margins convex or parallel-sided; ML not constricted just behind apex. 18

18. Dorsal colouration pale, yellowish or very pale brown, with elytral apices often dark brown (Ballantyne & Lambkin 2009 Fig. 4) 19
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 20

19. 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); inner margin of apical labial palpomere with 2 teeth (Ballantyne & Lambkin 2009 Fig. 4) . . . . *Aquilonia* Ballantyne
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; inner margin of apical labial palpomere irregular, not dentate (Ballantyne & Lambkin 2009; Figs 15, 16) . . . . *Gilvainsula* Ballantyne

20. Pronotal width subequal to humeral width; anterior hypomeron not flat to neck; 2–3 interstitial lines; antennae longer than GHW; inner margin of apical labial palpomere 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 (Ballantyne & Lambkin 2009 Figs 19, 20, 76, 80–82) . . . . *Lloydiella* Ballantyne
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 labial palpomere either laterally flattened, with inner margin having 2 or more teeth, or without 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 21

21. Pronotum wider across posterior margin than rest, never subparallel-sided (Ballantyne & Lambkin 2009 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 labial palpomere strongly flattened, shaped like a narrow to wide triangle, with inner margin either irregular and not dentate, or dentate with 2 teeth; dorsal colouration often orange pronotum with dark brown elytra having lateral margin orange (Ballantyne & Lambkin 2009 Figs 17, 18, 77) . . . . *Magnalata* Ballantyne
Pronotum often wider across posterior margin than rest (Ballantyne & Lambkin 2009; 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 (Ballantyne & Lambkin 2009 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 labial palpomere often strongly flattened, shaped like 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 labial palomerei often ovoid entire . . . . *Atyphella* Olliff

22. Median lobe of aedeagus bulbous along its length; apex of median lobe irregularly expanded. (Fu *et al*. 2012a Figs 10–12). . . . . *Luciola indica* Motsch. **Fig. 3 Node 11 Number 3**
Median lobe not bulbous along its length nor irregularly expanded at its apex.. 23

23. LO in V7 entire 24
LO in V7 bipartite. (e.g. Ballantyne & Lambkin Fig. 107). 27
24. Elytral apices with posterior emargination (Jeng *et al.* 2003 Fig. 2) . . . . *Luciola trilucida* Jeng *et al.* **Fig. 3 Node 8 Number 2**
Elytral apices without posterior emargination. 25
25. Elytral apices deflexed V7 always trisinuate, and abdominal ventrites with recurved posterior margins and PLP wider than or subequal in width to MPP, never narrower (e.g. Ballantyne & Lambkin Fig. 96) . . . . *Medeopteryx* **gen. nov.** Partim Fig. 3 Node 21
Elytral apices not deflexed 26
26. V7 sometimes trisinuate, often with only a MPP in V7; if V7 trisinuate no abdominal ventrites with recurved posterior margins and PLP narrower than MPP. . . . . *Australoluciola* **gen. nov.** Partim Fig. 3 Node 32
V7 always trisinuate, often with abdominal ventrites with recurved posterior margins; PLP wider than MPP . . . . *Medeopteryx* **gen. nov.** Partim Fig. 3 Node 19 numbers 7, 8
27. Aedeagal sheath with bulbous paraprocts (Ballantyne 1987a Fig. 4a–d; Ballantyne & Lambkin 2009 Figs 86–89, 94, 95); MFC present; elytral apices usually deflexed 28
Aedeagal sheath without bulbous paraprocts (Ballantyne 1987a Fig. 4e–h; Ballantyne & Lambkin 2009 Figs 90–93); without MFC 30
28. Deflexed elytral apices present . . . . *Pteroptyx* **s. str. Fig. 3 Node 16**
Deflexed elytral apices absent. 29
29. Posterior margin of V7 bearing bulbous incurving hairy lobes, without pointed projections; ventral surface of T8 without lateral depressed areas bearing spines. . . . . *Poluninius* **gen. nov. Fig. 3 Node 12 Number 4**
Posterior margin of V7 bearing narrow incurving hairy lobes, and pointed projections; ventral surface of T8 with lateral depressed areas with spined areas (Ballantyne & Lambkin 2009 Figs 106, 107). . . . . *Pyrophanes* Olivier
30. 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 (Ballantyne & Lambkin 2009 Figs 101–105); PLP often obliquely inclined to the median line. . . . . *Colophotia* Motschulsky[3]
Median carina absent; aedeagal sheath never very long and slender; antennal segments not shortened; T8 anterolateral arms not conspicuously elongated; PLP always horizontal; elytral apices often deflexed; V7 with broad PLP which are longer than the MPP (e.g. Ballantyne 1987b Fig. 2a, b) or subequal in length; abdominal V3 and often V4 may have recurved posterior margins; elytral apices often deflexed; apical labial palpomere about as wide as long or longer than wide . . . . *Trisinuata* **gen. nov. Fig. 3 Node 23**

1. Pacific Island species of *Luciola* distinguished here include *antipodum* and *hypocrita*, formerly assigned to *Bourgeoisia*.
2. *Luciola* **s. str.** As represented by *Luciola italica* is distinguished here.
3. 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.

Key to genera and species of Luciolinae using females

Couplets 17–19 modified from Ballantyne & Lambkin (2000)

Not all genera have females associated, nor are details of the reproductive system available for all genera.

1. Clypeolabral suture absent; labrum inflexible (e.g. Ballantyne & Lambkin 2009 Figs 27, 30) . . . . *Missimia* Ballantyne
Clypeolabral suture present; labrum flexible 2
2. Fore and hind wings fully developed and flight capable 3
Fore wings full length or shortened; hind wings shortened, vestigial or absent; not capable of flight. 15
3. Elytral punctation large and regularly spaced; pronounced humeral carina present (Fu *et al.* 2012 Fig. 34) . . . . *Curtos*. sp.
Elytral punctation not large and regularly spaced; humeral carina absent 4
4. Bursa plates present. 5
Bursa plates absent, or presence/absence not reliably determined 8
5. Bursa plates broad e.g. Figs 34,54,55,91,96–98,106, 160–167, 200–203 6
Bursa plates narrow, often hooked on inner surface 7
6. Wide elongate plates in each side of the bursa (Ballantyne *et al.* 2011 Figs 53, 54, 59, 60) . . . . *Pteroptyx maipo, valida*
Set of two plates in each side of the bursa (Figs 34,54,55,91,96–98,106, 160–167, 200–203) . . . . *Australoluciola* **gen. nov.** spp., *Colophotia* spp., *Medeopteryx* **gen. nov.** spp., *Pyrophanes* spp., some *Pteroptyx* s. str. spp., *Trisinuata* **gen. nov**. spp.
7. Bursa plates without hooks on inner surfaces . . . . *Aquatica* Fu *et al.*
Bursa plates with hooks on inner surfaces . . . . *Pygoluciola* spp.;
8. Bursa plates absent . . . . *Asymmetricata* spp.; *Luciola italica*
Nature of bursa plates unknown 9
9. Dorsal surface pale yellowish brown or yellowish orange, with dark elytral apices 10
Dorsal surface with orange pronotum, and dark brown elytra which may be pale margined, or yellowish brown elytra with brown markings at base and apex 11

10. Australian; orange elytra with very dark brown apices. . . . . *Aquilonia* sp.
New Guinean, mainly off shore islands in SE; elytra pale brownish yellow with light brown apices . . . . *Gilvainsula* sp.
11. Elytra dark brown, often with paler margins. 12
Elytra pale yellowish brown with extensive darker brown markings at base and apex . . . . *Pygatyphella* (Ballantyne)
12. Elytra dark brown without paler margins . . . .*Atyphella aphrogeneia*; *Lloydiella* spp., some *Pacifica* **gen. nov**. spp.
Elytra with paler margins 13
13. Pronotum smooth shiny, with punctures separated over the surface by their width; elytra convex-sided . . .*Convexa* Ballantyne
Pronotal punctures not widely separated. 14
14. Large (12.5–16 mm long); MS black . . . . *Magnalata* Ballantyne spp.
Smaller (not longer than 10 mm); MS pale coloured . . . . *Pacifica* **gen nov.** spp.
15. Elytra covering most if not all of the body (some abdominal segments may protrude in gravid females 16
Elytra very reduced (cover less than 1/3 of abdomen) 17
16. No hind wings . . . . *Atyphella atra* Lea
Hind wings present but reduced in length; fore wings slightly reduced in length; female may be capable of flight over short distances. . . . . *Luciola italica* (European species); *L. hypocrita* (known only from Fiji); *L. parvula* (Japanese species)
17. Elytra at least half as long as median pronotal length and contiguous in median line when abdomen is gravid . . . . *Aty. scintillans* Olliff
Elytra less than half as long as median pronotal length (Ballantyne & Lambkin 2000 Fig. 6c) 18
18. Elytra present as narrow lateral strips . . . . *Aty. lewisi* Ballantyne
Elytra about as long as wide 19
19. Pronotum smooth, shiny, with punctures separated by 1–2 times their width; posterolateral corners not projecting . . . . *Aty. similis* Ballantyne, *Aty. conspicua* Ballantyne
Pronotum not markedly smooth or shiny; punctures contiguous; posterolateral corners projecting . . . . . *Aty. inconspicua* (Lea)

Key to certain genera and species of Luciolinae using larvae

Fu *et al.* (2012b) give a key to Luciolinae larvae based primarily on adaptation to mode of life.

Australoluciola gen. nov.

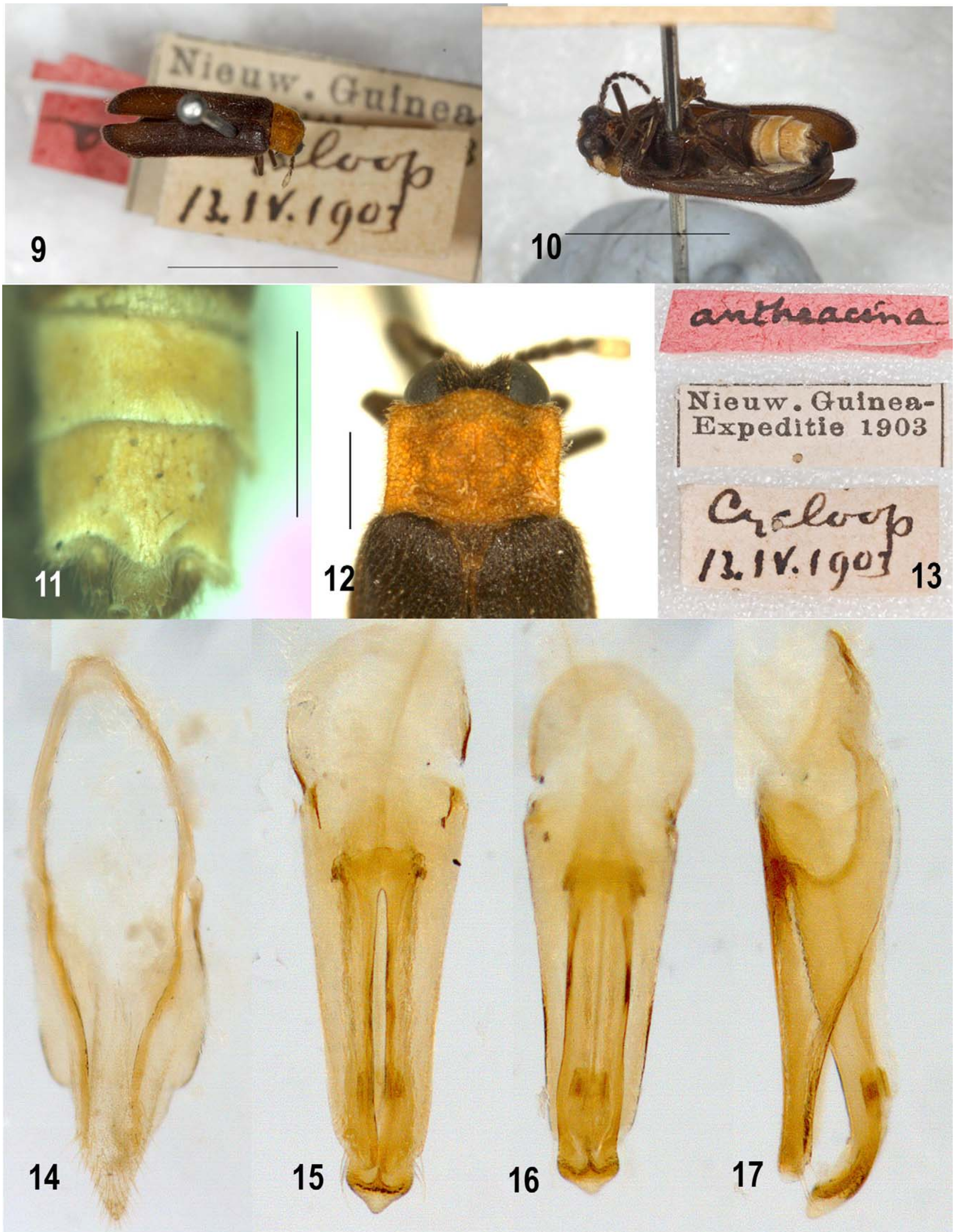
[Figs 9–91]

Type species: *Australoluciola australis* (F.).

Diagnosis. *Australoluciola* **gen. nov.** is an Australian and New Guinean genus belonging in a group of seven genera characterized by: pronotal width less than width across elytral humeri, parallel-sided elytra, no MFC, an elongate slender aedeagus with LL largely concealed behind the ML when viewed from beneath; aedeagal sheath elongate slender, widest across middle, without bulbous paraprocts, and with both sides of posterior half of sheath sternite tapering evenly towards a narrow entire apex. Males distinguished from *Colophotia* in having no median carina on V7, expanded and oblique PLP and bipartite LOs in V7; from *Pteroptyx* in having no MFC, deflexed elytral apices, bulbous aedeagal sheath paraprocts and bipartite LOs in V7; from *Pyrophanes* (which has a MFC) and *Poluninius* **gen. nov.** (which has no MFC) in lacking both incurving lobes along V7 and bipartite LO; from *Trisinuata* **gen. nov.** by the entire LOs in V7 (those of *Trisinuata* **gen. nov.** are bipartite); from most *Medeopteryx* **gen. nov.** in lacking deflexed elytral apices. It differs from *Luciola indica* in lacking the bulbous median lobe and paraprocts on the aedeagal sheath.

All but three species have orange pronotum and dark brown elytra similar to many species of *Medeopteryx* **gen. nov.** *Aus. aspera* has median brown pronotal markings, and in *Aus. flavicollis* the elytral base and/or margins may be pale. *Aus. japenensis* **sp. nov.** alone has pale yellowish brown dorsal colour and dark elytral apices, characteristic of many SE Asian fireflies (McDermott 1966). V7 may be trisinuate or with an MPP only, and PLP rounded, not produced; T8 has a well defined ventral groove margined by ridges and with short, wide and apically rounded flanges in *Aus. aspera* and *Aus. pharusaurea* **sp. nov.** only. Females macropterous and capable of flight. Larvae terrestrial, without laterally explanate tergal margins; laterotergites visible from above.

Male. Pronotum (Figs 12, 19, 25, 58): dorsal surface without irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense; anterior margin not explanate; either subparallel-sided, margins straight (A=B=C; e.g. Fig. 12), or lateral margins diverging posteriorly along their length (C>A, B), or lateral margins converging posteriorly (C<A, B); width < humeral width; anterolateral corners rounded obtuse or angulate; lateral margins without indentation at mid-point, and sinuousity in either horizontal or vertical plane; without indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners usually angulate, rounded obtuse in *Aus. australis*; posterolateral corners not usually projecting as far as median posterior margin; separated from it by scarce emarginations.



FIGURES 9–17. *Australoluciola anthracina* type male, Cyclops (MNHN). 9, 10 dorsal (9) and ventral; 11 V6, 7 ventral; 12 pronotum dorsal; 13 type labels; 14 aedeagal sheath ventral; 15-17 aedeagus, dorsal (15), ventral (16) and lateral. These figures share scale lines: 15–17.

Hypomera: closed; median area of hypomeron not elevated in vertical direction; median area more widely flattened than elsewhere except in *fuscamagna* **sp. nov.** where anterior and posterior areas very narrowly flat; pronotal width/ GHW 1.2.

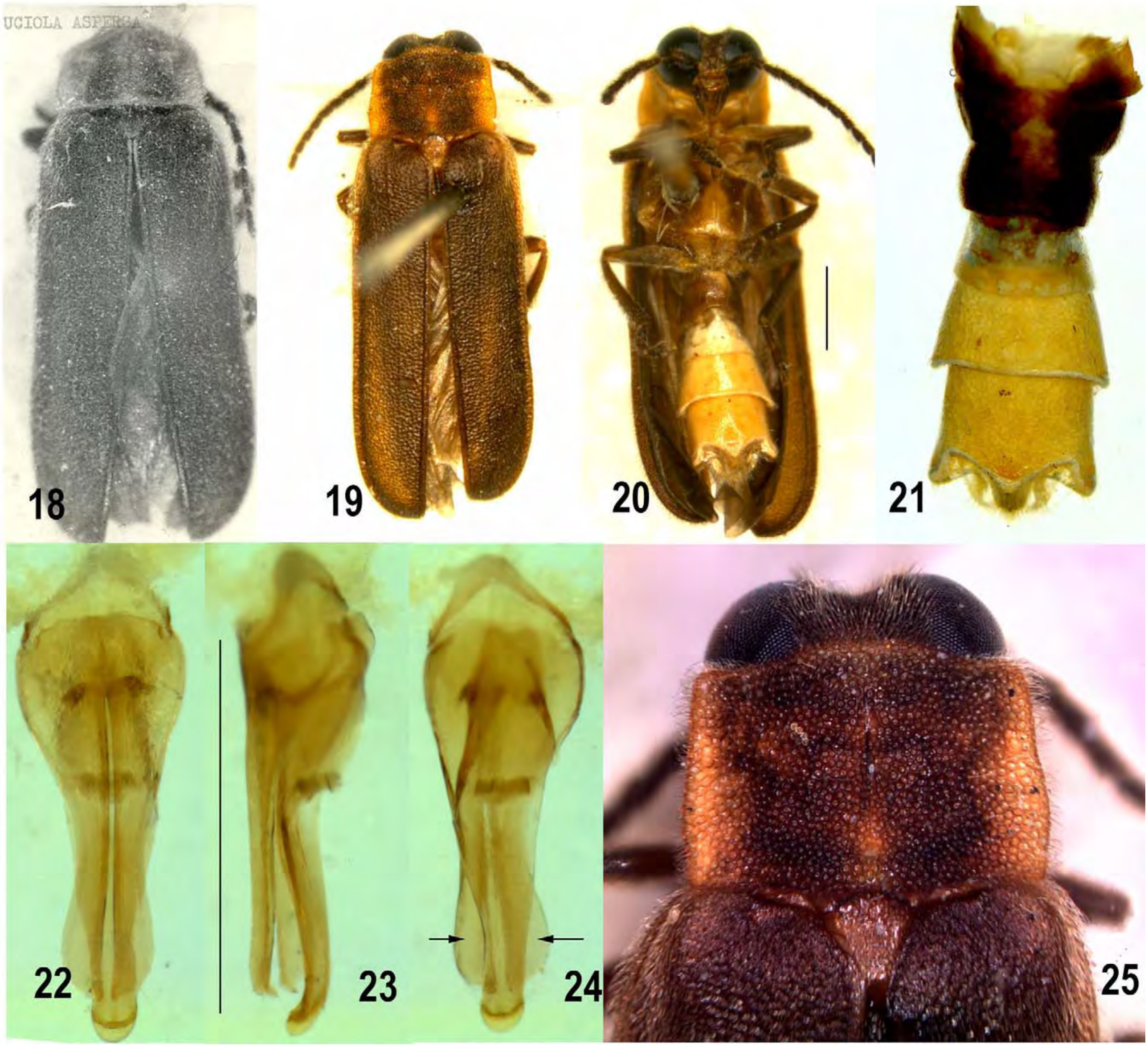
Elytron: punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and sutural ridge extend beyond mid-point, almost to apex but not extending around apex, neither thickened in apical half; no interstitial lines; elytral carina absent; in horizontal specimen viewed from below epipleuron at elytral base wide, covering humerus except in some *fuscaparva* **sp. nov.** where the humerus is narrowly visible; viewed from above anterior margin of epipleuron arises level with or 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 close to moderately separated; frons-vertex junction rounded, without 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 or ASW (except for some *flavicollis* where ASD >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 labial palpomere strongly flattened, shaped like narrow triangle (narrowest at base and L 2–3 X W), with inner edge entire (e.g. Ballantyne 1988 Figs 10, 11), and at least half as long as apical maxillary palpomere. Antennae 11 segmented; length>GHW up to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel.

Legs: with inner tarsal claw not split; without MFC; femora 3 swollen and curved and tibiae 3 curved in two species; no basitarsi expanded or excavated.

Abdomen (Figs 10,11,21,29,35,36,57,61,62,67,68,73,75,76,88): without cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment except in single male of *Aus. aspera*, where V3 is strongly recurved (Fig. 21); LO in V7 entire, either occupying most of V7, and reaching to sides but not posterior margin (Figs 11,20,21,28,35,61,68,73,75,87), or not reaching sides or posterior margin and occupying about half or less of V7 (e.g. Fig. 48); reaching into PLP where these are developed; 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 or truncate, either entire or shallowly emarginate, not laterally compressed, short or slightly longer than wide (L<W or L>W), not inclined dorsally nor engulfed by T8 apex, without dorsal ridge, median longitudinal trough. V7 without median carina, median longitudinal trough, anteromedian depression on face of LO, incurving lobes or pointed projections, median ‘dimple’, or reflexed lobes; posterior margin of V7 either trisinuate or with posterolateral corners rounded; if trisinuate then MPP longer than, and as wide as, PLP; if PLP not developed then posterolateral corners rounded and MPP well developed; PLP moderately produced, as wide as MPP, as long as wide or wider than long. T7 without prolonged anterolateral corners. T8: (Figs 29,30,36,62,76,77,88) well sclerotised, symmetrical, W=L, visible posterior area not narrowing abruptly, median posterior margin shallowly and narrowly emarginate; T8 widest across middle with lateral margins tapering evenly in both an anterior and posterior direction; without prolonged posterolateral corners, 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 with well developed median longitudinal trough, margined by well defined symmetrical ridges; anterior end of ridges either not produced, with rounded or angulate outline; or with short wide apically acute flanges in *aspera* and *pharusaurea*; without lateral depressed troughs, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 as long as, or slightly shorter than visible posterior portion of T8, not laterally emarginated before their origins, not expanded dorsoventrally, expanded only in horizontal plane; without bifurcation of inner margin and ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath: (Figs 14,30,42,43,52,53,81,82,89) approx. 3 times as long as wide; without bulbous paraprocts; symmetrical in posterior area where sheath sternite tapers evenly to a narrow rounded apex; anterior half of sternite relatively narrow, apically rounded; tergite without lateral arms extending anteriorly at sides of sheath sternite; tergite without projecting pieces along posterior margin of T 9, anterior margin without transverse band.



FIGURES 18–25. *Australoluciola aspera*, type female (18), Wewak male NHML 19–25. 18, 19 dorsal; 20, 21 ventral (21 abdomen only); 22–24 aedeagus dorsal (22), right lateral (23) and ventral (lateral projections of LL arrowed in 24); 25 pronotum dorsal. These figures share scale lines: 19, 20; 22–24.

Aedeagus: (Figs 15–17,22–24,31–33,39–41,49–51,63–65,69,70,78–80) L/W2.9–6.0; LL lack lateral appendages; apices of LL not visible from beneath at sides of ML, LL/ML narrow; LL of equal length, slightly shorter than ML, contiguous or closely approaching along inner dorsal margins except in *orapallida* where inner margins diverge and apices are very narrow; LL separated longitudinally by most of 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; LL without lateral hairy appendages along their outer ventral margins, not produced preapically nor narrowly on inner apical margin, apices of LL not inturned, nor out-turned; without projection on left LL; inner margins without slender leaf-like projection; ML symmetrical, without paired lateral teeth and tooth to left side, not strongly arched, apex not shaped like arrowhead, not bulbous, not inclined ventrally; bearing transverse ridge preapically on dorsal side; BP not strongly sclerotised, not hooded, not strongly emarginated along anterior margin.

Female (Fig. 18). Macropterous and observed in flight in *Aus. australis* (Ballantyne 1988 Fig. 12). Pronotum without irregularities in posterolateral areas; punctation moderate to dense; pronotal width less than humeral width; without 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; no interstitial lines; elytral carina absent. No legs or parts thereof swollen and /or curved. LO in V6 only, without any elevations or depressions or ridges on V7; median posterior margin of V7 widely emarginate, median area not broadly rounded; median posterior margin of V8 entire. Bursa plates (Figs 34,54,55,91) consisting of 2 wide paired plates in *Aus. australis*, *Aus. flavicollis* and *Aus. pharusaurea* **sp. nov.**

Larva. Reliably associated for *Aus. australis* only; terrestrial; elongate, slender, spindle shaped (Ballantyne & Buck 1979 Figs 32, 33, 37; Ballantyne 1988) of the form of *Pteroptyx valida* and *P. maipo* larvae (Ballantyne *et al.* 2011), without laterally explanate tergal margins and with laterotergites usually visible at sides; posterolateral corners of terga 1–8 rounded entire, of tergum 12 produced narrowly; median posterior margins of terga 1–11 with rounded projections beside mid line; without brush of hairs from apex of tibiotarsus; mandibles without inner teeth; antennal segment 3 short, sense cone adjacent to segment 3 short, wide.

Etymology. *Australoluciola* (feminine) is a compound noun indicating its origins (from the south) and previous affinities (seven of the species were described originally within the genus *Luciola*).

Remarks. *Australoluciola* **gen. nov.** includes eight New Guinean and four Australian species, one of which, *Aus. australis* (F.), is found in mangroves along the E coast of Queensland, while *Aus. orapallida* (Ballantyne) is known from one locality in mangroves in Cape York Peninsula.

The other Australian species, *Aus. flavicollis* and *Aus. nigra*, have an extensive distribution along the eastern coast of Queensland occurring in open sclerophyll forest and rain forest remnants especially around Brisbane (Ballantyne & Lambkin 2000). Three of the New Guinean species are distinguished by light patterns while nothing is known of their wider distribution.

List of species of *Australoluciola* gen. nov.

- *anthracina* (Olivier) **comb. nov**.
- *aspera* (Olivier) **comb. nov.**
- *australis* (F.) **comb. nov**.
- *baduria* **sp. nov**.
- *flavicollis* (MacLeay) **comb. nov**.
- *foveicollis* (Olivier) **comb. nov**.
- *fuscamagna* **sp. nov.**
- *fuscaparva* **sp. nov.**
- *japenensis* **sp. nov**.
- *nigra* (Olivier) **comb. nov**.
- *orapallida* (Ballantyne) **comb. nov**.
- *pharusaurea* **sp. nov.**

Key to species of *Australoluciola* gen. nov. using males

1. V7 trisinuate along its posterior margin (Figs 10,11,21,35,57,61,67,68,73,75) 2
   V7 not trisinuate along its posterior margin (Figs 28,48,87); posterolateral corners rounded, not produced; median posterior projection always developed sometimes longer than wide, may be apically emarginated 11
2. Hind femora swollen, hind tibiae curved (e.g.Fig. 37) 3
   Hind femora not swollen, hind tibiae not curved 4
3. Elytra dark brown . . . . *baduria* **sp. nov.**
   Elytra orange yellow with small dark area at apex . . . . *japenensis* **sp. nov.**
4. Pronotum all dark, or with dark markings around margins, or in centre 5
   Pronotum pale coloured with no dark markings 8
5. Pronotum entirely dark marked; rest of dorsal body and all of ventral surface except for LOs dark brown (Figs 66,67,71,72,74) 6
   Pronotum with dark markings around margins or in centre; ventral body may have paler markings 7
6. Medium sized (6.2–6.6 mm long) . . . . *fuscamagna* **sp. nov.**
   Small (3.5–4.0 mm long) . . . . *fuscaparva* **sp. nov.**
7. Pronotum orange with orange margins and extensive median dark markings (Fig. 25); elytra dark brown; ventral surface of body with pale areas including Los (Fig. 20) . . . . *aspera* (Olivier)
   Pronotum orange with dark markings around margins; ventral body (apart from LOs) dark brown . . . *anthracina* (Olivier) var.
8. Ventral aspect of body entirely dark brown except: posterior margin of abdominal V5 may be pale or apices of femora 1 may be paler; head between eyes dark brown; T7, 8 dark brown (Figs 9,10,75,75) 9

Ventral surface of body always with some pale markings i.e. parts of head, thorax and/or portions of legs and/or basal segments of abdomen pale, head between eyes yellow or brown; T7, 8 pale (Figs 57,83–86) 10

9. Large 9.9–10 mm long; known only from 3 males from Sea Falls Torricelli Mountains (Figs 75–82) . . . . *maxima* **sp. nov.**
Smaller (<8 mm); know from SE New Guinea. . . . . *anthracina* (Olivier) **var.**

10. New Britain; head between eyes yellow; elytral punctures small uniform (Figs 83–91) . . . . *pharusaurea* **sp. nov.**
Mainland New Guinea; head between eyes dark brown to black; punctures along some areas of elytra large and irregular (figs 56–65) *foveicollis* (Olivier)

11. Found in mangroves along east coast of Queensland as far south as Bundaberg; ventral body yellow except for white LOs; MPP short; head between eyes brown (Figs 26–34) . . . . *australis* (F.)
Open forest dweller; ventral body with extensive dark markings; MPP longer than wide, may be apically emarginate. 12

12. Elytra dark brown with no pale margins . . . . *nigra* (Olivier)
Elytra dark brown with paler margins 13

13. Elytra brown at bases and apices, and lateral margins widely pale; most of ventral . . . surface of body pale; aedeagus with LL very narrow and widely separated dorsally (Ballantyne & Lambkin 2000 Figs 19–22) . . . . *orapallida* (Ballantyne)
Elytra brown always with some orange markings, either across base, and/or sutural ridge, and/or lateral margin; most of ventral surface of body very dark brown; aedeagus with LL closely approaching dorsally (Fig. 45) . . . . *flavicollis* (MacLeay)

Table 8 lists species described originally as *Luciola* spp., having orange pronota and dark brown, non-margined, elytra, consistent with seven species assigned here to *Australoluciola* **gen nov.** Other genera/species with this colour pattern include *Lloydiella* spp. Ballantyne (Ballantyne & Lambkin 2009), *Atyphella immaculata* Ballantyne (Ballantyne & Lambkin 2000), species of *Medeopteryx* **gen nov.,** *Pacifica salomonis* (Olivier) **comb. nov.**, certain *Pyrophanes* species, and some *Curtos* (Jeng *et al*. 1998).

TABLE 8. SE Asian and Australopacific Luciolinae described as *Luciola* spp. (*sensu* McDermott 1966) with orange pronota and dark brown/ black elytra.

Species as listed in McDermott 1966	Comment	Action herein	Trisinuate V7
Luciola australis (F.)		*Australoluciola australis* (F.)	No
Luciola anthracina Olivier		*Aus. anthracina* (Olivier)	Yes
L. atripes Pic	Not reliably identified in collections	No action here; not recorded from New Guinea	No
L. calceata Olivier		No action here; not recorded from New Guinea	No
L. cerata Olivier	Redescribed by Fu & Ballantyne 2008;	No action here; not recorded from New Guinea	No
L. foveicollis Olivier		*Aus. foveicollis* (Olivier)	Yes
L. fukiensis Pic		No action here; not recorded from New Guinea	No
L. immarginata Bourgeois	Based on female, not reliably identified in collections	No action here; not recorded from New Guinea	
L. kagiana Matsumura	belongs in *Luciola* s. str clade (Fig. 4 Node 35.)	No action here; not recorded from New Guinea	No
L. kuriowae Matsumura		No action here; not recorded from New Guinea	?
L. limbalis Fairmaire	Based on a female	No action here; not recorded from New Guinea	?
L. nigra Olivier		*Aus. nigra* (Olivier)	No
L. pupilla Olivier		*Medeopteryx pupilla* (Olivier)	Yes
L. ruficollis Boisduval		*species incertae sedis*	?Yes
L. semilimbata Olivier / *L. venusta* Olivier		*Pyrophanes semilimbata* (Olivier)	Yes
L. timida Olivier		*species incertae sedis*	
L. filiformis (Olivier) *(yayeyamana)*		No action here; not recorded from New Guinea	No

Australoluciola anthracina **(Olivier) comb. nov.**
[Figs 9–17]

Luciola anthracina Olivier, 1885:363; 1902:74; 1913b:417.
Luciola (Luciola) anthracina Olivier. McDermott, 1966:99.

Holotype. Female. **NEW GUINEA**: 8.45 S, 146.25E, Central Pr., Yule Island, as "Isola Yule" (MCSN).

Code name. *Luciola* 10 (Lloyd 1973a).

Other specimens examined. NEW GUINEA: 2.34 S, 140.31E, Cyclops, 12.iv.1903 (bears pink paper label with Olivier's handwritten identification), male (MNHN). Mt Cyclops 3500 feet iii.1936 LEC male (BPBM). The following are tentative assignments: **NEW GUINEA**: 5.14 S, 145.45E, Madang Pr., Sek Harbor, 10 miles N Madang October 18, 1969, J.E. Lloyd, 3 males (G355–357) (JELC). 5.55S, 146.4E, Madang Pr., Finisterre Mts: Budemu, c. 4000 feet 15–24.x.1964 M E Bacchus 2 males, 2 females; Damanti c 3550 ft 3 females (BPBM). 6.35S, 147.51E, Morobe Pr., Finsch Haven, L Wagner male, female; Finschaven Wareo L. Wagner 3 males 2 females (SAMA). 7.20 S, 146.45E, Morobe Pr., 4 miles N Wau elevated 2800, near Kunai Creek Lae Rd., 1969, J.E. Lloyd. 3 males, Oct. 17 (G332, 335, 345); 2 males Oct. 18 (G347, 349); 2 males Nov. 12 (G569, 570) (JELC).

Diagnosis. Type female 5.0 mm long; entirely dark brown except for orange pronotum, and white LO. Males 7.3–7.6 mm long with orange pronotum and dark brown elytra; ventral colouration black except for pale LOs in V6, 7 and pale posterior margin of V5 in one male; posterior margin of V7 trisinuate, with MPP slightly longer than lateral projections; dorsal abdomen dark brown; most obviously distinguished from the similar *Aus. foveicollis* by the dark terminal abdominal tergites and the small even elytral punctation. Specimens from localities other than Mt Cyclops including those from elevation in Finschhaven and the Finisterre Mountains are tentatively assigned; they differ most obviously in the pale terminal tergites and some have dark marginal pronotal markings.

Male. Redescription (Cyclops males). 7.3–7.6 mm long. Colour (Figs 9, 10, 12): pronotum orange, MS brown, MN yellow; remainder of body very dark brown except for pale LOs in V6, 7, and narrowly pale posterior margin of V5. Pronotum (Fig. 12): 1.3–1.4 mm long, 1.8–2.0 mm wide, W/L 1.4; midanterior margin rounded and moderately produced beyond angulate anterolateral corners; lateral margins subparallel sided, A=B=C; posterolateral corners angulate approximately 90º; punctures broad, shallow mostly contiguous. Elytra: shiny, finely punctate; epipleuron visible at side of elytron level with posterior margin of MS. Head: moderately depressed between eyes, GHW 1.4 mm; SIW 0.3 mm; ASD subequal to ASW. Abdomen (Fig. 11) posterior margin of V7 trisinuate; LOs in V7 occupying most of the area and reaching to sides but not as far as posterior margin; MPP apically rounded, L=W; as wide as and slightly longer than PLP (Figs 10, 11). T8: ventral surface with well developed lateral ridges, no flanges; anterior area of ridges smoothly rounded; anterolateral prolongations of T8 wide, not as long as posterior entire portion. Aedeagus (Figs 15–17): relatively short and wide anterior prolongation of median lobe (viewed from beneath); lateral margins of LL straight, not expanded along apical ¼, outer margins narrowly visible beside ML near its apex, with apices of LL slightly obliquely truncate; L/W 3.4. Aedeagal sheath: (Fig. 14).

Males in Lloyd collection. 6–7.5 mm long (6–6.7 mm long except G570, G569). Colour: pronotum orange, MN cream; MS very dark brown; elytra entirely dark brown; head between eyes, antennae, palpi, all legs and all ventral surface of thorax dark brown except for yellow pronotal hypomera, brown precoxal bridges, and pale brown coxae 1; basal abdominal ventrites very dark brown; V5 white across posterior half; T6–8 white, T2–5 dark brown. Pronotum: 0.8–1.1 mm long, 1.4 mm wide; W/L = 1.3–1.7; median anterior margin often projecting moderately beyond rounded or angulate anterolateral corners; punctures contiguous over most of disc (slightly more widely separated in G356); subparallel-sided (B=C). Head: GHW 1.2–1.4mm; SIW 0.25mm; ASD = ASW; FS subequal in length, FS 1–4 slightly wider than remainder. Abdomen: MPP L>W; MPP subequal in width to PLP and slightly longer; posterior margin of MPP rounded. T8 without flanges; anterior margin of ridges rounded evenly. Aedeagus: slightly shorter and wider than type (L/W 3/1).

Males in SAMA collection. 6.4–7.1 mm long. Colour: pronotum orange without marginal dark markings (Wareo 1; Budemu 1); with dark marginal markings extending around all margins in Budemu (2), one with median dark sulcus; dark marginal markings except along midposterior margin in Finschaven (1); narrow anterior and lateral dark markings in Wareo (1), lateral markings only in Wareo (1); MN pale; MS dark brown; rest of ventral body except for white LOs and broad white posterior margin of V5 very dark brown; dorsal abdomen dark brown with T 6–8 pale whitish (T7, 8 dusky brown, lighter than preceding tergites in two Budemu males). Pronotum: 1.1–1.2 mm long; 1.6–1.8 mm wide; W/L 1.5; all corners angulate; lateral margins slightly divergent posteriorly (C slightly > B which is slightly > A); posterior margin slightly undulate with median posterior area broadly and shallowly emarginated. Elytron: 5.3–6.0 mm long. GHW 1.2–1.4 mm; SIW 0.2 mm; ASD slightly < ASW.

Female. Macropterous. Coloured as for male except white LO restricted to V6. Genitalia and internal reproductive not investigated on pinned specimens.

Larva. Not associated.

Remarks. Olivier (1885) described a single female, and subsequently assigned males from the type locality (Yule Island) and Mt Cyclops (Olivier, 1913b). We have been unable to relocate males from Yule Island and what we regard as the definitive redescription above is based on males (one identified by Olivier) from the Cyclops Mountains. The possibility of more than one species from these two localities should be considered. Olivier (1913b) described the dorsal end of the abdomen as white. The two Mt Cyclops males have T8 dark brown.

Assignment of the remaining specimens to this species is tentative only, and exacerbated by the difficulty in ascertaining the colour of the type male terminal abdomen. Both Lloyd's collections from lowland areas in Madang and Morobe Provinces, which lack dark margined pronota, and those from elevation in the Mt Lamington area with dark margined pronota, conform otherwise in ventral colouration and paler terminal abdominal tergites to Olivier's (1913b) description.

There are now five records of New Guinean Luciolinae having orange pronota with some dark marginal markings including the possible *anthracina* specimens described here e.g. *Luciola melancholica* Olivier (1913b) (treated here as Species Incertae); "Species D" and some *Pteroptyx* (now *Medeopteryx*) *cribellata* of Ballantyne and McLean (1970:247, 267); some *Pteroptyx* (now *Medeopteryx*) *fulminea* (Ballantyne 1987a). In all except *L. melancholica* the dark markings do not occur in all representatives, and in *cribellata* and *fulminea* most of the population described had no dark markings.

Australoluciola aspera **(Olivier) comb. nov.**

[Figs 18–25]

Luciola aspera Olivier, 1910a:344; 1913b:417; in Heyden, 1915:177.
Luciola (Luciola) aspera Olivier. McDermott, 1966:99.

Holotype. Female. **NEW GUINEA.** (Musée Senkenberg à Frankfort sur le main; (Senckenberg Forschungsinstitut und Naturmuseum).

Other material examined. NEW GUINEA: 3.30 S, 143.34E, East Sepik Province: Amok, 165 m, 6.i.1960, T. Maa, male (BPBM). 3.35 S, 143.35E, Wewak, 2–20 m, 11.x.1957, JLG, female (BPBM); Wewak F H Taylor, no date, male (NHML).

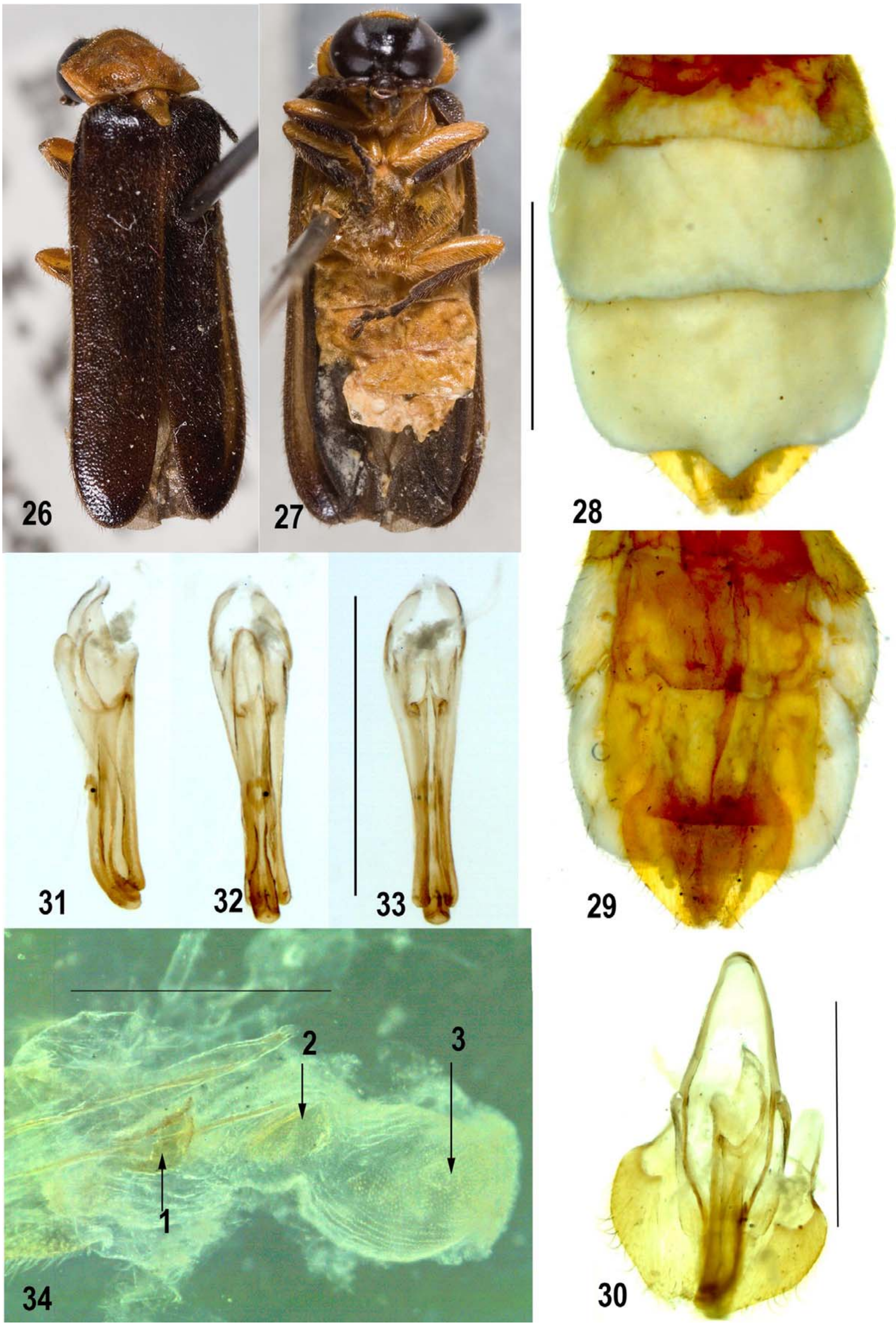
Diagnosis. The only species of *Australoluciola* with a wide dark median band on the orange pronotum; elytra dark brown; male V7 trisinuate.

Male. 5.7 mm long. Colour (Figs 19, 20, 25): pronotum orange with a median brown band (Figs 19, 25); MN orange, MS dark brown; elytra medium brown, lateral margin narrowly pale in anterior 1/3; ventral surface brown except for orange underside of pronotum, orange prosternum, pale yellow posterior half of V5, and creamy white V6, 7; legs brown except for pale coxae, trochanters and basal half of femora; basal tergites brown, T6, 7, 8 pale orange, semitransparent; dorsally reflexed margins of V6 and 7 white. Pronotum (Fig. 25): 1.3 mm long; 1.8 mm wide; W/L=1.4; dorsal surface irregular, with ridges and depressed areas; midanterior margin broadly rounded and projecting only a little in front of angulate anterolateral corners; lateral margins diverging posteriorly, C>A, B; posterolateral corners angulate; punctures broad, shallow, most contiguous. Elytra: 4.4 mm long; punctures minute, sublinear in parts of elytra over short distances. Abdomen (Figs 20, 21): V3 strongly, V4 very weakly recurved; anterior margin of V4 projecting into the posterior area of V3; posterior margin of V7 trisinuate; LOs occupying most of V7 and reaching sides but not posterior margin; MPP apically rounded, short; as wide as and slightly longer than PLP (Fig. 21). T8: Ventral surface with well developed lateral ridges and short, wide, apically rounded flanges; anterolateral prolongations of T8 wide, not as long as posterior entire portion. Aedeagus (Figs 22–24): short wide anterior prolongation of ML (view from beneath); lateral margins of LL curved, and expanded along apical 2/5 and visible beside ML; apices of LL slightly obliquely truncate; L/W 2.9.

Female (Type female Fig. 18). Macropterous. Genitalia and internal reproductive system not investigated.

Larva. Not associated.

Remarks. Association of males is made on the basis of the similarity of pronotal colour to that of the type female. Olivier's collection in MNHN has a small water colour of this species showing the dark pronotal markings as two dark patches along the posterior area only (Ballantyne examination 2002).



FIGURES 26–34. *Australoluciola australis*, male (ANIC). 26, 27 dorsal and ventral (27 terminal abdomen removed); 28–30 abdomen, 28 V5–7 ventral; 28 segments 6–8 dorsal; 30 tergite 8 with aedeagus and sheath in place, ventral; 31–33 aedeagus left lateral (31), ventral (32) and dorsal; 34 reproductive system, Ross River female, from side, anterior end to right of page. Figure legends: 1 median oviduct plate; 2 posterior and 3 anterior bursa plates. These figures share scale lines: 28, 29; 31–33.

Australoluciola australis **(Fabricius) comb. nov.**
[Figs 26–34]

Lampyris australis Fabricius 1775:201; 1781:253; 1787:162; 1792:102; 1801:104. Lacordaire, 1857:338. Motschulsky, 1854:53 (partim). *Nec* Guérin-Méneville, 1838:74. Boisduval, 1835:125, plate vi, Fig. 13.
Lampyris italica var. *australis* Fabricius. Olivier, G., 1790:18. Fabricius, 1792:104.*Luciola australis* (F.). Laporte, 1833:150. Lea, 1909:108 (partim). Masters, 1886:288; 1888:327. McDermott, 1966:99. (partim)**.** Ballantyne, 1988:161. Ballantyne & Lambkin, 2001: 57; 2009: 21. *Nec* Gorham, 1880:104; Olivier, 1883:330; 1885:362; 1902:74 (larva); 1907:50; 1909b:lxxxi; 1913b:417; Olliff, 1890:652; Lea, 1921a:197.
Luciola pudica Olliff, 1890:652. Lea, 1909:109 (female).Ballantyne, 1988:162 (Synonymy).
Luciola (*Luciola*) *pudica* Olliff. McDermott, 1966:112 (partim). Calder, 1998:178.

Lectotype. Male. NEW HOLLAND (designated by Ballantyne, 1988) in Hunterian collection, University of Glasgow (see below).

Other specimens examined. AUSTRALIA: Queensland: Townsville, banks of Ross River, 15–16.ix.1980, J. Case mating pair (ANIC).

Diagnosis. Male 5.5–7.0 mm long; pronotum orange, elytra very dark brown (Fig. 26, 27), ventral surface mostly yellow; eyes without any visible posterolateral excavation when head withdrawn; MPP rounded (Fig. 28); V7 without PLP; ventral surface of T8 with lateral ridges having an angulate anterior area (Fig. 30). Aedeagus (Figs 31–33) elongate slender, lateral margins of LL slightly curved such that lateral margins at apex are narrowly visible beside ML (view from beneath); L/W 5.0. Female macropterous, coloured like male except pale LO in V7 only; two wide separate pairs of plates in bursa (Fig. 34). Larva with small rounded protuberances along posterior margins of terga, found in coastal mangrove flats; distinguished from *Aus. nigra* by the presence of well developed tubercles along the anterior margin of the protergum (Ballantyne & Lambkin 2000 Fig. 22a).

Remarks. *Lampyris australis* F. was the only firefly collected along the Queensland coast during the voyage of Captain Cook in 1770, is thus among the first insect collection made in Australia by Joseph Banks, and was probably taken in mangroves at the Endeavour River near what is now Cooktown. The male in the Hunterian collection is pale brown ventrally, doubtless an attribute of age. Dorsal colouration of freshly collected specimens is similar to most of the New Guinean *Medeopteryx* species. The identity of this species was resolved by Ballantyne (1988) who redescribed males, females and larvae. With the exception of one record from New South Wales (no specific locality was given and this is probably a case of mislabelling) it appears restricted to coastal Queensland in mangrove areas.

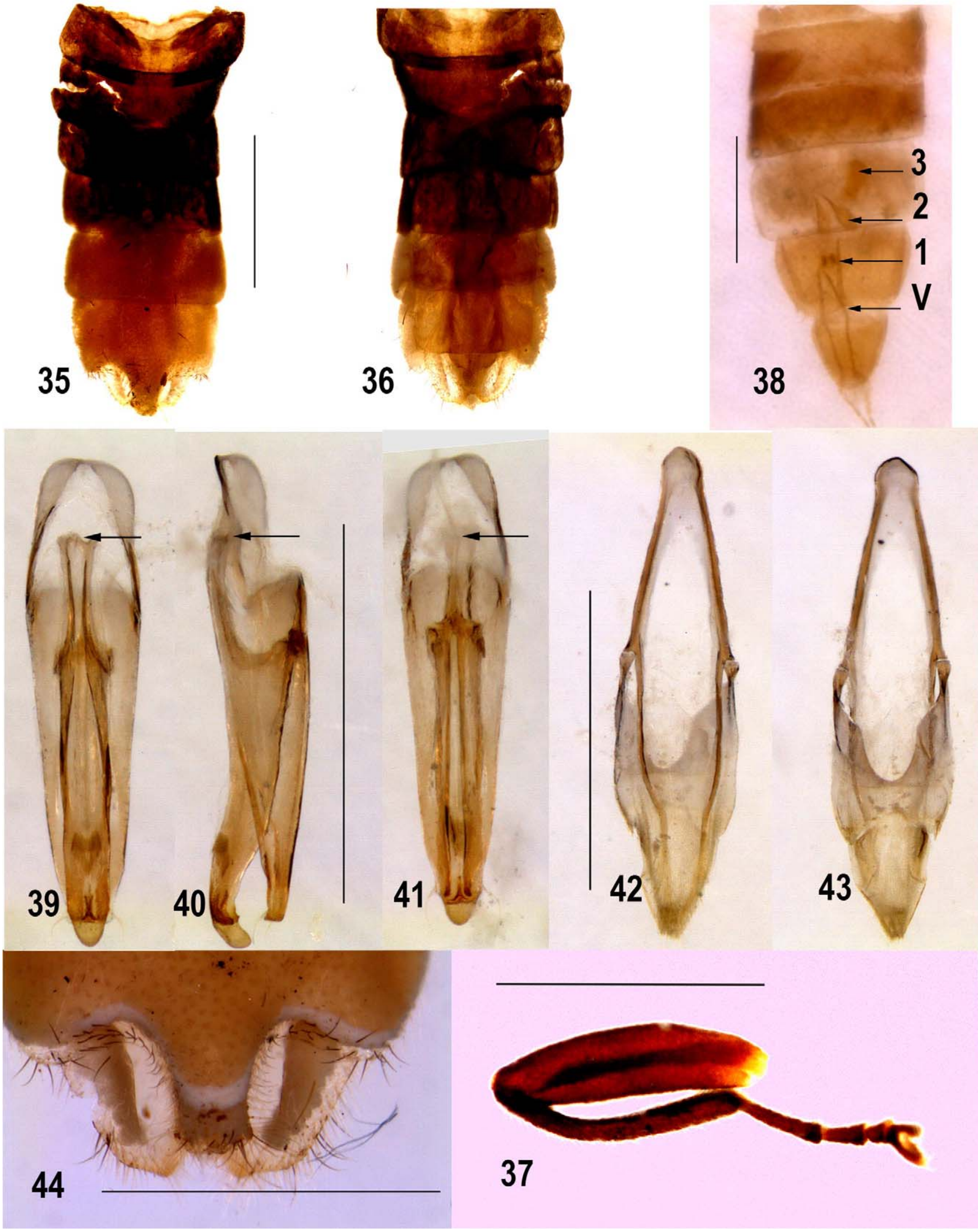
Australoluciola baduria **sp. nov.**
[Figs 35–37]

Holotype. Male. **INDONESIA** (as Dutch New Guinea): 1.45S, 136.08E Japen Island Mt Baduri 1000 feet viii.1938 LEC (NHML).

Paratypes (14). Same locality as holotype, 11 males. Japen Island: Mania**-**Undei 500 feet x.1938 LEC male (BPBM); Camp 2 Mt Eiori 2000 feet x 1938 LEC male; camp 3 central range Mt Oud 3000 feet xi.1938 LEC 2 males (NHML).

Diagnosis. Pronotum orange, elytra dark brown; distinguished from all other *Australoluciola* with similar dorsal colouration by the swollen and slightly curved femora 3 and the curved tibiae 3 in the male (Fig. 37); MPP longer than wide, considerably longer than the rounded PLP of V7.

Male. 4.9–6.1 mm long. Colour: pronotum orange; MN creamy white; MS dusky brown; elytra very dark brown almost black; all of ventral surface dark brown except for white LOs in V6, 7; T7, 8 pale semitransparent, remainder of tergites brown; dorsally reflexed margins of V6, 7 pale. Pronotum: 1.2–1.5 mm wide, 1.2–1.5 mm long; W/L = 2.4–3.0; midanterior margin broadly rounded, scarcely projecting beyond angulate anterolateral corners; lateral margins slightly divergent posteriorly (C slightly > B); punctures contiguous or separated by up to their width. Elytra: pin punctate, often irregularly so along margins, punctures separated by their width. Abdomen (Figs 35, 36): V3, V4 posterior margins not recurved; posterior margin of V7 trisinuate, LOs in V7 occupying most of the area and reaching sides but not posterior margin; MPP apex slightly produced, L>W; PLP rounded, not produced as far as MPP. T8: Ventral surface with anterior margins of lateral ridges effaced; no flanges. Aedeagus (similar to Figs 39–41): anterior portion of ML slender and prolonged; lateral margins of LL straight, tapering to apex; apices of LL narrowly rounded; L/W=5.0. Aedeagal sheath similar to Figs 42, 43.



FIGURES 35–44. *Australoluciola baduria* paratype male 35 -37. *Aus. japenensis* paratype male 39-44, paratype female 38 (BPBM). 35, 36, 38, 44 abdomen dorsal (36), ventral 35, 38; 44 detail of posterior margin of terminal abdomen; 37 ventral right hind leg (coxa and trochanter not visible); 39-41 aedeagus ventral (39), left lateral (40) and dorsal (41) (anterior margin of ML arrowed); 42, 43 aedeagal sheath ventral (42) and dorsal. Figure legends: V valvifers of ovipositor; 1, 2 and 3 median oviduct plate, posterior and anterior bursa plates; These figures share scale lines: 35, 36; 39–41; 42, 43.

Female, Larva. Unknown.

Etymology. The specific name is regarded as a noun in apposition, latinised from, and highlighting, the type locality.

Remarks. Two species of *Australoluciola* bearing expanded hind femora and curved tibiae, (a feature seen in most species of *Pyrophanes*), lack the MFC (seen in all species of *Pyrophanes*). The possible function of such male leg modifications is discussed subsequently.

Australoluciola flavicollis (Macleay) comb. nov.

[Figs 45–55]

Luciola flavicollis Macleay, 1872:263. Masters, 1886:289. Olliff, 1890:653. Olivier, 1902:79; 1907:52; 1910b:42. Lea, 1909:109; 1921a:197; 1921b:65. Ballantyne & Lambkin 2000:60; 2009:21. *Nec* Armitage, 1908:28.

Luciola (Luciola) flavicollis Macleay. McDermott, 1966:104. Calder, 1998:179.

Luciola Gestroi Olivier, 1885:366; 1902:79; 1907:52; 1910b:42; 1913b:417 (Synonymy). Masters, 1886:289. McDermott, 1966:104. [Fig. 47].

Luciola gestroi Olivier, 1909b:lxxxi. Lea, 1909:109. (Synonymy).

Luciola coarcticollis Olivier, 1888:59; 1902:76; 1907:51; 1909b:lxxxi; 1910b:42. Lea, 1909:109 (Synonymy)**.** [Fig. 46].

Luciola flavicollis var. *coarcticollis* Olivier. McDermott, 1966:104 (Synonymy).

Nec Luciola gestroi var. *nigra* Olivier, 1885:366. McDermott, 1966:104.

Holotype. Male **AUSTRALIA**: Queensland: 25.37 S, 151.37E, Gayndah (AMSA).

Other specimens examined. **AUSTRALIA**: Queensland, 13.59S, 143.33E Silver Plains Homestead, J. L. Wassell 1.iv.1960 6 females (ANIC).

Diagnosis. Males small (4.5–6.5 mm long); pronotum orange; elytra light or dark brown, always with some paler yellow or orange markings along sides or across base (Ballantyne & Lambkin 2000 Fig. 19; Fig. 45); ventral body very dark brown to black except for pale yellow prothorax, yellow areas of legs, and white LO which is restricted to a median basal area in V7 (Fig. 48); MPP of V7 prolonged, sub-parallel-sided or with sides tapering posteriorly, and apically emarginate; posterolateral corners of V7 rounded, not projecting (Fig. 48); aedeagus with relatively short and wide anterior prolongation of ML; lateral margins of LL straight, not expanded in apical ½ (Figs 49–51); aedeagal sheath (Fig. 52, 53). Female macropterous, coloured as for male except pale LO in V6 only; two wide pairs of plates in bursa, anterior pair with internal ridge (Figs 54, 55). Larva similar to that of *Aus.nigra*, distinguished by the arrangement of tubercles on the dorsum (Ballantyne & Lambkin 2000 Fig. 22 c).

Australoluciola foveicollis (Olivier) comb. nov.

[Figs 56–65]

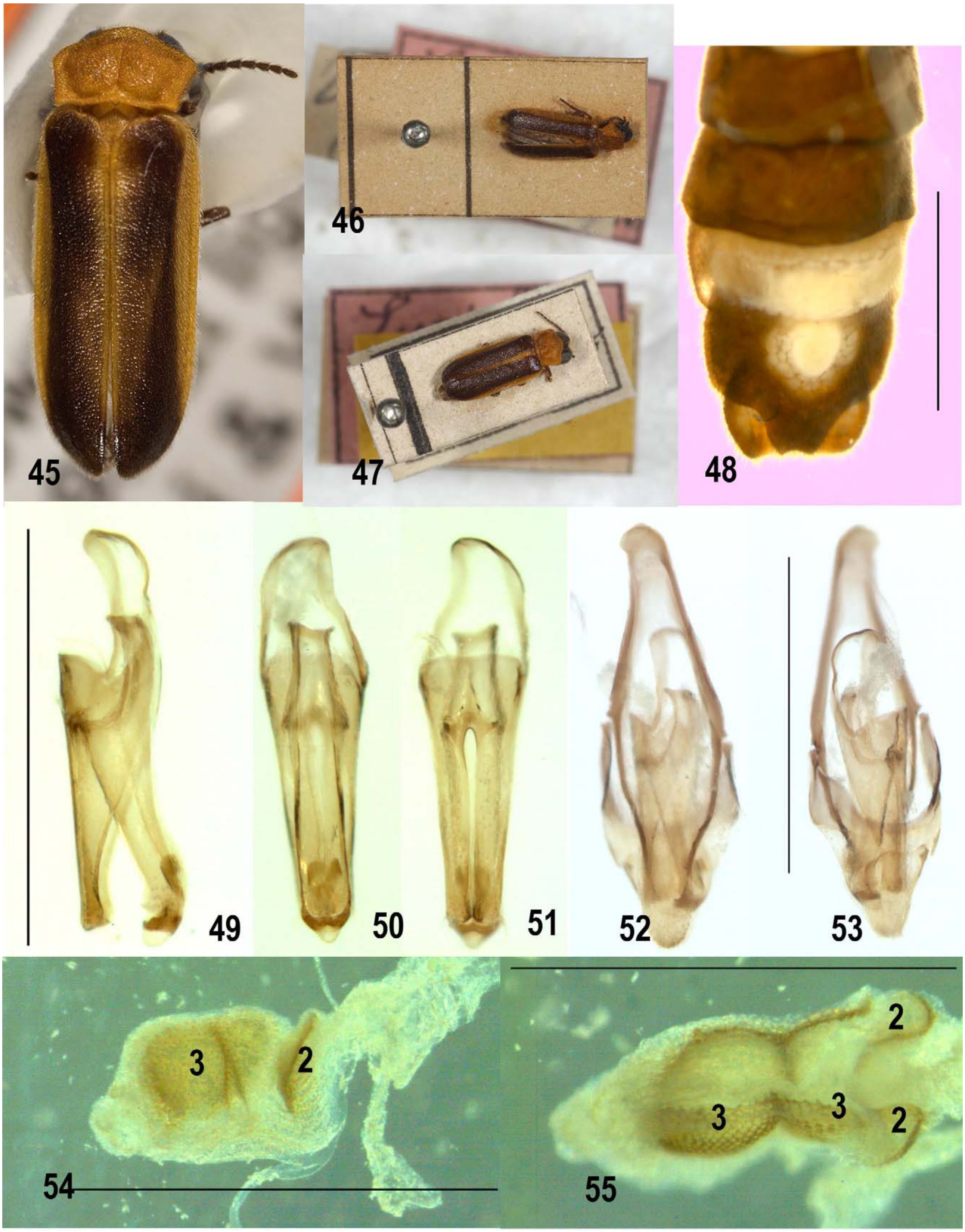
Luciola foveicollis Olivier, 1909a:316.

Luciola (Luciola) foveicollis Olivier. McDermott, 1966:104.

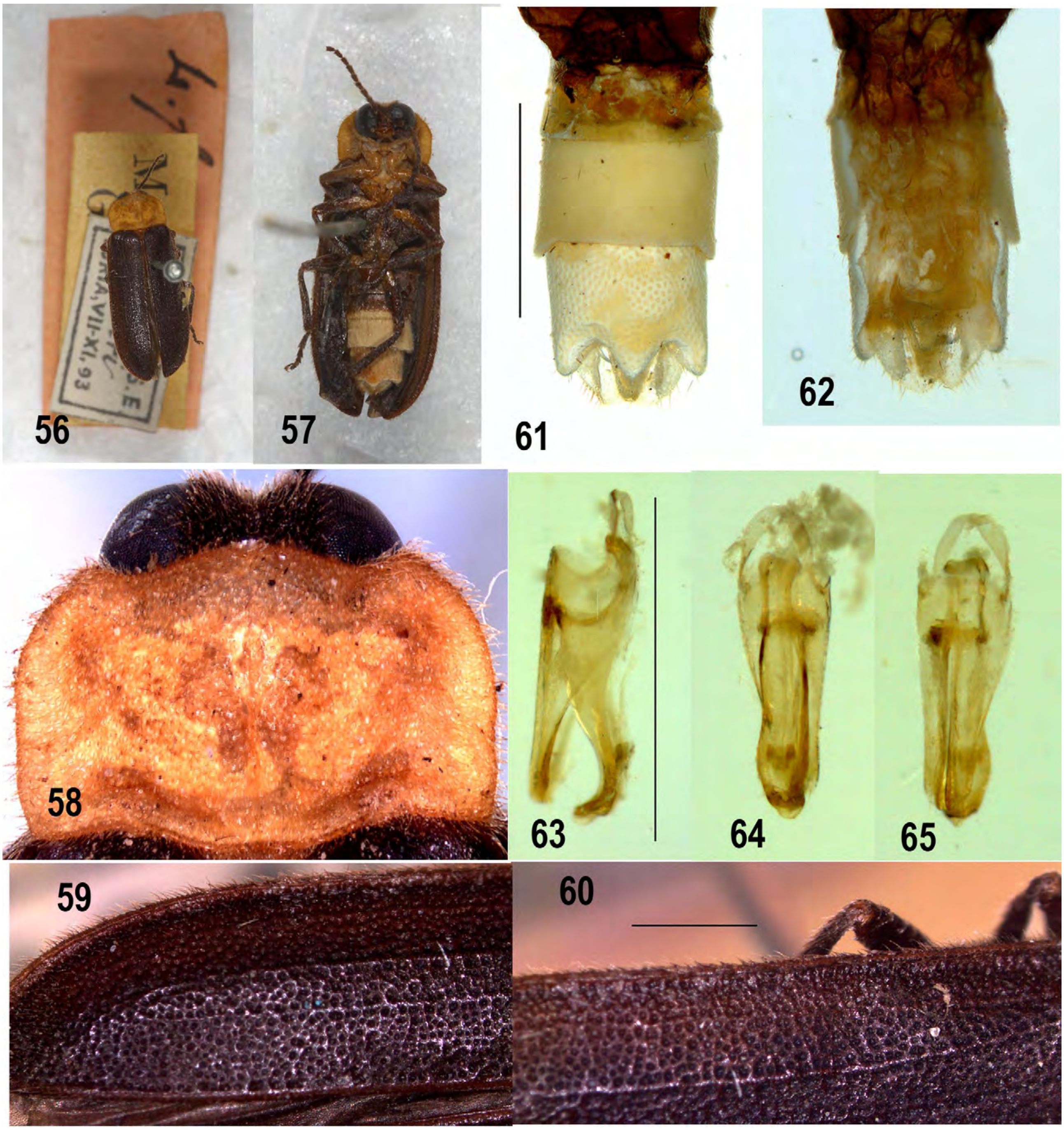
Lectotype. Male. **NEW GUINEA** 09.25S 147.35E, Central Province: labelled 1. New Guinea S. E. Haveri, Loria, VII–XI, 1893; 2. Typus in red print; 3. handwritten label foveicollis E. Oliv.; designated here (MCSN).

Other specimens examined. NEW GUINEA: 8.30S, 151.06E Milne Bay Province Kiriwini, Trobriand Island iii–iv–v.1895 A S Meek male (MNHN). 08.55S, 148.10E, Mt Lamington 1300–1500 feet C T McNamara 10 males 4 females (SAMA). 09.25S 147.35E, Central Province, Haveri vii–ix (18)93, Loria, male bearing pink handwritten label "L foveicollis Ern Oliv."(MNHN) Olivier Box 72. Paumomu Riv. Loria ix–xii (18) 92 male (MNHN). 9.30S, 150.40E Milne Bay prov., Fergusson Is ix x xi xii (18)94 A S Meek female (Pic box 40 id by Pic), male (Olivier box 72) (MNHN). Mamai Plantation near Port Glasgow 60 m, 12.11.1965 male RS (BPBM).

Diagnosis. One of three New Guinean *Australoluciola* with orange pronotum, dark elytra and trisinuate posterior margin of V7. Distinguished by the larger irregularly shaped punctures across parts of the elytra; distinguished from *Aus. anthracina* most obviously by the pale T7, 8 (those of some *anthracina* are dark), and from *Aus. pharusaurea*, which has only been recorded on New Britain, by the dark head (that of *pharusaurea* is golden yellow between the eyes).



FIGURES 45–55. *Australoluciola* spp**.** 45, 54, 55 *Australoluciola flavicollis*, male 45, female 54, 55 (ANIC). 46 *Luciola coarcticollis* type male (MNHN). 47 *Luciola gestroi* type male (MNHN). 45–47 dorsal; 48 ventral V4–7 and T8; 49–51 aedeagus left lateral (49), ventral (50) and dorsal; 52, 53 aedeagal sheath with aedeagus ventral (52) and dorsal; 54, 55 female bursa from side (54) and beneath (55). Figure legends: 2 posterior plates; 3 anterior plates. These figures share scale lines:49–51; 52, 53.



FIGURES 56–65. *Australoluciola foveicollis* male (56–60 Haveri, MNHN; 61–65 Mt Lamington SAMA). 56 dorsal; 57 ventral; 58 detail pronotum; 59, 60 lateral margins of elytron, posterior (59) and anterior half; 61, 62 abdomen ventral (61) and dorsal; 63–65 aedeagus right lateral (63), ventral (64) and dorsal. These figures share scale lines: 59, 60; 61, 62; 63–65.

Male. 8.0–9.2 mm long (lectotype 8.3mm). Colour (Figs 56, 57): pronotum pale yellow-orange; pale semitransparent areas of pronotum reveal fat body beneath; MN pale yellow; MS yellowish, brown posteriorly in lectotype, or pale yellowish brown; elytra shiny, dark often reddish brown, with sutural ridge narrowly paler in lectotype, sutural ridge and lateral margins narrowly reddish brown in Paumomu and some Mt Lamington males; head, labrum, antennae and palpi medium to dark brown; ventral surface of prothorax yellow; coxae, trochanters and basal 1/3 femora 1, 2 yellow, remainder of legs 1, 2 brown; ventral surface of mesothorax yellowish, semitransparent; ventral surface of metathorax medium brown; coxae 3 light brown, trochanters and bases of femora pale, semitransparent, remainder of legs 3 medium to dark brown; basal abdominal ventrites medium brown, may be semitransparent; posterior margin of V5 narrowly pale; LOs in V6, 7 yellowish; T6–8 clear cream, semi-transparent; basal abdominal tergites medium brown, semi-transparent. Pronotum (Fig. 58): 1.4–2.9 mm wide, 0.9–1.7 mm long; W/L = 1.5–1.7; densely clothed in short yellow hairs; surface dull; punctures contiguous; midanterior margin gently rounded, projecting only a little beyond broadly rounded anterolateral corners with lateral margins subparallel-sided (B=C) in lectotype and Trobriand male where anterolateral corners are angulate; lateral margins usually strongly divergent posteriorly with anterolateral corners acute, posterolateral corners usually acute, broadly rounded in Paumomu River male. Elytron (Figs 59, 60): 3 slightly elevated interstitial lines visible; punctures over lateral surface broader than pronotal punctures and somewhat irregular in outline. Head: moderately excavated between the eyes; GHW 1.6 (lectotype)–2.0 mm; SIW 0.3 mm; ASW = ASD in lectotype, ASD < ASW in remainder; FS subequal in length. Abdomen (Figs 61, 62): LOs occupying V6, 7 entirely except for narrow posterior margin of 7 and extending into MPP and PLP; MPP of V7 rounded, W>L and longer than PLP; posterior margin of T8 gently trisinuate with lateral margins diverging anteriorly (Fig. 62); ventral face of T8 gently concave in median area, with lateral ridges slightly developed, and flanges absent. Aedeagus (Figs 63–65): relatively short and wide anterior prolongtion of ML; lateral margins of LL straight, not expanded in apical ½, apices obliquely truncate; L/W=3.5.

Remarks. A lectotype male (first in a syntype series) was designated to overcome inconsistent descriptions of this species, which did not allow adequate categorisation of *foveicollis.* Olivier (1909a) recorded *foveicollis* from Haveri in Central province (Sogeri Plateau) on the mainland of New Guinea, and described unusual pronotal sculpturing. LB saw nothing distinctive on the lectotype and other Haveri specimens pronotum (Fig. 58) except the midposterolateral depressed areas which Olivier did not highlight. However *Medeopteryx sublustris* has distinctive pronotal sculpturing (Fig. 184), but resembles *foveicollis* in colouration only. The male of *Aus. aspera* has distinctive pronotal sculpturing, but differs from *Aus. foveicollis* in pronotal colouration (Fig. 25). Olivier (1909a) described the "apparent" similarity of *foveicollis* to the female of *aspera*. Olivier (1913b) recorded the species from Haveri*, Paumomu River, Kiriwini*, Trobriand* and Fergusson* of which the last three are islands (the Trobriand Islands are now officially known as the Kiriwina Islands). Specimens from * have been relocated and are addressed here.

Australoluciola fuscamagna sp. nov.

[Figs 66–74]

Holotype. Male. **NEW GUINEA**: 7.20S, 146.45E, Morobe Pr., 4 mi n Wau. elev. c 2800' nr Kunai Creek Lae Rd. 1969, J.E. Lloyd (G322) (ANIC).

Paratypes (4). All same locality as holotype; Oct. 17 male (G317); Nov. 12 male (G568) (JELC); Nov. 12 male (G579); Nov. 14 male (G608) (ANIC).

Code names. *Luciola* 7, "Big Black" (Lloyd, 1973a).

Diagnosis. Males dark brown (see Table 9) except for white posterior margin of V5, white LOs in V6, 7 and pale T6–8; distinguished from the similarly coloured *Aus. fuscaparva* **sp. nov.** by its larger size and light patterns, and from *Tri. papuana* by the entire LO in V7.

Male. 6.2–6.6 mm long. Colour (Figs 66, 67, 68, 71): entirely dark brown except for white posterior margin of V5 (Fig. 68), white LOs in V6 and 7, pale semitransparent T6–8, and white dorsally reflexed margins of V6 and 7; pronotum viewed under strong illumination is paler in convex areas and very dark brown in concave areas. Pronotum (Fig. 71): 0.8–1.2 mm long; 1.2–1.4 mm wide; W/L = 1.1–1.5; midanterior margin rounded, projecting moderately beyond angulate anterolateral corners; lateral margins subparallel-sided (A=B=C); punctures small, shallow, separated over most of the disc by twice their width. Elytra (Fig. 66): 5.4 mm long; shiny, punctures dense, many contiguous. Abdomen (Figs 67, 68): V3, V4 posterior margins not recurved; posterior margin of V7 trisinuate; LOs in V7 occupying most of the area and reaching to sides but not to posterior margin; MPP apically rounded, L=W; as wide as and slightly longer than PLP. T8: Ventral surface of T8 with well developed lateral ridges without flanges, anterior inner area of ridges rounded; anterolateral prolongations of T8 wide, not as long as posterior entire portion. Aedeagus (Figs 69, 70): anterior prolongation of ML short and wide; lateral margins of LL straight, converging posteriorly with apical ½ of lateral margins not visible beside ML; apices LL obliquely truncate and narrow; L/W=4.0.

FIGURES 66–74. *Australoluciola* spp. 66–71 *Aus. fuscamagna* **sp. nov.** holotype male (ANIC). 72–74 *Aus. fuscaparva* **sp. nov.** holotype male (ANIC). 66, 72 dorsal, 67 ventral; 68, 73 terminal abdomen with LO; 69, 70 aedeagus ventral (69) and left lateral; 71, 74 pronota, dorsal. These figures share scale lines 69, 70.

Remarks. The specific name *fuscamagna* emphasizes the dark dorsal colouration (Latin, fuscus = dark or black) and the size difference (magnus = big) between this and *fuscaparva (Luciola* species 8, "Little Black") to which it is most similar. Males "emitted a rapid, 1–sec flicker of 7–11 modulations each 3–4 sec" (Lloyd, 1973a).

TABLE 9. Luciolinae males with dark brown, grey or black dorsal colouration.

Species	Locality	Reference
Aus. fuscamagna **sp. nov.**	New Guinea	
Aus. fuscaparva **sp. nov.**	New Guinea	
Luciola antipodum (Bourgeois)	New Caledonia	Ballantyne & Lambkin 2009
L. hypocrita (Olivier)	Fiji	Ballantyne & Lambkin 2009; Deheyn & Ballantyne 2009
L. aquilaclara **sp. nov**.	New Caledonia	
L. oculofissa **sp. nov**.	New Caledonia	
L. flebilis Olivier	Sumatra	Olivier 1909
L. picea Gorham	Sumatra	Gorham 1882
Magnalata carolinae (Olivier)	Caroline Islands	Olivier 1911a; Ballantyne & Lambkin 2009
Trisinuata papuana (Olivier)	New Guinea	Olivier 1913b
Tri. papuae (McDermott)	New Guinea	McDermott 1959; Ballantyne & McLean 1970; Ballantyne 1987a
Tri. similispapuae (Ballantyne *et* McLean)	New Guinea	Ballantyne & McLean 1970; Ballantyne 1987a

All listed species are characterised by recent taxonomic treatments except for *Luciola flebilis* and *L. picea* from Sumatra, both of which have entirely dark colouration except for the white V5–7, and may have been based on the same species.

Australoluciola fuscaparva sp. nov.

[Figs 72–74]

Holotype. Male. **NEW GUINEA**: 7.20S, 146.45E, Morobe Pr., 4 mi n Wau elev. c 2800', nr Kunai Creek, Lae Road, Oct. 18, 1969, J.E. Lloyd, (G352) (ANIC).

Paratypes. Same locality as holotype, Oct. 18 3 males (G348); Nov. 13 male (G590) (JELC); Oct. 17 male (G315); Nov. 16 male (G613); Nov. 12 male (G573); Oct. 18 male (G350) (ANIC).

Code Names. *Luciola* 8, "little black" (Lloyd, 1973a).

Diagnosis. Males dark brown (see Table 9) except for white posterior margin of V5, white LOs in V6, 7 and pale T6–8; distinguished from *Aus. fuscamagna* by its smaller size and different light patterns. Table 9 lists Luciolinae species having dark dorsal colouration.

Male. 3.5–4.5 mm long. Colour (Figs 72, 74): entirely dark brown except for white V6 and 7 (LOs), white posterior 1/5 of V5, pale semitransparent T6–8 (Fig. 72), and small reddish brown elevated areas of pronotal disc. Pronotum (Fig. 74): 0.8–1.2 mm long, 0.9–1.4 mm wide; W/L = 1.2–1.3; median anterior margin projecting moderately beyond angulate anterolateral corners; lateral margins subparallel-sided (A=B=C); punctures shallow, separated at most by their width; median convex areas of disc smooth, shiny, almost apunctate. Elytra (Fig. 72): shiny, punctures dense, subcontiguous. Abdomen (Figs 72, 73): V3, V4 with posterior margins not recurved; posterior margin of V7 trisinuate (some ethanol preserved specimens appear to have PLP not produced); LOs in V7 occupying most of the area and reaching to sides but not to posterior margin; MPP apically rounded, L=W; as wide as and slightly longer than PLP (Figs). T8: Ventral surface of T8 with well developed lateral ridges without flanges, anterior inner area of ridges rounded; anterolateral prolongations of T8 wide, not as long as posterior entire portion. Aedeagus: anterior prolongation of ML short and wide; lateral margins of LL straight, converging posteriorly with apical ½ of lateral margins not visible beside ML; apices LL rounded; L/W=4.0.

Remarks. This species is named for its similarity to *Aus. fuscamagna* and its smaller size (Latin, fuscus = dark, or black; parvus = small). *Aus. fuscaparva* flew in "a jerky, erratic manner while emitting 3–8 (usually 4–6) rapid flashes; each flash had a duration of ca 0.14 sec." in contrast to *Aus. fuscamagna* which "emitted a rapid, 1 sec. flicker" (Lloyd 1973b). Lloyd (1977) remarked "the flicker frequency of the little black *Luciola* is about half that of its relative" (*Aus. fuscamagna*).

Australoluciola japenensis **sp. nov.**
[Figs 38–44]

Holotype. Male. **INDONESIA** (as Dutch New Guinea): 1.45S, 136.08E, Japen Island Mt Baduri 1000 feet viii.1938 LEC (NHML).

Paratypes (13). Same locality as holotype, 2 males, 11 females (NHML).

Diagnosis. Dorsal surface yellowish orange except for narrow dusky brown apex of elytra; distinguished from all other *Australoluciola* by the dorsal colouration; one of two *Australoluciola* with expanded and curved femora 3 and the curved tibiae 3 in the male (similar to Fig. 37). Distinguished from *Aus. baduri* **sp. nov**. by the elytral colouration; MPP longer than wide, considerably longer than the rounded posterolateral corners of V7 (Fig. 44).

Male. 4.8–5.5 mm long. Colour: pronotum, MS, and elytra yellowish orange, elytra with restricted dusky apical area; MN whitish due to underlying fat body; head between eyes yellowish, labrum brown, antennae and apical palpomeres dark brown; ventral surface of body (excluding LOs) yellowish except for brown apices of femora 1, 2 and brown tibiae and tarsi 1, 2; LO in V6, 7 whitish, extending into PLP and MPP except for a very narrow posterior margin; dorsal surface of abdomen including terminal tergites yellowish. Pronotum: 1.4–1.5 mm wide, 0.8–1.0 mm long; W/L = 1.5–1.8; midanterior margin rounded, not projecting beyond angulate anterolateral corners; lateral margins subparallel-sided (A=B=C or B=C); punctures contiguous or separated by up to their width. Elytra: pin punctate, often irregularly so along margins, punctures separated by their width. Head: gently excavated between eyes; GHW 0.9–1.0 mm; SIW 0.2 mm; ASD > ASW. Abdomen (Fig. 44; similar to Figs 35, 36): V3, V4 posterior margins not recurved; posterior margin of V7 trisinuate, posterolateral corners rounded, not produced as far as MPP (Fig. 44); LOs in V7 occupying most of the area and reaching to sides and well into PLP and MPP except for a very narrow posterior margin; MPP apex truncate slightly rounded, L>W. T8: posterior margin straight (Fig. 44); ventral surface with lateral ridges effaced anteriorly, no flanges. Aedeagus (Figs 39 -41): anterior portion of ML slender and prolonged (arrowed in Figs); lateral margins of LL straight, tapering to apex; apices of LL narrowly rounded; L/W 5.0. Aedeagal sheath (Figs 42, 43).

Female. Associated by label data only. Macropterous, coloured as for male except for ventral abdomen where ventrites preceding LO are brownish; LO white; V7, 8 semitransparent yellowish. Bursa plates (Fig. 38) observed through whole abdomen soaked in cold KOH, wide and paired.

Etymology. The specific name (latinised, genitive case) derives from the type locality, meaning "of japen".

Remarks. Two species of *Australoluciola* bear swollen hind femora and curved tibiae, a feature seen in most species of *Pyrophanes*, but lack the MFC. The possible functions of such male leg modifications are discussed subsequently.

Australoluciola maxima **sp. nov.**
[Figs 75–82]

Holotype. Male. **NEW GUINEA**: 3.22S 142.14E, West Sepik Province, Torricelli Mt Sea Falls near Afua, 1700 feet 1939 P G Moore (NHML).

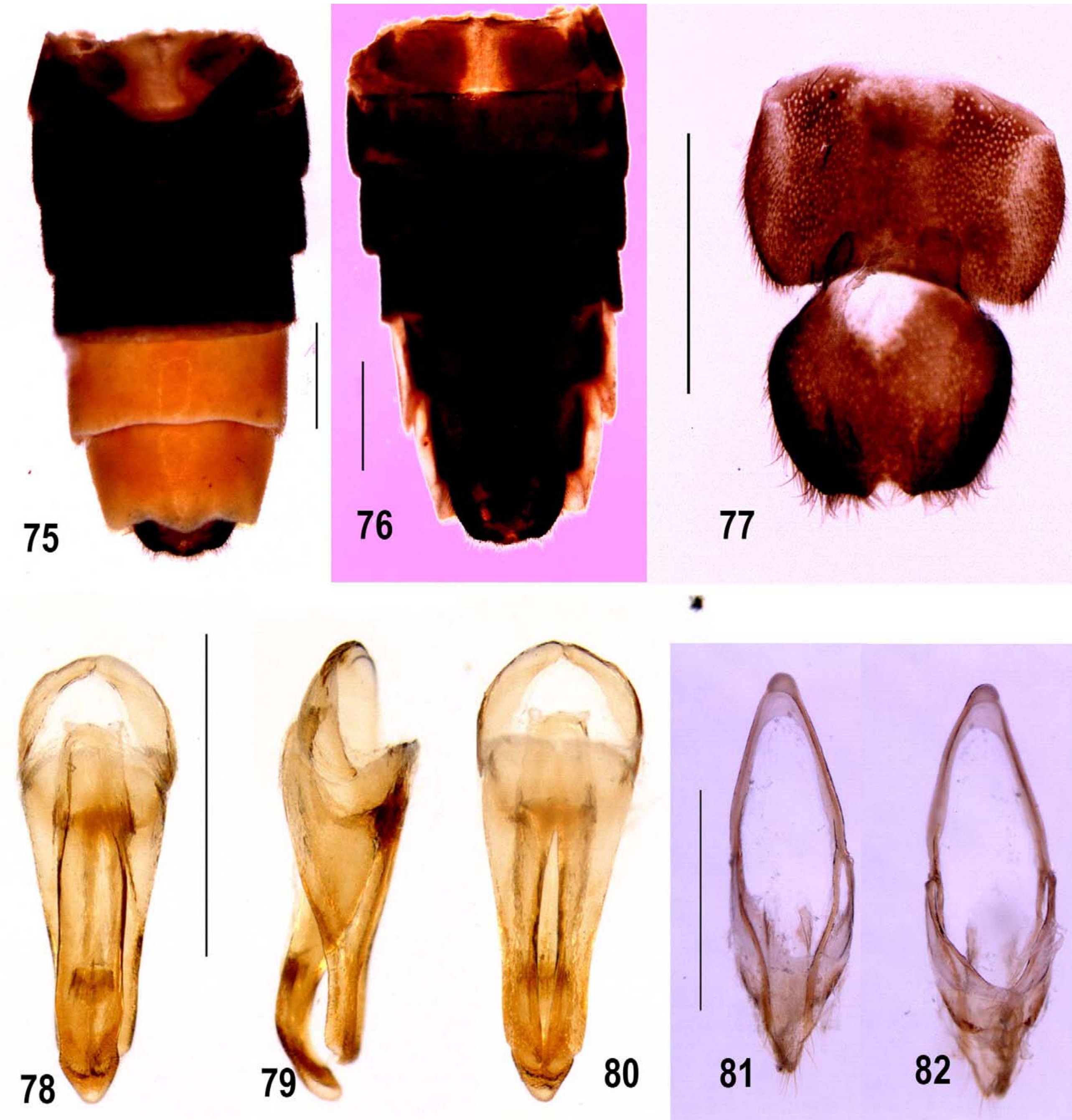
Paratype (1). Male, same data as holotype (NHML).

Diagnosis. The largest species of *Australoluciola* (9.9–10 mm long) with orange pronotum, dark brown non margined elytra and trisinuate posterior margin to V7; abdominal tergites dark brown.

Male. 9.9–10 mm long. Colour (Figs75–77): pronotum and MN orange, MS dusky brown, elytra very dark brown; all of ventral surface including head mouthparts and antennae, very dark brown except for white LO in V6, 7, and white posterior margin of V5; basal portion of MPP behind LO clear semitransparent, tip of MPP very dark brown; LO in V6, 7 whitish, extending into PLP and MPP except for a narrow posterior margin; dorsal surface of abdomen including terminal tergites dark brown (Figs 76, 77). Pronotum: 2.9 mm wide, 1.7–1.9 mm long; W/L = 1.5–1.7; midanterior margin rounded, barely projecting beyond anterolateral corners; lateral margins divergent posteriorly (C, B>A); punctures contiguous or separated by less than their width. Elytra: pin punctate, punctures separated by their width; two to three weakly defined interstitial lines visible. Head: strongly excavated between eyes; GHW 1.9–2.0 mm; SIW 0.3 mm; ASD < ASW. Abdomen (Figs 75–77): V3, V4 posterior margins not recurved; posterior margin of V7 trisinuate, posterolateral corners rounded, not produced as far as MPP; LOs in V7 occupying most of the area and reaching to sides and well into PLP and MPP, except for a narrow posterior margin; MPP apex slightly rounded, L>W. T8: posterior margin slightly obliquely truncate beside median emargination (Fig. 77); ventral surface with lateral ridges rounded anteriorly, no flanges. Aedeagus (Figs 78–80): margins of ML subparallelsided; anterior prolongation of ML short and wide; lateral margins of LL straight, not expanded in apical ½; apices of LL obliquely truncate; L/W=3.2. Aedeagal sheath (Figs 81, 82).

Female and **Larva.** Unknown**.**

Etymology. Named for its size (Latin maximus, a, um large).



FIGURES 75–82. *Australoluciola maxima* **sp. nov.** holotype male (ANIC). 75–77 abdomen, ventral (75), dorsal (76), tergites 7, 8, dorsal (77); 78–80 aedeagus ventral (78), left lateral (79) and dorsal; 81, 82 aedeagal sheath ventral (81) and dorsal. These figures share scale lines: 78–80.

Australoluciola nigra (Olivier) comb. nov.

Luciola Gestroi var. *nigra* Olivier, 1885:366.
Luciola (Luciola) nigra Olivier stat. nov. Ballantyne in Calder, 1998: 179. Ballantyne & Lambkin 2000:63; 2009:21.
Luciola humilis Olivier, 1896:2; 1902:80; 1907:52. Lea, 1909:108; 1921a:7. Ballantyne in Calder, 1998:179.
Luciola (Luciola) humilis Olivier. McDermott, 1966:105. Ballantyne in Calder, 1998:179 (synonymy).
Luciola scutellaris Lea, 1929:344. Ballantyne in Calder, 1998:179 (synonymy).
Luciola (Luciola) scutellaris Lea. McDermott, 1966:113.

Holotype. Male. *Luciola humilis* **QUEENSLAND**: Cairns (NHML).

Other specimens examined. **NEW GUINEA**: 8.51S, 143.11E, Western district Oriomo 3m, 6.viii.1964 H Clissold male (BPBM). 146.40E, 7.22S, Wau Morobe Dist Big Wau Creek 1300m xi.1965 JLG malaise trap male (BPBM).

Diagnosis. Males small to medium (4.8–7.6 mm long); pronotum orange, MS orange or black; elytra very dark brown, almost black; ventral surface of metathorax, and of V2–5 black; white LO occupying all of V6 (lateral margins sometimes dark brown); LO restricted to median basal area of V7, which is otherwise black; pronotal punctures small, shallow, mostly contiguous; MPP of V7 conspicuously produced, and may be slightly emarginate at apex; ventral surface of T8 with lateral ridges without flanges. Female macropterous, coloured as for male except for pale cream LO in V6. Larva dorsally pale with a broad pale median band (Ballantyne & Lambkin 2000 Fig. 22c), distinguished from the very similar larvae of *Aus. australis* and *Aus. orapallida* in without marginal tubercles along the anterior margin of the protergum.

Australoluciola orapallida (Ballantyne) comb. nov.

Luciola (*Luciola*) *orapallida* Ballantyne. Ballantyne & Lambkin 2000:67.

Holotype. Male. **QUEENSLAND**: 13.57S, 143.12E, Cape York Peninsula, east coast, Silver Plains: Massey River, 12.xii.1964, salt-water couch, L. Powell (QMBA T62935).

Diagnosis. Male 6.0–7.2 mm long; similar to *Aus. australis* (F.) and *Aus. flavicollis* (Macleay), distinguished by the broad pale lateral bands on the elytra, the pale colour of the venter and the outline of V7, and the narrow, widely separated aedeagal LL. Female macropterous, coloured as for male. Presumed larva similar to that of *Aus. australis* (Ballantyne & Lambkin 2000 Fig. 22b).

Australoluciola pharusaurea sp. nov.
[Figs 83–91]

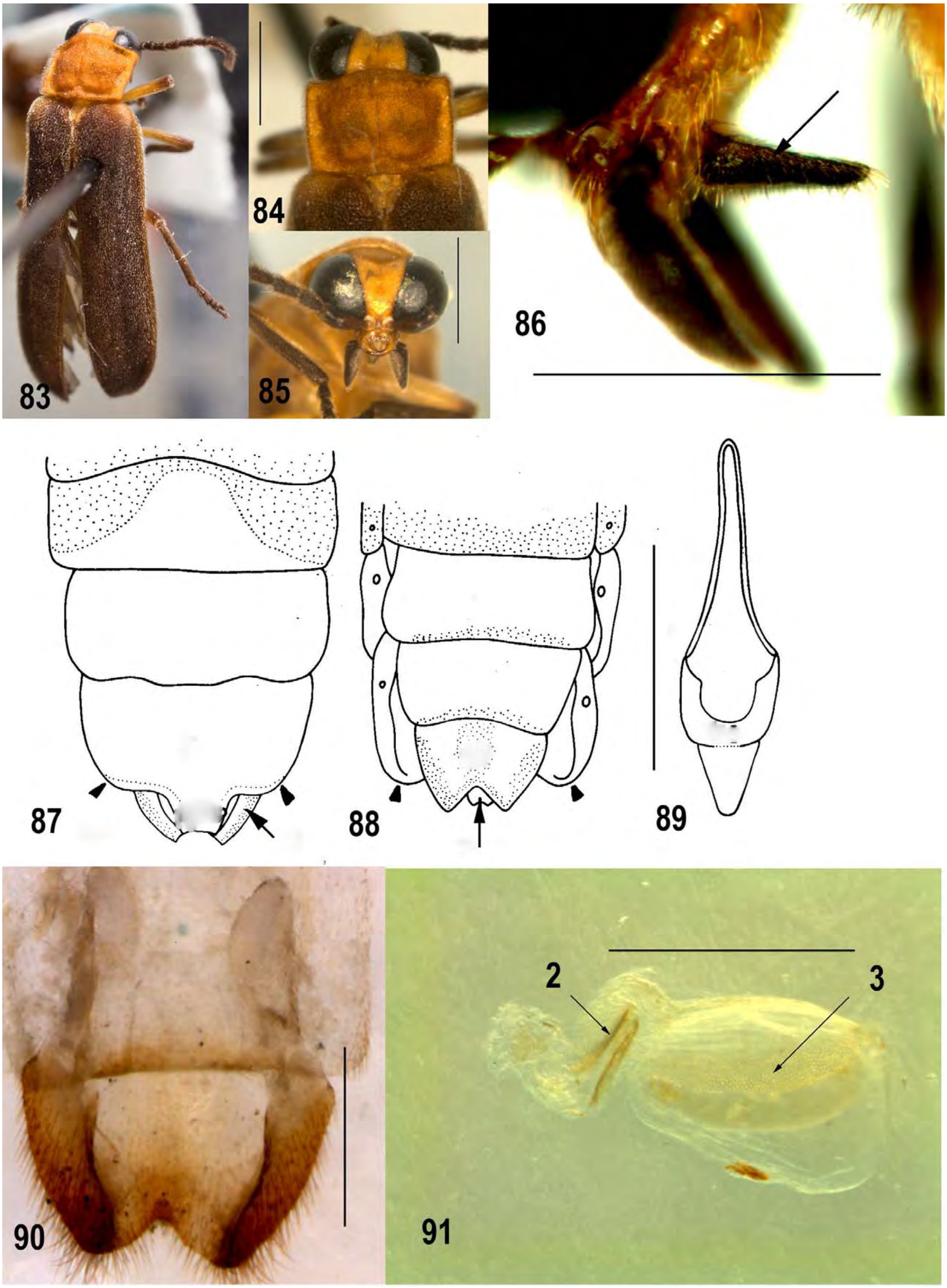
Holotype. Male. **NEW GUINEA**: 4.12S, 152.11E, New Britain, Gazelle Pen., 8.2 miles S. Rabaul, Nov. 23, 1969, J.E. Lloyd (G642) (ANIC).

Paratypes (8). Same locality as holotype, 4 males, female Nov. 23 1969 (G638, 639, 640, 643, 645) (JELC); Rabaul, Nov. 24 1969 J.E. Lloyd 3 males, female (G648) (ANIC). Kerevat, 19.Xi.1969, J. Buck 2 females (Tube KE/31 #31/III/21) (ANIC).

Code Name. *Luciola* 4 (Lloyd, 1973a).

Diagnosis. Pronotum orange, elytra dull reddish brown; head between eyes yellow; posterolateral corners of V7 rounded, not appearing produced in dried pinned specimens.

Male. 5.5—6.8 mm long. Colour (Figs 83–86): pronotum dull deep orange; retraction of fat body beneath cuticle leaving irregularly shaped darker areas; pronotal punctures margined in deeper orange; MS and MN yellow; elytra deep reddish brown, dusky brown on humeral angle, basal 1/4 of epipleuron and basal 1/8 of sutural ridge narrowly dusky orange; (pubescence of dorsal body appears golden yellow under high illumination; if not so illuminated elytral surface appears dull); head between eyes pale clear yellow, semitransparent (Fig. 85); labrum light brown; apices of palpi dark brown; scape and pedicel dark red brown, shiny, FS dull dark brown; pro and mesosterna and pleura yellow; coxae, trochanters 1, 2 and femora 1, 2 yellow; tibiae, tarsi and apices of femora 1, 2 dark brown; ventral surface of metathorax medium brown; coxae 3 brown; anterior face trochanters 3 brown,



FIGURES 83–91. *Australoluciola pharusaurea* **sp. nov.** (83–89 holotype male ANIC; 90 paratype male G648 ANIC; 91 paratype Kerevat female ANIC). 83 dorsal; 84 pronotum dorsal; 85 anterior head; 86 left lateral apical palpomeres maxilla and labium, apical labial palpomere arrowed; 87, 88 abdomen ventral (87) and dorsal; 89 aedeagal sheath dorsal; 90 Tergite 7, 8 ventral; 91 bursa lateral. Figure legends: 2 posterior plate, 3 anterior plate.

posterior face yellow; femora 3 yellow except for brown apical fourth; remainder of legs 3 brown; basal abdominal ventrites dark brown; V5 dark brown, with irregular white markings across posterior margin (Fig. 87); V6 and 7 white; basal abdominal tergites dark brown; terminal 3 tergites very pale brown, semitransparent, T8 narrowly brown along lateral and posterior margins (Figs 88, 90); dorsally uprolled lateral margins of V6 and 7 creamy white (Fig. 88). Pronotum (Fig. 84): 1.6 mm wide, 1.2 mm long; W/L = 1.3; midanterior margin broadly rounded, projecting considerably beyond angulate anterolateral corners; lateral margins subparallel; punctures contiguous over most of disc. Elytra (Fig. 83): dull, with dense subcontiguous punctures. Head: GHW 1.3–1.4 mm; SIW 0.2 mm; ASD <ASW. Abdomen (Figs87, 88): posterior margin of V7 not trisinuate, posterolateral corners appearing rounded and not produced posteriorly in pinned specimens, and slightly angulate in ethanol preserved specimens; LOs occupying most of V7, reaching sides but not posterior margin; MPP medianly shallowly emarginated or truncate, L=W. T8 (Fig. 90): Ventral surface with well developed lateral ridges and short, wide rounded flanges. Aedeagus: prolongation of ML short and wide; lateral margins of LL straight, not expanded along outer ½; apices obliquely truncate; L/W=6.0. Aedeagal sheath (Fig. 89).

Female. 4.5 mm long; coloured as for male except for narrowly white posterior margin of V5; white LO in V6 only; V7 pale in median area (due to fat body), dark laterally and along posterior margin; V8 brown. Bursa plates (Fig. 91).

Etymology. The specific name, *pharusaurea* [pharus (Greek) = lighthouse and aureus (Latin) = golden] emphasizes the pattern of light production observed for one male which "emitted 40 consecutive flashes without an omission" (Lloyd, 1973a), as well as the golden colour of the head and pronotum.

Remarks. McDermott (1966) recorded only *Luciola leucura* Olivier from New Britain, but listed six New Guinea species having orange pronotum, and uniformly dark elytra. All were described with a trisinuate posterior margin to V7, inconsistent with this species. Of these *Luciola venusta* and *L. timida* may not be from New Guinea and are discussed; *Aus. foveicollis* and *M. pupilla* are characterised here. Olivier (1885) based *Luciola anthracina* on a female; male specimens assigned subsequently (Olivier, 1913b) were described with trilobed V7 and the ventral surface of the abdomen black except for the white V6 and 7 and white posterior margin of V5 (males are redescribed here). *Aus. pharusaurea* differs from *Aus. anthracina* in its distribution, ventral colouration, and non trisinuate posterior margin of V7. *Luciola ruficollis* was described with black head, V7 trilobed, ventral thorax reddish and ventral abdomen yellow [Guérin-Méneville (1838)]. McDermott's (1966) reference to Plate XXXV in Girard (1873) for *L. ruficollis* is to a species with lateral prolongations of the antennal FS, inconsistent with any known Luciolinae. Ballantyne (1987a) considered *Pteroptyx antennata* and *L. ruficollis* could be conspecific. *Aus. pharusaurea* differs from *L. ruficollis* in its darker ventral colouration and presently known distribution. The latter is not identifiable in collections, and is treated under *Species Incertae.*

Lloyd (1973a) observed that no more than two males of this species were seen flying at any one time, and that these "emitted series of single short flashes ... with a period of about 0.5 seconds", and he described the pursuit of a flying female by a male. *Aus. pharusaurea* is sympatric in New Britain with the orange head *Medeopteroptyx effulgens*, males of which flashed "single short flashes at a flash period of about 1.2 secs", contrasting with a flash period of 0.5 secs for *Aus. pharusaurea*. These two orange headed species from New Britain are morphologically distinctive, differing in colour, punctation of pronotum and elytra, pronotal outline, and possession of the deflexed elytral apex.

Colophotia Motschulsky

[Figs 92–108]

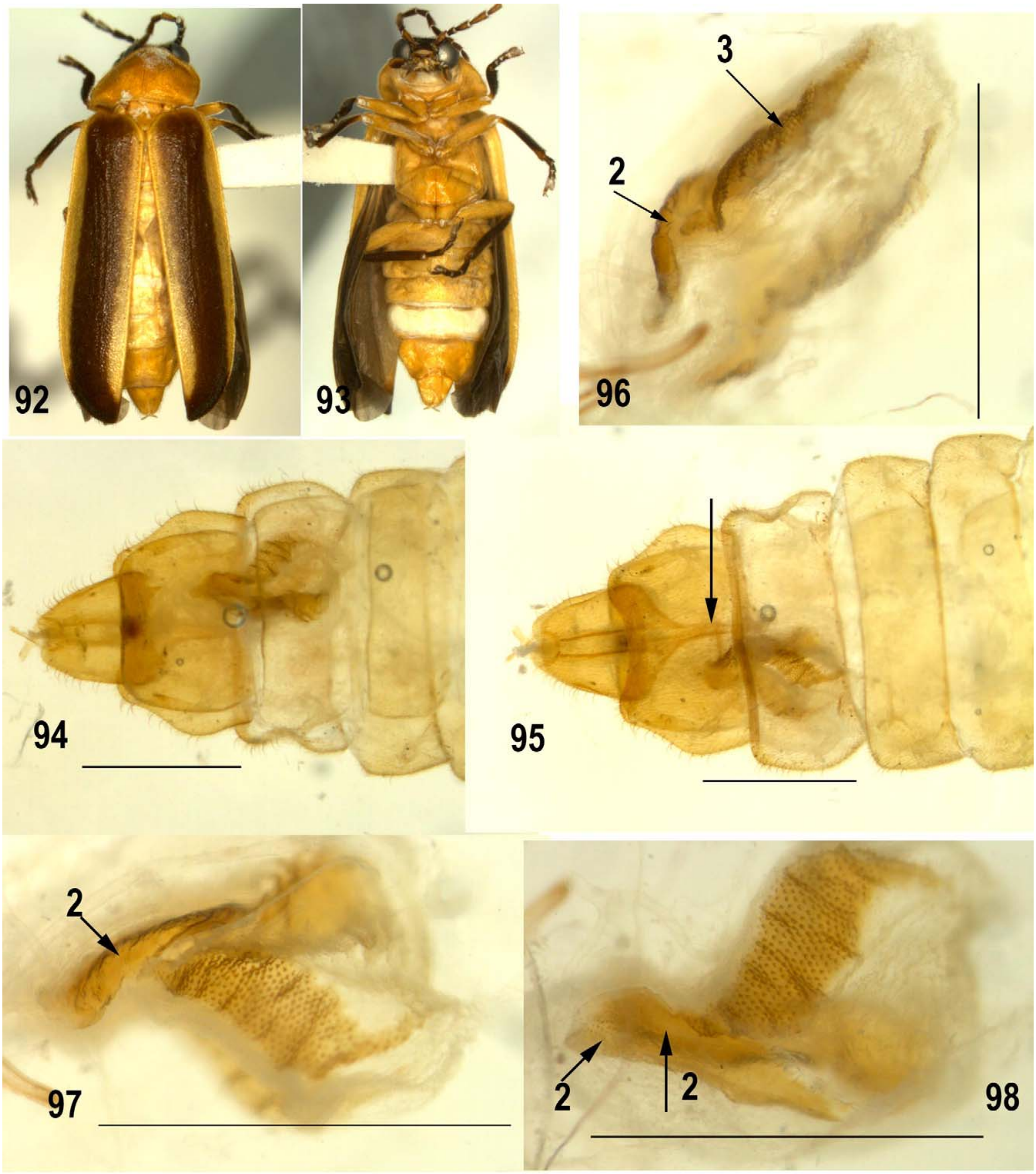
Colophotia Dejean, 1833:103 (catalogue name only).

Colophotia Motschulsky, 1853: 51. Olivier, 1885: 367; (in Baer), 1886: 132; 1907: 56; 1910b: 48; 1911b: 102; 1913a: 59. McDermott, 1966: 116. Ballantyne, 1968: 106; 1987b: 173, 175–177. Ballantyne and McLean, 1970: 234. Ballantyne & Lambkin 2009:155, Figs 98–105).

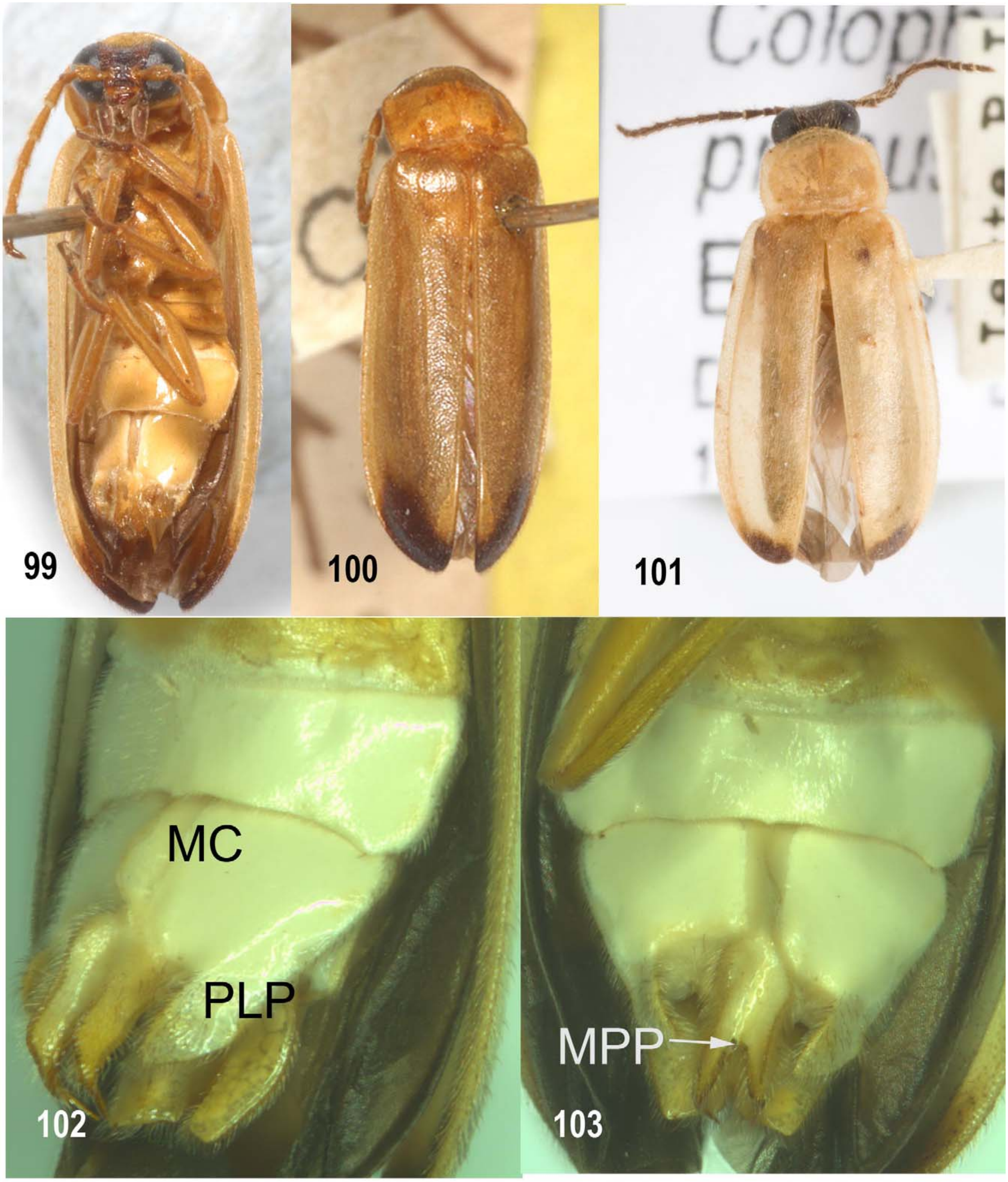
Type species: *Lampyris praeusta* Eschscholtz, 1822, designated by Motschulsky (1853).

Diagnosis. *Colophotia* is probably a heterogeneous assemblage of species and this definition is based on three species (*praeusta*, the type species, *concolor* and *plagiata*) scored by Ballantyne and Lambkin (2009) and herein. Males most obviously distinguished by the bipartite LO in V7 separated by a longitudinal carina (Figs 99, 102, 103, 107, 108), oblique PLP, deeply emarginate MPP prolonged into two hooks curving dorsally, FS 7–9 conspicuously shorter than remaining FS [Fig. 101), anteriorly prolonged anterolateral corners of T7, very elongate paired anterior prolongations of T8, very elongate aedeagal sheath and shortened aedeagal LL (Fig. 198) (Ballantyne & Lambkin 2009 Figs 98–105).

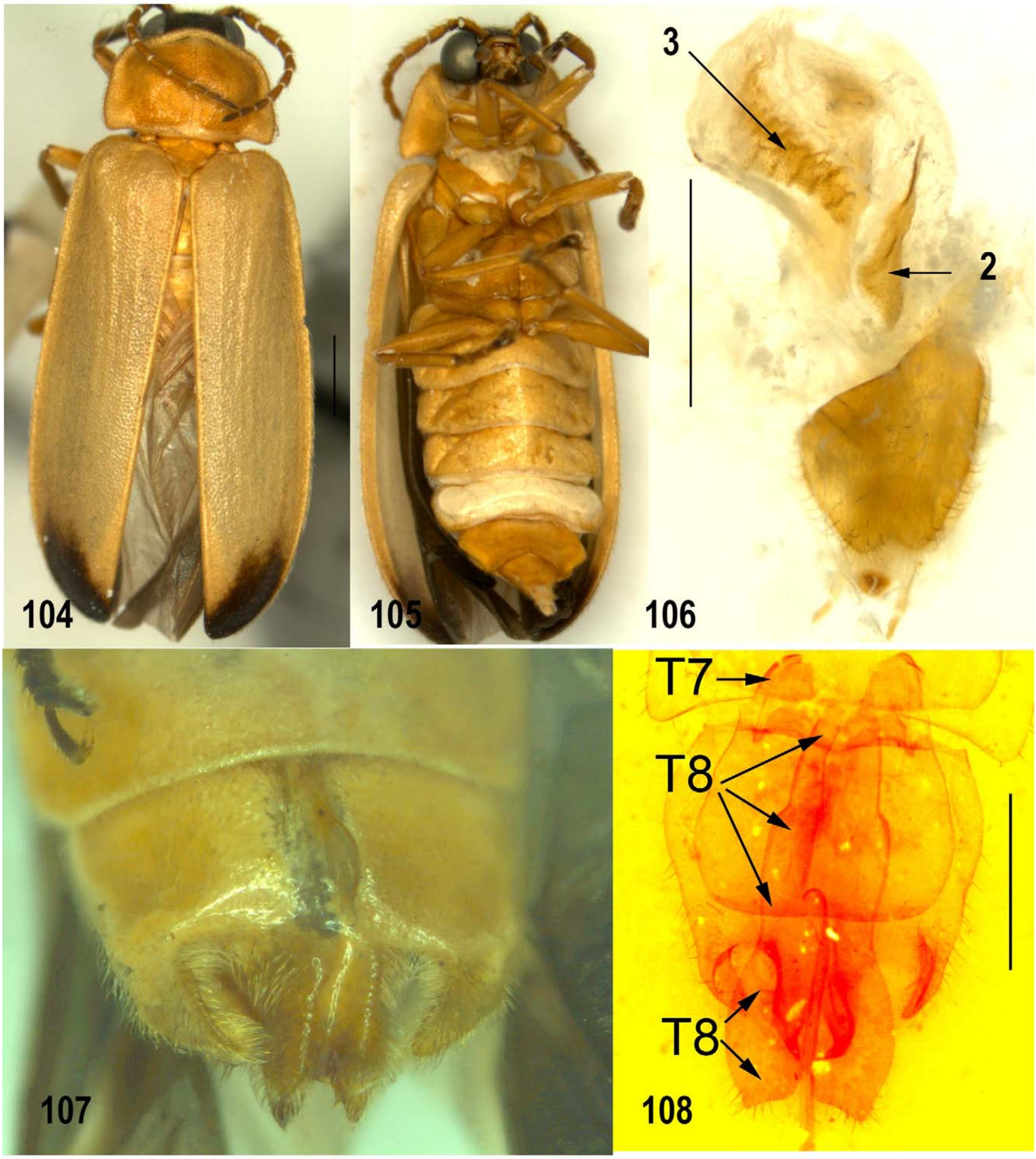
Female (Figs 92–98, 104–106)**.** Macropterous and assumed capable of flight. Pronotal outline similar to that of male. No legs or parts thereof swollen and /or curved. Median posterior margin of V7 widely emarginate, median area not broadly rounded. Bursa with wide paired plates on each side, anterior pair larger and inner margins rugulose (Figs 94–98, 106).



FIGURES 92–98. *Colophotia plagiata* bred female (USNM). 92, 93 dorsal (92) and ventral body; 94, 95 dorsal (94) and ventral abdomen (soaked in cold KOH), anterior apodeme of V8 arrowed in 95; 96–98 bursa ventral (96), and lateral (97, 98). Figure legends: 2 posterior plate; 3 anterior plate.



FIGURES 99–103. *Colophotia praeusta* male. 99 ventral (MNHN); 100, 101 dorsal (100 MNHN; 101 USNM); 102, 103 abdomen ventral LO segments ventrolateral (102) and ventral. Figure legends: MC median carina V7; MPP median posterior projection V7; PLP posterolateral projections V7.



FIGURES 104–108. *Colophotia* females. 104–106 *Colophotia praeusta* female (USNM). 107, 108 *C. plagiata* male (USNM). 104, 105 dorsal (104) and ventral; 106 bursa and V8 ventral (2 posterior plate; 3 anterior plate); 107 abdomen LO segments ventral; 108 abdomen cleared in cold KOH from beneath. Figure legends: T7 tergite 7 anterior prolongations right side; T8 tergite 8.

Larva. (Associated by breeding for *C. praeusta* only). Terrestrial; elongate, slender spindle shaped (Ballantyne and Lambkin 2009 Fig. 517), of the form of *Pteroptyx maipo* and several Australian *Australoluciola* sp. larvae (Ballantyne & Lambkin 2000; Ballantyne *et al* 2011).

Remarks. All references to *Colophotia* subsequent to and including Motschulsky (1853) attributes the genus to Dejean (1833). This latter reference is a catalogue name only. Motschulsky (1853) gave the first description and designated a type species.

McDermott (1966) listed ten species from either the Philippines or Indonesia. Few are well defined and the genus requires an extensive revision which is not currently possible here. Most are dorsally pale with black tipped elytral apices except for *C. plagiata* which has dark elytra, and the totally pale *C bakeri* Pic, *C. concolor* Olivier and *C. miranda* Olivier. *Colophotia miranda* was described with a single recurved appendage on the male terminal abdomen, suggestive of *Pygoluciola*, and subsequently (Olivier, 1913a) with 2 appendages. Its status is uncertain and it may have been based on a female. *Luciola truncata* Olivier, 1886 is known only from a female; McDermott (1966) erroneously assigned it to *Colophotia*. *C. brevis* Olivier lacks a median carina between LO halves and its status needs investigation (Ballantyne obs.). Blair's (1927) description of a *C. brevis* larva without laterally explanate tergal margins cannot be confirmed.

McDermott (1962:24) described "the apical ventral (abdominal) plate bears two parallel longitudinal hooked carinae with a slot between them through which projects a triangular plate", and considered figure 23b of the lateral aspect of the abdominal apex showed the "projecting aedeagus" and the "triangular plate". The aedeagus is not visible in this unlabelled figure and McDermott's reference is either to the bifurcate MPP of V7, with its well developed and dorsally curving hooks, or to the posterolateral projections of that ventrite; anterior to these and between the light organ halves is a median (single) carina projecting to the right of the figure. McDermott (1962) incorrectly represented the aedeagus of *Colophotia praeusta;* he probably extracted the aedeagus still enclosed in the aedeagal sheath and appears to have figured both.

List of species of *Colophotia* Motschulsky *Sensu* McDermott (1966)

- *bakeri* Pic
- *brachyura* Olivier
- *brevis* Olivier
- *concolor* Olivier
- *elongata* Pic
- *miranda* Olivier*
- *particulariventris* Pic
- *plagiata* Erichson
- *praeusta* Eschsch.
- *truncata* Olivier*
- * Species Incertae

Key to species of *Colophotia* using males

This is a key to the three species scored by Ballantyne and Lambkin (2009), Fu *et al.* (2012a) and here.

1. Elytra totally pale yellow dorsally; median carina between LO halves .low and wide; apical hooks on MPP strongly asymmetrical; posterolateral corners of T8 strongly prolonged (Ballantyne and Lambkin 2009 Figs 510–512) . . . .*concolor* Olivier
 Either elytra dark brown with pale lateral and sutural margins (e.g. as in Fig. 92), or if pale dorsally elytral apices dark brown (Figs 100, 101); narrow high median carina present between lightorgan halves (Figs 102, 103, 107); apical hooks on MPP not strongly asymmetrical; posterolateral corners of T8 not strongly prolonged (Ballantyne and Lambkin 2009 Figs 98–105) . . . 2
2 Dorsal colour pale brownish yellow with elytral apices dark marked (Figs 99–101) . . . . *praeusta* Eschsch.
 Dorsal colouration with pale yellow pronotum and brown elytra which are pale margined (as in Fig. 92). . . .*plagiata* Erichson

Luciola Laporte s. str.
[Figs 109–138]

Luciola Laporte. Laporte 1833:146. Lacordaire 1857:335. Motschulsky, 1853:52. Gorham 1880:99. Olivier 1902:69; 1907:50. Lea 1909:106.
Type species: *Luciola pedemontana* Motschulsky designated by Motschulsky 1853.
Luciola (Luciola) Laporte. McDermott, 1966:103 (Partim). Nec Calder, 1998: 178.
Lampyroidea Costa. Costa 1875:clxix. Olivier 1902:69; 1907:49; 1911:102. McDermott 1966:115. Type species: *Lampyroidea syriaca* Costa monobasic.
Bourgeoisia Olivier. Olivier 1908:17; 1911b:102. McDermott, 1966:117. Deheyn & Ballantyne 2009:47. Type species: *Luciola antipodum* Bourgeois designated by McDermott 1966.

Diagnosis. *Luciola* **s. str.** belongs in a group of genera with aedeagal LL visible beside the ML; distinguished by the separation of the LL dorsally, the often strongly curved/arched ML terminating in a preapical ventral point, and the presence in some species (including *italica*) of elongate slender apically pointed lobes arising from the inner ventral margins of the LL. Dorsal colour pattern of orange pronotum and dark brown elytra occurs in several species including the type (which may have a median dark pronotal marking); Pacific Island species have deep grayish brown to black dorsal colour (see Table 9) and several have eye emarginations of varying depth. Females macropterous in *L. kagiana*, or with varying degrees of fore and hind wing loss in other species. Larvae reliably associated only for *kagiana* and *parvula* where they are probably terrestrial and have laterally explanate tergal margins (e.g. Chen 2003:168).

Male. Pronotum: dorsal surface without irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense; anterior margin not explanate; lateral margins either diverging posteriorly along their length (C>A, B), or converging in posterior 1/3; width < or subequal to humeral width; anterolateral corners rounded obtuse; lateral margins without indentation at mid-point, or sinuousity in either horizontal or vertical plane; without indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners usually rounded obtuse, angulate in Pacific Island species where they are 90° approximately and incline obliquely to the median line; posterolateral corners either not projecting, or extending as far as median posterior margin and separated from it by scarce emarginations except in *kagiana* where the emarginations are well developed.

Hypomera: closed; median area not elevated in vertical direction; posterior area not flat in *italica*, *syriaca* and *hypocrita*, narrowly flat in remainder, where dorsal and ventral surfaces are strongly adpressed; pronotal width/ GHW 1.2–1.6.

Elytron: punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and sutural ridge extending beyond mid-point, almost to apex but not extending as a ridge around apex, neither thickened in apical half; no interstitial lines; elytral carina absent; in horizontal specimen viewed from below epipleuron at elytral base wide, covering humerus; viewed from above the anterior margin of the epipleuron arises level with or 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 except for *hypocrita* where they are slightly convex-sided.

Head: minimally to 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 in L. *italica*, contiguous ventrally in Pacific Island species (Fig. 111); eyes above labrum close, sometimes contiguous; frons-vertex junction rounded, without median elevation; posterolateral eye excavation strongly developed, visible in resting head position in some Pacific Island species only (Figs 110,120,121,122); antennal sockets on head between eyes, contiguous, or separated by < ASW or = 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: probably functional; apical labial palpomere either strongly flattened, shaped like broad triangle (widest at base), with inner edge dentate in *L. italica*, or ovoid, longer than wide with margins entire; at least half as long as apical maxillary palpomere in the remaining species described below. Antennae 11 segmented; length >GHW up to twice GHW except in Pacific Island species where antennal length is subequal to GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel.

Legs: with inner tarsal claw not split; without MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Figs114,119,124,125): without cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment; LO absent in *L. oculofissa* **sp. nov**. (Figs 124,125); LO absent in V7 and restricted to anterolateral plaques in V6 in *L. hypocrita* (Deheyn & Ballantyne 2009 Fig. 5 a,b); LO in V7 in remaining species entire, either occupying most of V7, and reaching to sides and almost to posterior margin (Fig. 119), or not reaching sides or posterior margin and occupying about half or less of V7 (Fig. 114); posterior half of V7 not arched or swollen, muscle impressions not visible in this area; neither anterior nor posterior margin of LO emarginate; if LO present in V6, occupying almost all V6 except in *hypocrita*. MPP present, symmetrical, apex rounded or truncate, not laterally compressed, short, not inclined dorsally nor engulfed by T8 apex, without dorsal ridge, median longitudinal trough. V7 without median carina, median longitudinal trough, anteromedian depression on face of LO, incurving lobes or pointed projections, median 'dimple', or reflexed lobes. T7 without prolonged anterolateral corners. T8 symmetrical, W=L, visible posterior area not narrowing abruptly, median posterior margin shallowly and narrowly emarginate; widest across middle with lateral margins tapering evenly in both an anterior and posterior direction; without prolonged posterolateral corners, 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 without well developed median longitudinal trough, lateral depressed troughs, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 either not as long as visible posterior portion of T8, or shorter, not laterally emarginated before their origins, not expanded dorsoventrally, expanded only in horizontal plane; without bifurcation of inner margin and ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath: approx. 3 times as long as wide; without bulbous paraprocts; either symmetrical in posterior area where sheath sternite tapers evenly to a narrow rounded apex or slightly emarginated on right side; tergite without lateral arms extending anteriorly at sides of sheath sternite; tergite without projecting pieces along posterior margin of T9, anterior margin without transverse band.

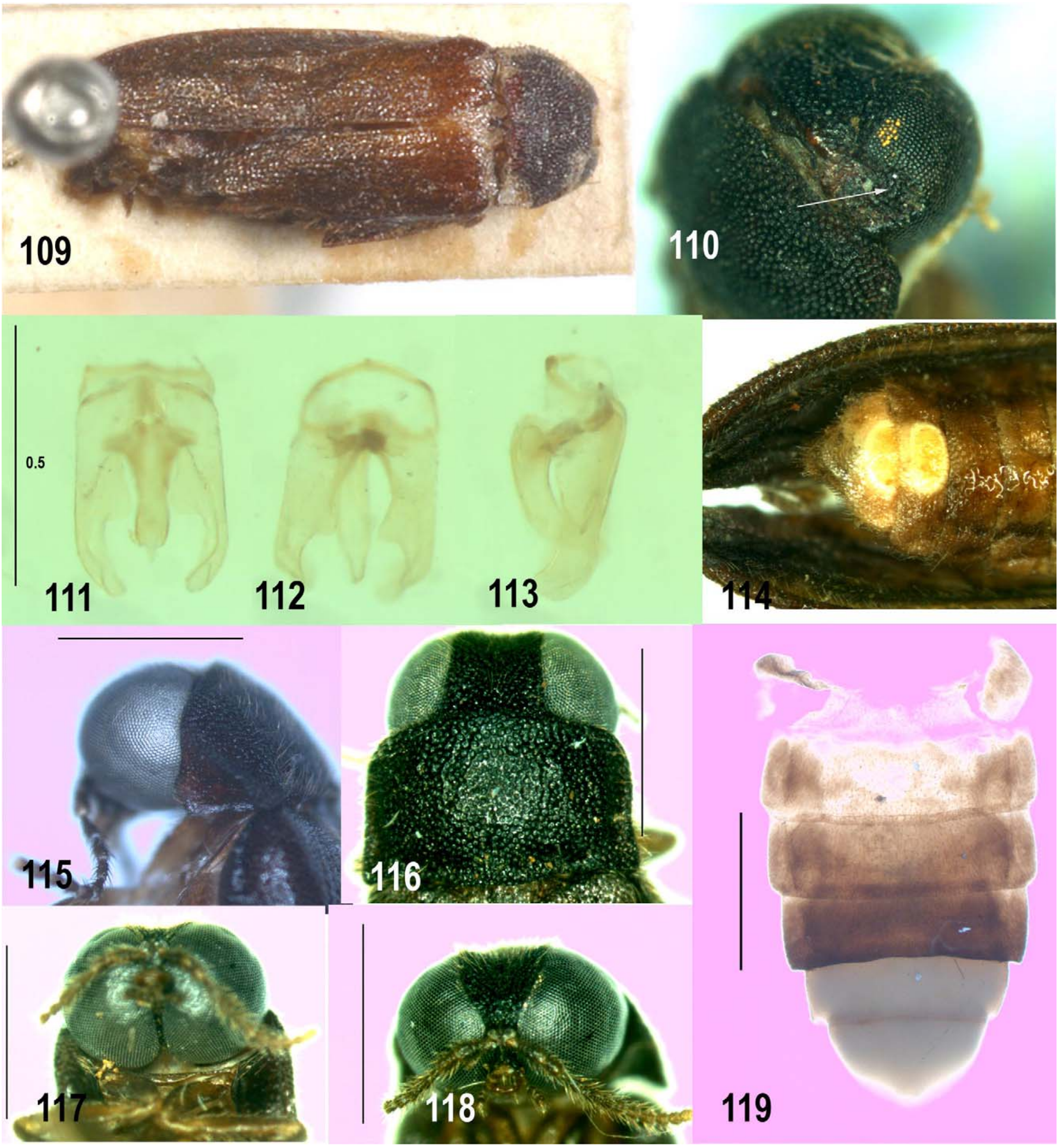
Aedeagus (Figs 111–113, 122,126) (e.g. Ballantyne 1968 Figs 162–169; Jeng *et al.* 2003 Figs 21A–C): LL lack lateral appendages; LL visible from beneath beside ML, LL/ML moderate to wide; LL of equal length, slightly longer than ML, either diverging along their length or not diverging basally; separated longitudinally by most of their length; LL base width often narrower than LL apex width which may be wider than that of ML; LL apices often more widely expanded than elsewhere and enfolding the ML at the sides; dorsal base of LL symmetrical, not excavated; LL without lateral hairy appendages along their outer ventral margins; narrowed apices of LL sometimes inturned; without projection on left LL; inner margins often with slender leaf-like projection; ML symmetrical, without paired lateral teeth and tooth to left side, usually strongly arched, preapical ventral area produced and pointed; BP not strongly sclerotised, not hooded, not strongly emarginated along anterior margin, often very narrow.

Female. Macropterous in *kagiana* (Chen 2003:168), or with varying degrees of fore and hind wing loss. Pronotum without irregularities in posterolateral areas; punctation moderate to dense; pronotal width less than, subequal to or greater than humeral width; without 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; no interstitial lines; elytral carina absent. No legs or parts thereof swollen and /or curved. LO in V6 only, without any elevations or depressions or ridges on V7; median posterior margin of V7 widely emarginate, median area not broadly rounded; median posterior margin of V8 entire. Bursa plates not observed in dissections of ethanol preserved specimens of *italica*.

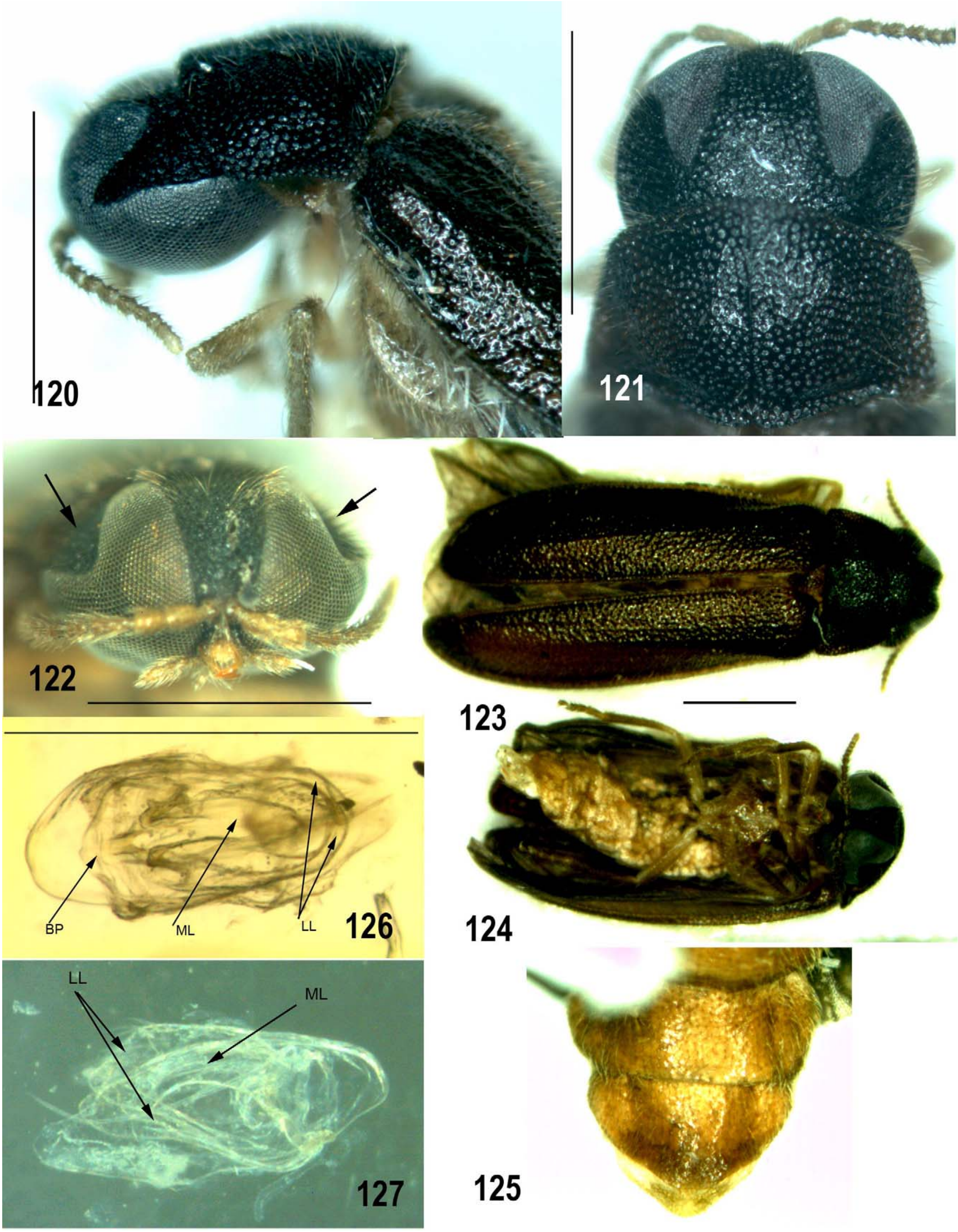
Larva (Figs 128–138). Here only *L. hypocrita*, and New Caledonian larvae associated by label data are described (Tables 10, 11 indicate rationale for association). Elongate, slender, tapering somewhat in front and behind; with 3 thoracic and 9 abdominal segments; external plates of the dorsal surface very well sclerotised with no obvious dorsal areas of exposed membrane except between segments; all body segments except the last with a median dorsal longitudinal line; lateral margins of tergal plates explanate thickened (except for terminal segment which is parallel-sided), and projecting beyond sides of body and usually covering laterotergites in the abdomen, visible only if they are laterally prolonged. Head: antennal segment 3 surmounted by a ring of hairs and subequal in length to the elongate sense cone. Mouthparts: mandibles without inner teeth; apical palpomeres of maxilla and labium with terminal sense organs. Thorax (Figs 128, 131, 132, 135, 137, 138): prothorax longer than wide, always with lateral projections especially at posterolateral corners; meso and metathoracic segments shorter than prothorax and with 2 or 3 lateral projections. Legs: tibiae with an apical brush of fine white hairs reaching over the apical claw (tarsungulus) (Fu *et al.* 2012b Fig. 55). Abdomen (Figs 129, 130, 133, 134): median sternal plates of segments 1–6 and laterotergites of segments 1–6 with short posterior projections in Pacific Island species; posterolateral corners of laterotergites angulate, often narrowly prolonged and may be visible at sides of body from above when lateral margins of terga are narrowed and prolonged (Fig. 134) (Fu *et al.* 2012b Fig. 54).

Remarks. *Luciola* **s. str.** is addressed from scoring a population from Pisa of *Luciola italica*, the type species (Ballantyne and Lambkin 2000, 2001, 2006, 2009). *Bourgeoisia* and *Lampyroidea* (based only on its type species *syriaca*) are submerged under *Luciola*. *Luciola italica* exists in a variety of morphological forms across Europe, and such an investigation while necessary is currently beyond our capacity. Suggestions for possible subdivisions below relate to Figs 3, 4 and the key to genera and species groups incorporates all these possible subdivisions of *Luciola*.

1. Fig. 3 Node 1 two aquatic Japanese species *Luciola cruciata*, *L. owadai*.
2. Fig. 3 Node 8 blue number 2 (*Luciola trilucida*).
3. Fig. 3 Node 11 blue number 3 (*Luciola indica*).
4. Fig. 4 Node 44 blue number 20 Species 8.
5. Fig. 4 Node 45 includes species with elytral punctures in lines, an emarginated LO in V7 and sclerites surrounding the aedeagal sheath (*L. carinata*–*L. aquatilis*).
6. Fig. 4 Node 46 (*Luciola dejeani*–*L. aegrota*).



FIGURES 109–119. *Luciola* spp. Males. 109–114 *Luciola antipodum* Bourgeois (MNHN). 115–119 *Luciola aquilaclara* **sp. nov.** paratype male (QMBA). 109, 116 dorsal (116 head and pronotum only); 110 right posterolateral head (eye excavation arrowed); 111–113 aedeagus ventral (111), dorsal (112) and right lateral; 114 terminal abdomen and elytra ventral; 115–118 head and pronotum left lateral (115), dorsal (116), anteroventral (117) and anterior; 119 abdominal ventrites 3–7 ventral. These figures share scale lines: 111–113.



FIGURES 120–127. *Luciola oculofissa* **sp. nov.** paratype males (QMBA). 120, 121 head and pronotum, left lateral (121) and dorsal (Pic du Grand Kaori); 122 head anterior (Foret du Nord); 123, 124, whole body dorsal (123) and ventral (Foret du Nord); 125 V6, 7 ventral (Col de Petchecara); 126, 127 aedeagus in aedeagal sheath ventral (126, anterior end to left of page), ventrolateral (127, anterior end to right of page (Rive Bleu). Figure legends: BP basal piece; LL lateral lobes; ML median lobe. These figures share scale lines: 123, 124.

TABLE 10. Localities for New Caledonian species.
Adults type 1 with LO; adult type 2 no LO

Larvae only	Larval Type	Adults only	Adult Type	Adults and larvae	Type
Col d'Amieu	B, C				
Mandjelia	B, C				
		Nehoue camp	1		
Touho Tower	A				
Mt Taom	B				
				Aoupinie	1, C
		Col de Petchecara	1		
Gelima	B				
Mt Rembai	B				
		Mt Do	1		
				Dzumac road	1, B, C
Mt Mou base	B, C				
				Rive Bleu	2, A
Houp Geant	C				
Foret Electrique	A				
Mt Koghis	A				
		Pic du Pin	*		
		Pic du Grand Kaori	2		
				Port Boise	2, A

Footnote: *1 hand collected at night; 2 yellow pan in day

TABLE 11. Characteristics New Caledonian *Luciola* spp. larvae

Feature	*L. hypocrita*	*L. aquilaclara* sp. nov.	*L. oculofissa* sp. nov.
Lateral projections of protergum	2 weak	4 strong	2 strong
Lateral projections of mesotergum	3 weak	3 strong*	2 (posterior projection at corner is weak)
Lateral projections of metatergum	3 weak	3 strong*	Same as above
Posterolateral projections of abdominal terga	2 strong	1 narrow# +	1 narrow
Posterior projections of abdominal sterna	2 weak	2 strong	2 moderate
Posterior projections of abdominal laterosternites	strong	Strong #	moderate
Posterior projections of abdominal laterotergites	Angulate barely projecting	strong	Angulate corner not projecting
Projections to side of median line on thoracic and abdominal terga 1–8	Broad wide separation	Short close	Not developed

* single larva from Foret du Nord lacks the anterolateral projection; #curved towards rear in 1 larva from Col d'Amieu, 3 Aoupinnie larvae from top camp and sawmill, and in one of two larvae taken on 23.xi.2001; + outer posterior margin of lateral tergal projections with small tooth in Mt Taom, Mt Mou base, one Dzumac Road larva and Foret du Nord larva.

List of species of *Luciola* s. str.

- *antipodum* (Bourgeois)*
- *aquilaclara* **sp. nov.***
- *italica* L.
- *hypocrita* Olivier*
- *oculofissa* **sp. nov.***
- *syriaca* (Costa)

Here we address specifically only the fauna of New Caledonia and Fiji*.

Luciola antipodum Bourgeois
[Figs 109–114]

Luciola antipodum Bourgeois, 1884:285.
Rhagophthalmus antipodum (Bourgeois). Olivier, 1902:87. Fauvel, 1904:140.
Bourgeoisia antipodum (Bourgeois). Olivier, 1908:17. Heller, 1916:243. Ballantyne, 1968:123. Ballantyne & Lambkin 2009:Figs 59, 513, 515.
Bourgeoisia antipoda (Bourgeois). McDermott, 1966:117. Ballantyne, 1968:123 (synonymy).

Type. Not reliably located. LB located a specimen in the Bourgeois collection (Box 22 MNHN) in 2003 labelled 1. (hand written) *Bourgeoisia antipodum* Bourg; 2. Kanala Fauvel. The specimen lacks head and pronotum, and is discussed below.

Other specimens examined (* = tentative inclusion only, discussed below). **NEW CALEDONIA**: 21.31S, 165.57E Kanala 2 males (Olivier collection Box 59 MNHN), one male labelled 1. (handwritten) Kanala; 2. Luciola?? antipodum FvL (? Fauvel collector) N. Caledonia. Mt St Arago, 19.vi.1914, P D Montague, male ("under side of abdomen highly luminous") (NHML). Grotte de Ninrin-Reu nr Poya, 4.i.1965 G Gross Biospel. Exped., male (SAMA)*. 21.37S, 165.46E, Farino 750m 3–10.ii.2002 male Malaise trap, C Darling (QMBA). SOLOMON ISLANDS: San Cristobal, Kira Kira 0–50m, 10.xi.1964 RS, male (BPBM)*.

Diagnosis. Specimens identified as *L. antipodum* Bourgeois conform in size, extent of eye emargination, and extent of LOs in V6, 7 to the Kanala males in the Olivier collection, and extent of LOs to the fragment of abdomen in the Bourgeois collection (MNHN) with the exception of those indicated by * above which are discussed below. A small species known only from New Caledonia, with deep grey dorsal colouration (Fig. 109), large head with eyes subcontiguous ventrally, and a well developed dorso-lateral eye emargination (Fig. 110); LOs in V6, 7 oval in outline and not reaching margins of either segment, nor to the posterior margin in V7 (Fig. 114). Females and larvae not associated.

Male. 3.6–4.7 mm long; 1.6–1.7 mm wide; W/L 0.4. Colour (Figs 109, 110): Pronotum very dark brown; MS, MN and elytra lighter brown; ventral surface of body lighter brown than elytra except for pale LOs in V6, 7 which are retracted from the lateral margins on both segments and assume an oval outline (Fig. 114). Pronotum (Fig. 109): 1.3–1.5 mm wide; 0.9–1.0 mm long; W/L 1.4–1.5. Elytron: 3.1–3.7 mm long. Head: GHW 0.9–1.3 mm; SIW 0.1 mm; ASD < ASW (sockets very close almost contiguous); eye emargination well defined, visible when head retracted (Fig. 110). Abdomen (Fig. 114): LO in both V6, 7 small, entire, not reaching sides of V6, not reaching sides or posterior margin of V7 except: Ninrin-reu male where LO in V6 especially reaches almost to sides; Mt St Arago male where LOs do not reach sides but remaining area of both ventrites occupied by diffuse fat body and appear white; Kira Kira male where LO plaques occur at sides of V6, and rest of V6 and V7 occupied by diffuse fat body which may not be luminous (LO in this male gives appearance of being bipartite in V6). Aedeagus (Figs 111–113): ML with very narrow apex, shorter than LL which curve inwards at their narowed rounded apices; LL widely separated along middorsal line, with a rounded projection along inner margins, at approximately half their length from the apex; BP very narrow.

Remarks. We consider the specimens in the Olivier collection (MNHN) most closely approach the original designation of this species by Bourgeois. The specimen Ballantyne located in the Bourgeois collection (MNHN) is labelled *Bourgeoisia.* Whether it can be regarded as a type is questionable. Olivier (1908) assigned the species to *Bourgeoisia;* it may have been relabelled by Bourgeois or possibly Olivier himself. It is without a head and pronotum and both elytra are incomplete. However the abdomen shows features consistent with the Kanala males in the Olivier collection viz. oval LOs in V6, 7 not reaching either the sides, or the posterior margin of V7. The Kanala males (MNHN) also have well defined eye emarginations visible when the head is withdrawn.

This species may be very poorly represented now in New Caledonia, as despite extensive collecting there by the team from Queensland Museum only a single Farino male has the strong eye excavation and appears to have a very reduced LO in both V6 and 7.

Alternatively (see below) the retraction of the light organ in the older pinned specimens may be simply a postmortem effect. Determination of critical features in some specimens which are in poor condition has been difficult. Ballantyne and Lambkin (2009 Fig. 59) figured the specimen from Ninrin-reu (SAMA) with well defined eye emarginations. A large and widespread population of a second species with extensive LOs in V6, 7 was a recent collection, but this population, described here as *Luciola aquilaclara* sp. nov., lacks the eye emargination. A second extensive population without LOs and with very strong dorsal eye emarginations is described as *L. oculofissa* sp. nov. All three New Caledonian species share a similar dorsal colouration and almost identical pattern of aedeagus and aedeagal sheath. The possible function of the eye emargination is discussed subsequently. No larval associations for this species were made.

Ballantyne (1968) redescribed a single male from the Solomons with a well defined eye emargination, but could not determine the extent of the LO material in V6, 7, and it may belong here. The LL of the male aedeagus are closely approximate dorsally (Ballantyne 1968 Figs 174, 175) unlike the specimens depicted here. A second specimen from San Cristobal included here has eye emarginations but LO in V6 may be bipartite (they are separated by fat body and thus extent of the actual light organ is difficult to determine). Ballantyne and Lambkin (2009:46, Figs 142, 143) described *Atyphella kirakira* from San Cristobal with bipartite LO in V6 separated by extensive fat body, and non aggregated fat body in V7.

Existing information about the New Caledonian firefly fauna is confusing. *L. antipodum* may have been represented in the recent QMBA field collections by a single male. *L. caledonica* Bourgeois was described, probably from a female, as 10 mm long, with an orange pronotum having a dark anterior mark and dark brown elytra. No specimens approaching this size have been collected recently on New Caledonia and Ballantyne and Lambkin (2009) synonymised *caledonica* with *plagiata* Blanchard and assigned the species to *Pygatyphella*. Fauvel's (1904) account of luminous *L. caledonica* from New Caledonia is at best second hand and the observations he refers to may well have been luminous fungi. Heller's (1916) list is a catalogue entry only.

***Luciola aquilaclara* sp. nov.**

[Figs 115–119, 130–134, 136, 137]

Holotype. Male. **NEW CALEDONIA**: 22.19S, 166.53E Foret de Thi, 100–300m, 23–25.iii.1961, JS (BPBM).

Paratypes. **NEW CALEDONIA**: 20.18S 164.24E Col d'Amein 3 km WSW 520m 14.XII.2004 1 larva (Type C), rainforest, sieved litter; 20.18S 164.24E 520m 6.i.2005 3 larvae (2 type C, 1 type B), rainforest sieved litter; 21.37S, 165.49E 470m 27.i.2004 larva (Type B) QMBA 1120, rainforest sieved litter; 21.37S, 165.49E Col d'Amieu west slope upper 480m 3.v.2005 3 larvae (Type B, 1 larva Type C). 20.24S, 164.32E Mandjelia Summit 780m, 6–7.xi.2001 3 larvae (Type C) QMB 1055 rainforest, 12.xii.2004 7 larvae (Type C) sieved litter; 20.24S 164.31E Mandjelia lower creek 580m 12.xii.2004 3 larvae (1 type C, 2 type B), rainforest sieved litter. 20.26S, 164.14E Nehoue campground 50m 2 males hand collected. 20.47S 164.35E Mt Taom summit site 1 980m 7.xii.2004 larva (Type B), rainforest sieved litter; Mt Taom summit site 2 940m 7.xii.2004 larva (Type B), rainforest sieved litter; Mt Taom summit site 3 7.xii.2004 2 larvae (Type B) rainforest sieved litter. 21.09S 165.19E Aoupinie: sawmill 500m 17.xii.2004 larva (Type C) rainforest sieved litter; 21.11S 165.19E top camp 3 males; 850m, 20–21.xi.2000 2 males; 850m 23.xi.2001 3 larvae (Type C) QMB 1045 rainforest, sieved litter; 850m 23.xi.2001 male hand collected; 750m 2.v.2005 larva (Type C). 21.25S, 166.24E, Grotte de Ninrin-Reu nr Poya, Biospel. Exped. 4.i.1965, at light, G. Gross, male (SAMA). 21.34S 166.07E Col de Petchecara S end 22.xi.2003–29.i.2004 FIT male; 21.34S 166.06E Col de Petchecara middle FIT male. 21.35S, 165.59E Gelima 5 kms S 485m 15.xi.2002 larva (Type B) QMB 1083 rainforest, sieved litter. 21.35S 165.50E Mt Rembai 700m 30.xii.2004 1 larva (Type C) rainforest, sieved litter. 21.45S 166.00E Mt Do Summit 1000m 22.xi.2003–28.i.2004 male Min. FIT. 22.02S 166.28E Dzumac Road junction 950m 9.xi.2002 3 larvae (Types B, C) QMB 1077 rainforest, sieved litter; Dzumac Road 22.03S 166.28E 700m 5.xii.2003–26.i.2004 male FIT GM (taken with male *L. oculofissa* **sp.**

nov.). 22.05S 166.22E Mt Mou base 350m 4.ii.2004 2 larvae (Types B, C) QMB 1119 rainforest, sieved litter. 22.06S, 166.39E Riv. Bleue panoramic track 160m 12 males (9 males 20.xi–11.xii.2000) malaise trap. 22.09S 166.41E Houp Geant 320m 6.v.2005 2 larvae (Type C). 22.15S 166.49E Pic du Pin site 1 QM party 26.xi.2004 10 males night hand collected rainforest, male pyrethrum knock down (4 males *L. oculofissa* **sp. nov**. taken at this site). 22.19S, 166.53E Foret de Thi, 100–300m, 23–25.iii.1961, JS 19 males (BPBM). 22.19S, 166.55E, Foret de Nord sites 1, 2 QM party, 480m, 2.xii.2004, male (site 1), male (site 2) rainforest at night hand collected; 210m site 2 21.iv.2005, larva (Type C). All specimens in QMBA unless indicated otherwise; QMBA specimens taken by a team of P. Bouchard, C. Burwell, P. Grimbacher, G Monteith and S. Wright.

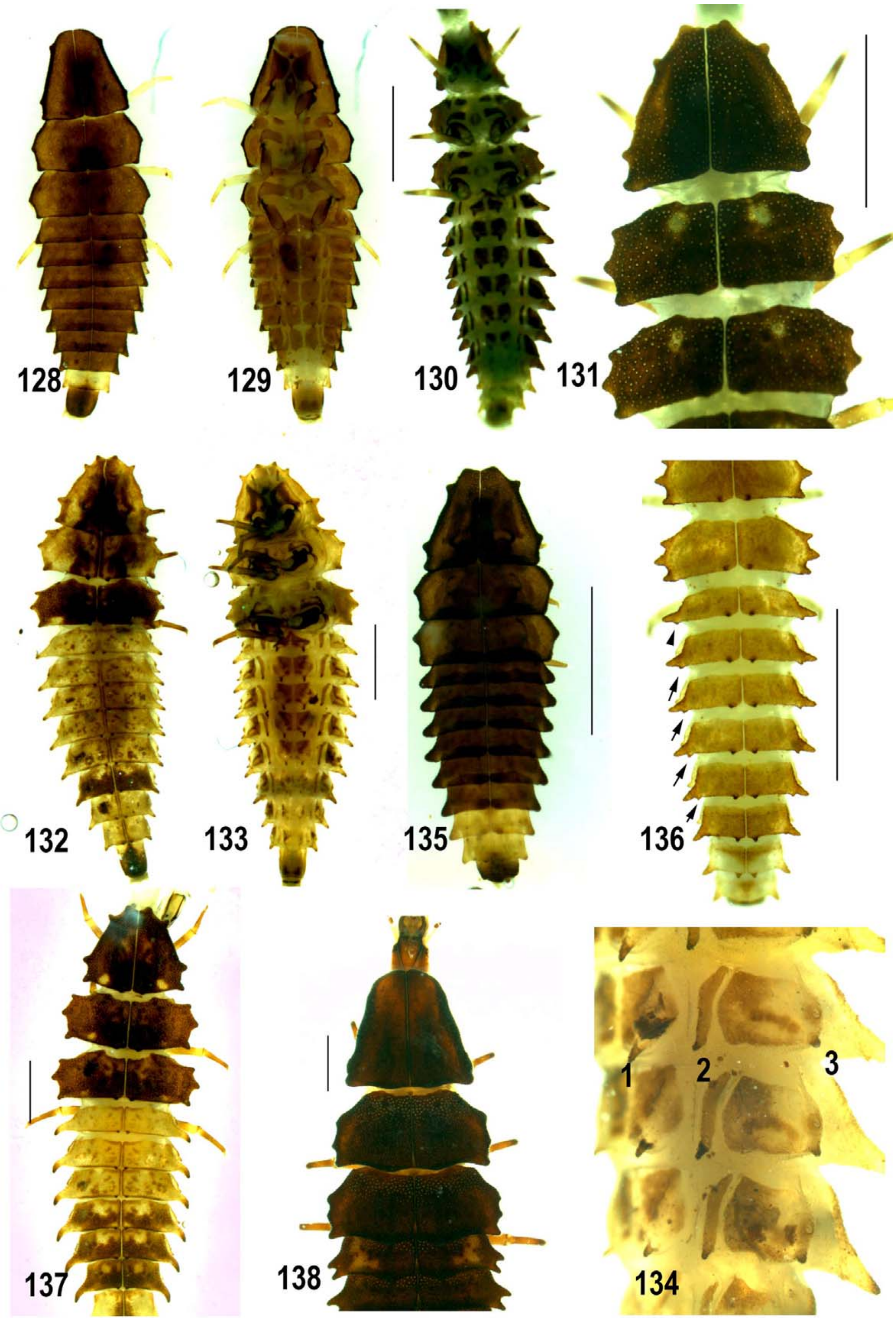
Diagnosis. Known only from New Caledonia; dorsal colouration deep grey as for *L. antipodum*, *L. oculofissa* **sp. nov**. and *L. hypocrita*. Distinguished by the well developed LOs in V6, 7 (Fig. 119) occupying all but a very narrow posterior margin of V7, and the lack of any obvious eye emargination when head is withdrawn (Figs 115, 116).

Male. 4.1–6.0 mm long. Colour (Figs 116, 119): body very dark brownish grey, pronotum very dark and often contrasting with the slightly paler elytra; T8 paler brown and semitransparent; white LOs occupying all of V6, 7 except for a narrow posterior margin in V7 (Fig. 119). Pronotum (Fig. 116): 0.8–1.2 mm long; 1.2—1.7 mm wide, W/L 1.3–1.5; pronotal width subequal to humeral width or slightly less in some pinned specimens. Elytron: 3.3–4.8 mm long; subparallelsided. Head (Figs 117, 118): GHW 1.1–1.4mm; SIW 0.1–0.15mm; antennal sockets almost contiguous; the small mouthparts may indicate that this species does not feed as an adult. Aedeagus (Figs 111–113): ML with very narrow apex, shorter than LL which curve inwards at their narrowed rounded apices; LL widely separated along middorsal line, with a rounded projection along inner margins at approximately half their length from the apex; BP very narrow.

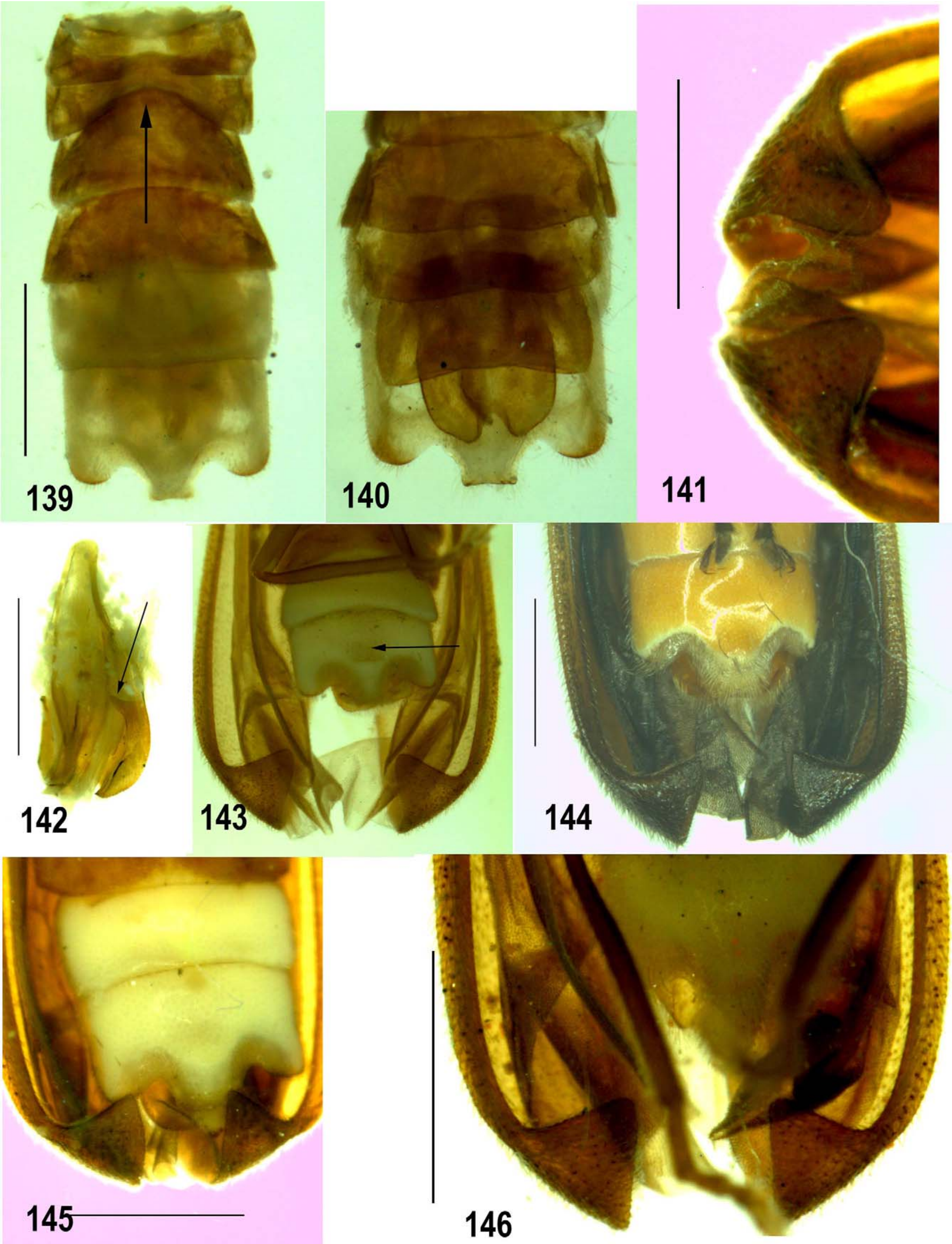
Female. Unknown. Probably flightless. Males have most of the ventral head area devoted to compound eyes (Fig. 117) and have simple short antennae so are probably relying on sighting the female response from above.

Larva (Figs 130**–**134, 136, 137). Associated by correspondence of collecting data with that of males and distinguished by features outlined in Table 11, and below. Larvae are described as either Type B or C of which B may represent earlier instars of C and differs only in colouration as described below. Both types were often taken at the same site. Instars not identified.

Colour: Type B: (e.g. Col d'Amieu, Gelima Figs 130, 131) (Fu *et al*. 2012b Figs 52–54) thoracic terga light to quite dark brown; some with terga 2 and 3 dark with 2 pale markings along anterior area near mid line on each (Fig. 131), abdominal terga dark brown with pale markings scattered, terga 7 and 8 largely pale with dark markings along median line, and 9 dark with pale anterolateral corners. Paler Type B larvae (e.g. Mt Taom summit Fig. 136) with light brown thoracic terga and abdominal terga 1–6, with 7, 8 largely pale, having dark markings along mid line and anterior margin only. Type C (Figs 132, 133, 134, 137): thoracic terga 1–3 quite dark with some paler markings (along posterior margins in Aoupinnie larvae Fig. 137, towards posterior margin and to sides in Mandjelia larvae Fig. 132); abdominal terga (Figs 132, 137) 1–3 or 1–5 pale yellow with irregular brown markings, abdominal terga 4–6 largely brown, dark markings sometimes restricted to tergum 6; terga 7, 8 largely pale yellow with some dark markings; most of tergum 9 brown. Ventral plates on both larval types are brown. Dorsal surface (Figs 131, 132, 136, 137): well sclerotised, with pale punctures scattered evenly over the surface; well defined pale median line running from anterior margin of protergum to posterior margin of abdominal tergum 8; all terga with short paired projections along posterior margin beside mid line (Fu *et al.* 2012 Fig. 52); Mt Taom summit larva with short paired teeth along posterior margin of abdominal terga 1–6 (Fig. 136). Thorax: protergum wider than long, with 4 lateral projections on each side including produced posterolateral corners (e.g. Figs 131–133, 137); meso and metaterga much wider than long, shorter than protergum, with 3 lateral projections on each side including the produced posterolateral corners. Abdomen (Figs 130, 132, 133, 134): depending on orientation of specimen and degree of lateral extension laterotergites may be visible from above on one or both sides. Abdominal terga 1–8 with posterolateral corners prolonged narrowly and apically rounded; terga 1–8 diminish in width and increase in length; posterolateral corners narrowly prolonged (Figs 130, 132) and slightly curved in some Aoupinnie and Col d'Amieu larvae (Fig. 137). Ventral surface (Figs 130, 133, 134) (Fu *et al.* 2012 Fig. 54): posterior margin of median sterna plates of abdominal segments 1–6 with paired narrow projections, of segments 7, 8 with shorter projections; posterior end of laterosternites (coloured part) dark, projecting; posterolateral corners of laterotergites of segments 1–8 narrow and projecting.



FIGURES 128–138. *Luciola* spp. Larvae (QMBA). *Luciola oculofissa* **sp. nov.** 128, 129 (Foret electrique), 135 (Touhu TV Tower). *Luciola aquilaclara* **sp. nov.** 130–134 (130, 131 Col d'Amieu, 132–134 Mandelia summit), 136 (Mt Taom summit), 137 (Aopinnie). 138 *Luciola hypocrita*. 128, 132, 135 dorsal whole body; 131 dorsal thorax only; 136 dorsal thoracic terga 2, 3, abdominal terga 1–8 (teeth along posterior margins of terga arrowed); 137 dorsal thorax and abdominal segments 1–7; 129, 130, 133 ventral; 134 left ventrolateral 3 abdominal segments. Figure legends: 1 left projection of sternum; 2 posterior projection of laterosternite; 3 posterior projection of laterotergite. These figures share scale lines: 128–130; 132, 133.



FIGURES 139–146. *Medeopteryx* spp. Males (ANIC). 139–142 *M. corusca***.** 143 *M. cribellata*. 144 *M. effulgens*. 145 *M. fulminea*. 146 *M. flagrans*. 139, 140 abdomen, ventral (139, anterior margin of V4 arrowed) and dorsal; 141 apices of elytra ventral; 142 tergite 8 ventrolateral, flange arrowed; 143–146 terminal abdomen and elytral apices, ventral. These figures share scale lines: 139, 140.

Etymology. The specific name highlights both the dark dorsal colouration and the large LO (aquilus, a, um latin dark coloured; clarus, a, um latin bright).

Remarks. Discovery of the existence of two new species of Luciolinae in New Caledonia has only been made possible by the extensive collecting activities of the team from the Queensland Museum. The partial or complete loss of LO material with expansion of the ventral head area as well as the development of a posterolateral eye excavation in *L. antipodum* and *L. oculofissa* sp. nov. is discussed subsequently. This species is distributed from north to south in New Caledonia and at altitudes both above and below 300m.

Luciola hypocrita Olivier

[Fig. 138]

Luciola hypocrita Olivier, 1888:202; 1902:80.

Bourgeoisia hypocrita (Olivier). Olivier 1908:17. McDermott 1966:118. Ballantyne 1968:124. Ballantyne & McLean, 1970:234. Deheyn & Ballantyne 2009: 47. Ballantyne & Lambkin 2009:Fig. 514.

Luciola nigra McDermott, 1966:110 (unnecessary new name for *L. atra* Pic).

Luciola atra Pic, 1928:58. Deheyn & Ballantyne 2009: 47.

Nec *Luciola atra* (G.A. Olivier). Branham, 2010 Fig. 4.15.2D.

Holotype. Male. *Luciola atra* Pic. **FIJI:** 18.00S, 178.00E labelled 1. Handwritten Luciola sp. (Olivier dit); 2 handwritten *Luciola atra* n s; 3 symbol; 4 printed black ink Ins. Fiji (MNHN).

Holotype. Male. *Luciola hypocrita* Olivier). Male. **FIJI:** 18.00 S, 178.00E labelled 1. Handwritten on pink paper Luciola hypocrita; printed Ern. Oliv.; 2 printed SPECIMEN TYPICUM ORIGINALE AUCTORIS Ern. Olivier; 3. Handwritten Fidjie Ins. (MNHN).

Diagnosis. Males known only from Fiji. Dark grayish dorsal colour with small posterolateral eye excavation; male LOs restricted to anterolateral plaques in V6 only; female flightless, with elytra covering much of the abdomen, coloured as for male; larvae dorsally deep grey with a tuft of fine white hairs at the apex of the tibiotarsus. Ballantyne (1968) redescribed males, and described a female and larva. Deheyn and Ballantyne (2009) characterized light production in the female and expanded the redescription of males, females and larvae. Larval characters are expanded in Table 11, Fig. 138 and Fu *et al*. (2012b Figs 50, 51).

Remarks. Branham's (2010) reference to *Luciola atra* (G. A. Olivier) larva was misspelled and is a reference to *Lucidota atra*.

Luciola oculofissa sp. nov.

[Figs 120–127]

Holotype. Male. **NEW CALEDONIA:** 22.06S 166.39E Riv. Bleue panoramic track 160m 20.xi–11.xii.2000 malaise trap (MNHN).

Paratypes. NEW CALEDONIA: 20.39S 165.13E Touho TV tower 400m 30.I.2004 QMB 1114 rainforest sieved litter 1 larva. 22.06S 166.39E Riv. Bleue panoramic track 160m 20.xi–11.xii.2000 malaise trap, 11 males; Riv. Bleue (Mois de Mai) 400m 19.xi.2001 QMB 1046 rainforest sieved litter 1 larva. 22.09S 166.41E Foret Electrique 220m 23.iv.2005 larva. 22.11S 166.01E 700m 3.xi.2002 QMB 1072 rainforest sieved litter 1 larva. 22.15S 166.49E Pic du Pin site 1 rainforest yellow pan 25–26.xi.2004 4 males. 22.17S 166.53E Pic du Grand Kaori site 2 250 m 22.xi–21.xii.2004 malaise trap rainforest 3 males; 22.17S 160.54E Pic du Grand Kaori site 2 21.xi.2001–29.i.2002 malaise trap 2 males. 22.19S 166.55E Foret du Nord sites 1, 2 480m 2.xii.2004 yellow pan 23 males. 22.21S 166.58E Port Boise, 20m 22.xi.2001–29.i.2002 4 males (FIT) 1 larva (pitfall trap). (QMBA).

Diagnosis. Known only from New Caledonia; dorsal colouration deep grey as for *L. antipodum, L. aquilaclara* **sp. nov**. and *L. hypocrita*. Distinguished by lacking any trace of LOs, and the huge anteriorly projecting eye emargination clearly visible from above when head is withdrawn. Female not associated. Larvae associated by correspondence of collecting data with that of males and distinguished by features outlined in Table 11, Figs 128, 129, 135 and below.

Male. 3.6–4.5 mm long. Colour (Figs 120–125): pronotum very dark almost black, elytra slightly paler; underside of body pale brown except for black head. Pronotum (Figs 121, 123): 0.8–1.2 mm long; 1.2 mm wide, W/L 1.2–1.5; pronotal width subequal to humeral width or slightly less in some pinned specimens. Elytron: 2.8–3.5 mm long; subparallelsided. Head (Figs 120, 121, 122, 123): elongate and protruding beyond anterior margin of pronotum (Fu *et al.* 2012b Figs 48, 49). GHW 1.2; SIW 0.1 mm; ASD < ASW; antennal sockets contiguous; the small mouthparts may indicate that this species does not feed as an adult. Aedeagus (Figs 126, 127): ML with very narrow apex, shorter than LL which curve inwards at their narrowed rounded apices; LL widely separated along middorsal line, with a rounded projection along inner margins at approximately half their length from the apex; BP very narrow.

Female. Unknown. Probably flightless.

Larva. Associated by correspondence of collecting data with that of males and distinguished by features outlined in Table 11 (as larva type A), Figs 128, 129, 135 and below.

Colour (Fig. 128, 129, 135): Dorsal surface quite dark brown with either only tergum 8 pale (Fig. 128), or both terga 8, 9 pale (Fig. 135). with narrow dark markings along posterior margin; ventral plates well defined, brown except for pale yellow underside of abdominal segments 7, 8 (Fig. 129). Dorsal surface (Figs 128, 135): well sclerotised; large pale punctures scattered along anterior and lateral margins of protergum, and at sides of remaining terga; well defined pale median line running from anterior margin of protergum to posterior margin of abdominal tergum 8; terga without any short paired projections along posterior margin beside mid line (Fig. 128, 135). Thorax (Figs 128, 135): protergum not much wider than long, with 3 short lateral projections on each side including barely produced posterolateral corners (Fig. 128, 135); meso and metaterga much wider than long, shorter than protergum with 2 lateral projections on each side including the produced posterolateral corners. Abdomen (Figs 128, 129, 135): laterotergites not visible from above; abdominal terga 1–8 with lateral margins expanding towards posterior end and posterolateral corners narrowed and apically acute (Fig. 128) or rounded (Fig. 135). Ventral surface (Fig. 129): posterior margin of median sternal plates of abdominal segments 1–6 with paired narrow projections, sterna areas of segments 7, 8 ill defined; posterior end of laterosternites dark, projecting; posterolateral corners of laterotergites of segments 1–8 narrowed, angulate, and slightly projecting towards rear.

Etymology. The specific name emphasizes the huge eye emargination (oculus, **-**i (m) Latin eye; fissus, a, um Latin split, cloven).

Remarks. This species was mainly collected during daylight hours using yellow pans (shallow plastic dishes with the inside painted bright yellow). A 1 cm deep layer of detergent water was placed in them and they were laid out on the forest floor during the day. G. B. Monteith (of the Queensland Museum team which collected these insects) noted that flying insects patrolling the forest floor zoom down to investigate the bright colour, land on the bright yellow surface, and drown. The dorsal eye excavation is enormous and discussed subsequently. Larval associations are tentative only. It is known from the southern area of New Caledonia at elevations lower than 300m, with two exceptions. The southern Foret Nord record at 480m is of many males. Monteith considers the northerly record at the Touho TV tower in the north east of the island may have been mislabelled; it is based on a single larva.

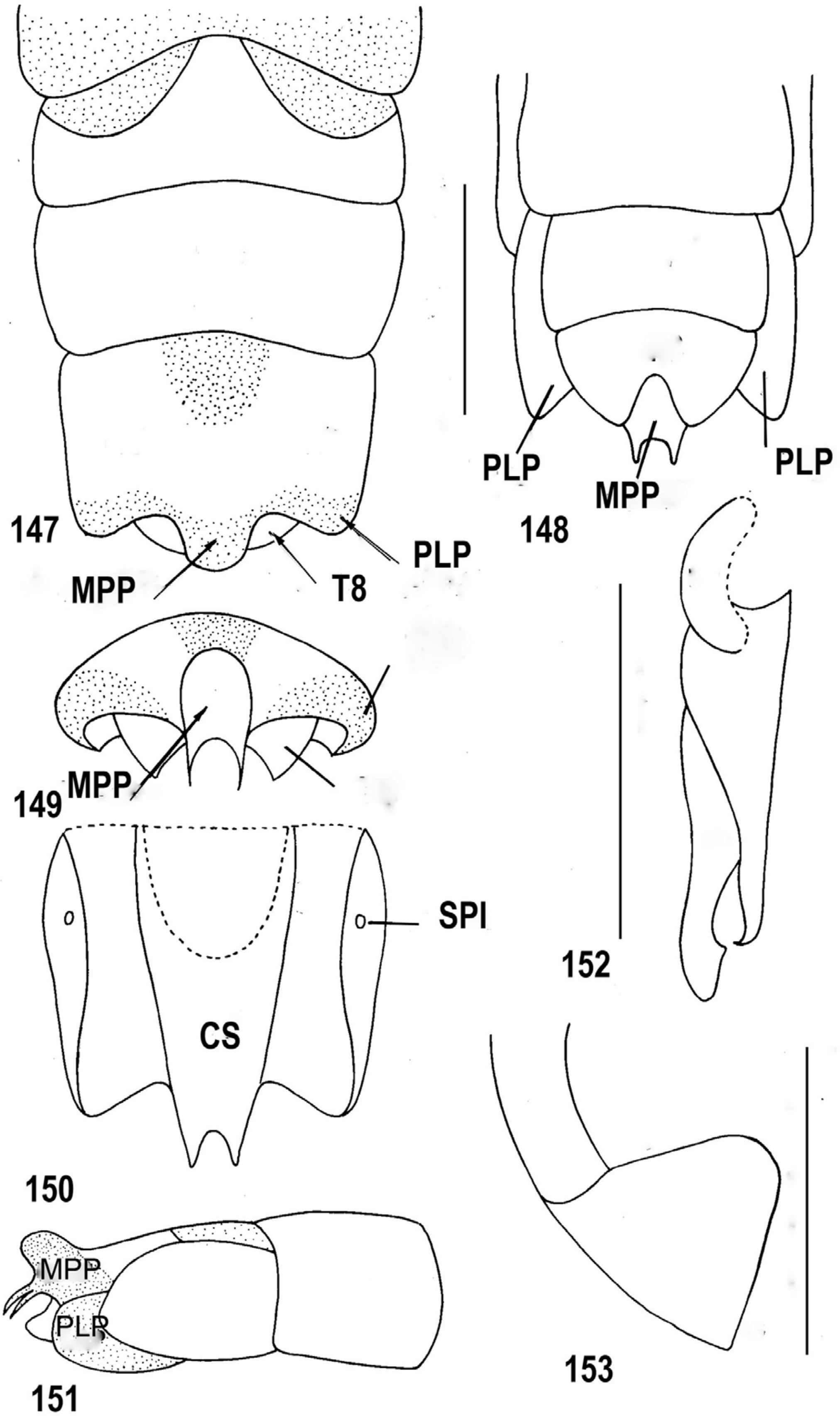
Medeopteryx gen. nov.

[Figs 139–184]

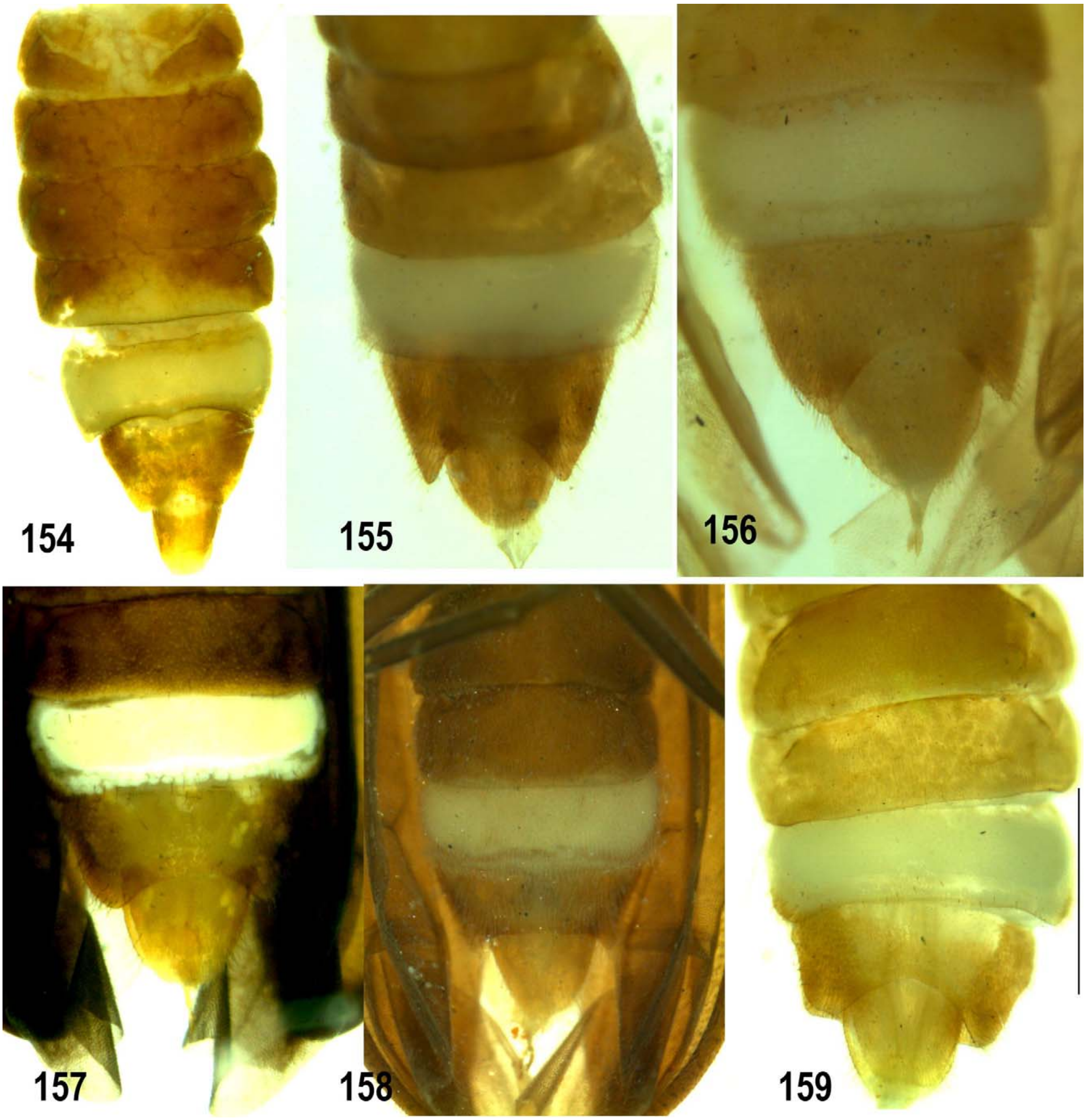
Type species: *Pteroptyx effulgens* Ballantyne.

Diagnosis. *Medeopteryx* **gen. nov**. is a new genus based mainly on New Guinean bent-winged fireflies formerly assigned to *Pteroptyx*, and is proposed for New Guinean and Australian species with an entire LO in V7, the posterior margin of which is trisinuate with PLP no longer or wider than the MPP. All but two species have deflexed elytral apices. It is most obviously distinguished from *Pteroptyx* **s. str.** in having an entire LO in V7, without a MFC and bulbous paraprocts on the aedeagal sheath.

Male. Pronotum: dorsal surface without irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense; anterior margin not explanate; W/L 1.3–1.7; either subparallel-sided, margins straight (A=B=C), or lateral margins diverging with posterior rounded convergence (C>A, B); pronotal width < humeral width; anterolateral corners rounded obtuse; lateral margins without indentation at mid-point, or sinuousity in either horizontal or vertical plane; without indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners usually angulate, 90º to median line, or rounded obtuse; posterolateral corners not usually projecting as far as median posterior margin and separated from it by scarce emarginations.



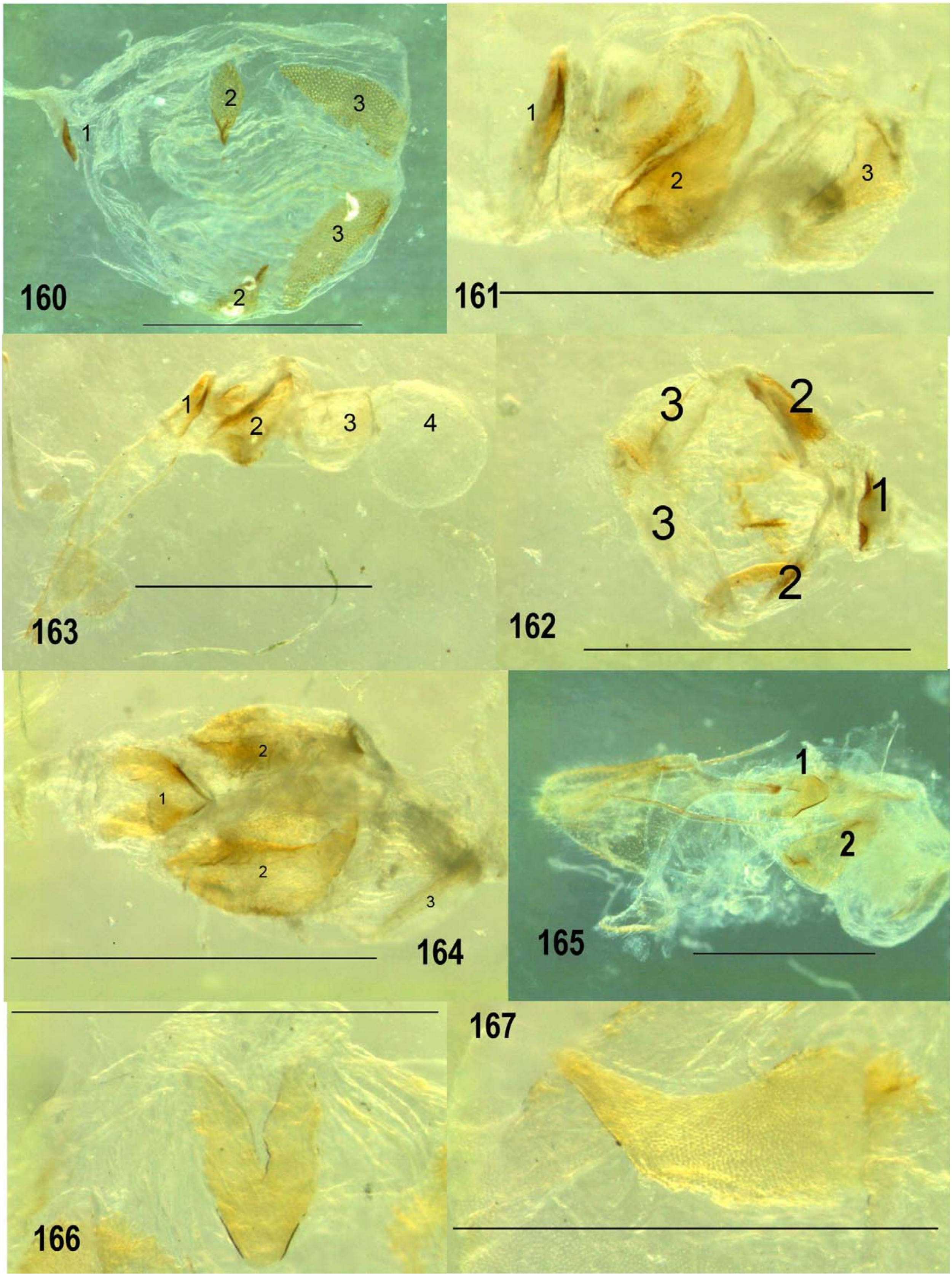
FIGURES 147–153. *Medeopteryx clipeata* **sp. nov.** holotype male (BPBM). 147–151 abdomen, ventral (147), dorsal (148), from behind with ventral surface uppermost (149), dorsal V7 (150), left lateral (151); 152 aedeagus left lateral; 153 ventral apex right elytron. Figure legends: CS cuticular strips; MPP median posterior projection of V7; PLP posterolateral projections of V7; SPI spiracle; T8 tergite 8. These figures share scale lines: 147–151.



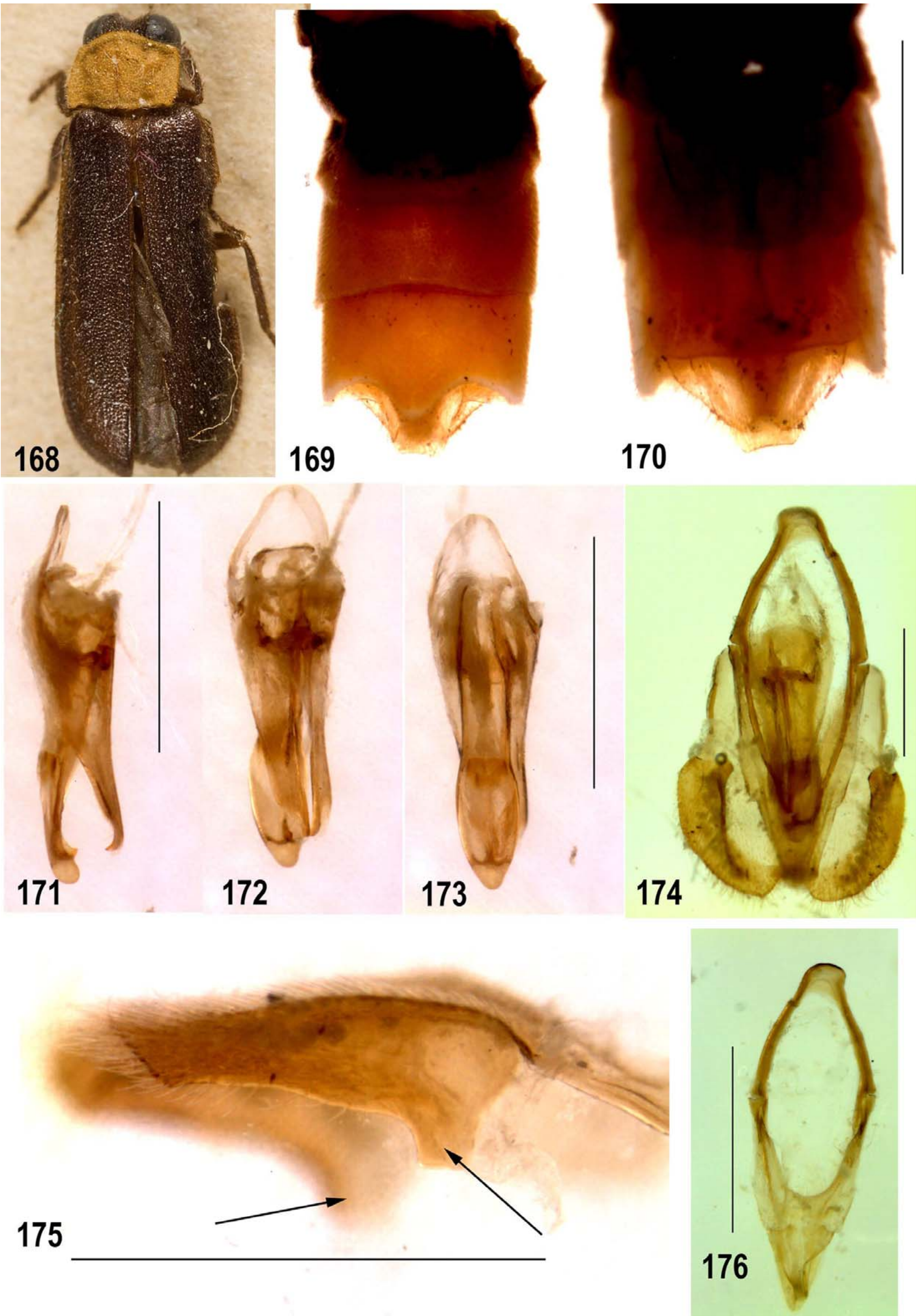
FIGURES 154–159. *Medeopteryx* spp. female abdomens ventral (not to scale) (ANIC). 154 *M. antennata*. 155 *M. corusca* (mating pair Catherine Mission). 156 *M. cribellata* (G381 mating pair). 157 *M. effulgens* (Kah New Ireland). 158 *M. flagrans* (G535). *M. fulminea* (Kar Kar Island).

Hypomera: closed; median area not elevated in vertical direction; median area more widely flattened than elsewhere; pronotal width/ GHW 1.2.

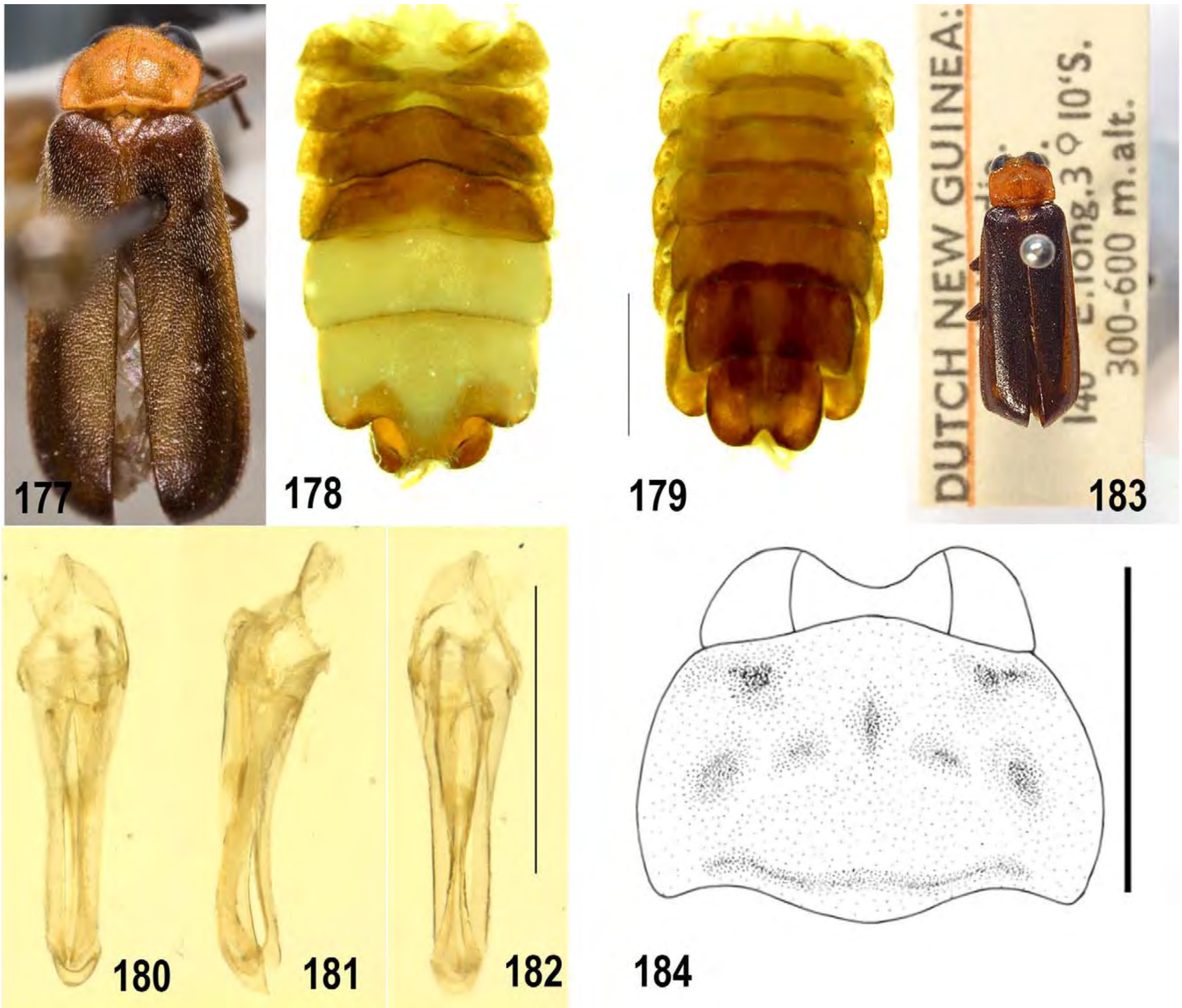
Elytron: punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices either deflexed or not; deflexed apex rounded, pointed or truncated, truncated apices short (Figs 141,143–146,153); epipleuron and sutural ridge extending beyond mid-point, to deflexed apex; no interstitial lines; elytral carina absent; in horizontal specimen viewed from below epipleuron at elytral base wide, covering humerus, viewed from above epipleuron arises anterior to or level with posterior margin of MS; epipleuron developed as a lateral ridge along most of length until deflexed apex; sutural margins approximate along most of length in closed elytra; lateral margins parallel-sided.



FIGURES 160–167. Female *Medeopteryx* spp. bursa. 160 *Medeopteryx antennata* female of mating pair Sek Bridge (ANIC). 161, 162 *M. corusca* female of mating pair Kondiu (ANIC). 163 *M. cribellata* Kar Kar Island (ANIC). 164–167 *M. similispupillae* **sp. nov.** 164 bursa ventral; 165 reproductive system excluding ovaries lateral; 166 median oviduct plate ventral (anterior end to foot of page); 167 anterior plate lateral. Figure legends: 1 median oviduct plate; 2 posterior bursa plate; 3 anterior bursa plate; 4 spermatophore digesting gland.



FIGURES 168–176. *Medeopteryx pupilla* male Mt Lamington (AMUS). 168 dorsal; 169, 170 abdomen ventral (169) and dorsal; 171–173 aedeagus left lateral, dorsolateral and ventral; 174, 175 tergite 8 (174 ventral with aedeagal sheath; 175 from right side, dorsal surface uppermost, flanges arrowed); 176 aedeagal sheath dorsal. These figures share scale lines: 171–173.



FIGURES 177–184. *Medeopteryx* spp. Males. 177–182 *M. similispupillae* **sp. nov.** paratypes. 183 *M. torricelliensis*. 184 *M. sublustris*, diagrammatic representation of pronotal sculpturing. 177, 183 dorsal; 178, 179 abdomen, ventral (178) and dorsal; 180–182 aedeagus dorsal (180), left lateral (181) and ventral (182). These figures share scale lines: 180–182

Head: moderately-deeply depressed between eyes; well 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 moderately separated; frons-vertex junction rounded, without median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous, usually separated by up to ASW or > ASW in the "*cribellata* complex" (Ballantyne 1987a:131); clypeolabral suture present, flexible, not in front of anterior eye margin when head viewed with labrum horizontal; outer edges of labrum reach to or beyond inner edges of closed mandibles. Mouthparts functional; apical labial palpomere strongly flattened, shaped like narrow triangle (narrowest at base), with inner edge entire; 2–3 X as long as wide. Antennae 11 segmented; length>GHW, usually twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel.

Legs: with inner tarsal claw not split; without MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Figs 139–146): without cuticular remnants in association with aedeagal sheath; V3 and/or V4 often with curved posterior margins and V4 extending anteriorly into emarginated posterior margin of V3 (this feature varies between different specimens in the one species and may be difficult to determine on dried pinned abdomens); posterior margin of V7 trisinuate; LO in V7 entire and occupying most of V7, reaching to sides but not posterior margin; posterior half of V7 not arched or swollen, muscle impressions not visible, anterior margin of LO emarginate only in *clipeata* **sp. nov**. (Figs 147–151); LO present in V6, occupying all or almost V6. MPP present, symmetrical, apex emarginate, often shallowly so and emargination may not be visible from beneath; MPP not laterally compressed, short (L=W), not inclined dorsally nor engulfed by T8 apex, without dorsal ridge, median longitudinal trough; MPP longer than or subequal in length to, and wider than or subequal in width to, horizontal PLP. V7 often with median 'dimple' (depressed area Fig.143 arrowed) anterior to MPP, in which case the ventral surface of the MPP is elevated (Ballantyne & McLean 1970 termed this a 'hump'); V7 without median carina, median longitudinal trough, anteromedian longitudinal depression on face of LO, incurving lobes or pointed projections, or reflexed lobes on dorsal surface; dorsal face of light organ bearing paired cuticular strips running from the sides of the MPP over the surface of the LO and attaching anteriorly to longitudinal abdominal muscles, in *antennata, corusca, cribellata, effulgens, elucens, flagrans, fulminea, platygaster, pupilla, similisantennata, similispupillae, sublustris, torricelliensis* (Ballantyne 1987a; 1993), or a wide single strip in *clipeata* **sp. nov**. (Fig. 150 CS). T7 without prolonged anterolateral corners. T8 well sclerotised, symmetrical, W=L, visible posterior area not narrowing abruptly, median posterior margin emarginate, often widely so; usually widest across middle with lateral margins tapering evenly in both an anterior and posterior direction; without prolonged posterolateral corners, 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 with a well developed median longitudinal trough margined by well defined ridges; anterior end of ridges usually with flanges which may be symmetrical/asymmetrical, narrow or broad, and with rounded or pointed apices (Figs 142,174,175); without lateral depressed troughs, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 either as long as visible posterior portion of T8 or slightly shorter, not laterally emarginated before their origins, not expanded dorsoventrally, expanded only in horizontal plane; without bifurcation of inner margin and ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath (Figs 174,176): approx. 3 times as long as wide; without paraprocts; symmetrical in posterior area where sheath sternite tapers evenly to a narrow rounded apex; anterior half of sternite relatively narrow, apically rounded; tergite without lateral arms extending anteriorly at sides of sheath sternite; tergite without projecting pieces along posterior margin of T9, anterior margin without transverse band.

Aedeagus (Figs 152,171–173, 180–182): L/W approx. 5/1; LL lack lateral appendages; apices of LL not visible from beneath at sides of ML, LL/ML narrow; LL of equal length, very slightly shorter than ML, contiguous or slightly separated longitudinally by most of their length along inner dorsal margins; 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; LL without lateral hairy appendages along their outer ventral margins, not produced preapically nor narrowly on inner apical margin, apices of LL not inturned, nor out-turned; without projection on left LL; inner margins without slender leaf-like projection; ML symmetrical, without paired lateral teeth and tooth to left side, not strongly arched, apex not shaped like arrowhead, not bulbous, not inclined ventrally; BP not strongly sclerotised, not hooded, not strongly emarginated along anterior margin.

Female (Figs 154–167)**.** Macropterous and some species observed in flight. Pronotum without irregularities in posterolateral areas; punctation moderate to dense; pronotal width less than humeral width; without 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; no interstitial lines; elytral carina absent. No legs or parts thereof swollen and /or curved. LO in V6 only, without any elevations or depressions or ridges on V7; median posterior margin of V7 widely emarginate, median area not broadly rounded; median posterior margin of V8 entire (Figs 154–159). Bursa (Figs 160–167) with paired wide plates; posterior oblique pair broad ventrally narrowing to pointed dorsal ends.

Larva. Not reliably associated.

Etymology. *Medeopteryx* (feminine noun; Greek *mede* = genitals, and *pteryx* = a wing, thus highlighting the shape of V7 and the deflexed elytral apices).

Remarks. Two groups within *Pteroptyx* Olivier have been recognized (Ballantyne 1987a) and successive phylogenetic analyses of the Luciolinae support this move to further subdivide the bent-winged fireflies (Ballantyne & Lambkin 2000, 2006, 2009).

List of species of *Medeopteryx* gen. nov.

- Species * have an exclusively Australian distribution
- *amilae* (Satô) **comb. nov.**
- *antennata* (Olivier) **comb. nov.**
- *clipeata* **sp. nov.**
- *corusca* (Ballantyne) **comb. nov.**
- *cribellata* (Olivier) **comb. nov.**
- *effulgens* (Ballantyne) **comb. nov.**
- *elucens* (Ballantyne) **comb. nov.**
- *flagrans* (Ballantyne) **comb. nov.**
- *fulminea* (Ballantyne) **comb. nov.**
- *hanedai* (Ballantyne) **comb. nov.**
- *platygaster* (Lea) **comb. nov.**
- *pupilla* (Olivier) **comb. nov.**
- *similisantennata* (Ballantyne) **comb. nov.**
- *similispupillae* **sp. nov.**
- *sublustris* (Ballantyne) **comb. nov.**
- *tarsalis* (Olivier) **comb. nov.**
- *torricelliensis* (Ballantyne) **comb. nov.**

Key to species of *Medeopteryx* using males

Modified from Ballantyne (1987a, 2001)

1. Elytral apices not deflexed 2
   Elytral apices deflexed 4
2. T7, 8 dark brown ((Fig. 179). . . . . *similispupillae* **sp. nov**.
   T7, 8 pale (Fig. 170) . . . . *pupilla* (Olivier)
3. Anterior margin of entire LO in V7 emarginated (Fig. 147). . . . . *clipeata* **sp. nov.**
   Anterior margin of LO in V7 not emarginated 3
4. Elytral apices pointed, angle between junction of sides B & C < 45°; e.g. Fig. 144 (Ballantyne 1987a Figs 2g, 8h, 9g, 13o) . . 5
   Elytral apices rounded or truncate, angle between junction of sides B & C > 45°, usually obtuse (Ballantyne 1987a Figs 4b, g, 5g, 6i, 7m, 10h, 11h, 12g, n, 13h) 7

5 Head between eyes orange; endemic to New Britain (Ballantyne 1987a Figs 5, 8) . . . . *effulgens* (Ballantyne)
  Head between eyes brown 6

6 Endemic to Cebu island, Philippines; light patterns unknown; flanges not determined. . . . . *amilae* (Satô)
  Endemic to mainland New Guinea; light patterns described in Ballantyne 1987a: 156); flanges wide, apices may be rounded in Kar Kar Island specimens (Ballantyne 1987a Fig. 9) . . . . *fulminea* (Ballantyne)

7 Elytra pale yellow with apex black; flanges broad, apically rounded (Ballantyne & McLean 1970 Fig. 11) . . *tarsalis* (Olivier)
  Elytra entirely medium to dark brown 8

8 Dimple (depressed area) present on V7; Figs 143, 145 (Ballantyne & McLean 1970 Figs 7, 11; Ballantyne 1987a Figs 2, 7–11) 9
  Dimple (depressed area) absent on V7 (e.g. Ballantyne 1987a, Figs 12, 13) 12

9 Elytral apices truncate, (short, wider than long) . . . . *platygaster* (Lea)
  Elytral apices strongly deflexed (long, at least as long as wide) 10

10 Elytral apices with A and C subequal, slightly longer than B; dimple shallow, hump only gently elevated; median posterior projection of V7 apically scarcely emarginate; dorsally reflexed margins of Vs 6 and 7 entirely brown; flanges of T8 short, wide, apically rounded; ASD subequal to ASW (Ballantyne 1987a Fig. 11). . . . . *elucens* (Ballantyne)
   Elytral apices with A, B and C subequal, or B and C subequal, slightly longer than A; dimple deep, or at least moderately developed, as is hump; MPP of V7 apically emarginate; dorsally reflexed margins of V6 and 7 white, or dorsally reflexed margin of V6 partly brown, and reflexed margin of V7 white; flanges elongate, narrow, apically acute; ASD > ASW 11

11 Elytral apices with A, B, C subequal; dimple deep; (Fig. 143) (Ballantyne 1987a Fig. 7) . . . . *cribellata* (Olivier) **s. str.**
   Elytral apices with B and C subequal, slightly longer than A; dimple only . moderately depressed (Fig. 141) (Ballantyne 1987a Fig. 10) . . . .*corusca* (Ballantyne)

12 Pronotum with pronounced ridges and depressed areas in midlateral areas of disc (Fig. 184); flanges short, wide, apically acute (Ballantyne 1987a Fig. 12) . . . . *sublustris* (Ballantyne)
   Pronotum smooth over most of disc, without any pronounced ridges in midlateral areas 13

13 Antennal FS 7–9 shorter than remainder. 14
   Antennal FS 7–9 not shorter than remainder 15

14 MPP of V7 apically emarginate in ventral aspect, and longer than wide across posterior face; apex of elytron moderately acute (Ballantyne 1987a Figs 3, 4) . . . . *similisantennata* (Ballantyne)

MPP of V7 entire in ventral aspect, and about as long as wide across posterior face; apex of elytron broadly rounded (Ballantyne 1987a Figs 3, 4) . . . . *antennata* (Olivier)
15 Pronotum with median dark spot on disc (Ballantyne & McLean 1970 Fig. 15) . . . . *hanedai* (Ballantyne)
Pronotum without dark markings on disc 16
16 MPP of V7 apically expanded, bearing 2 short fine, dark, dorsally projecting hooks, and a fine lateral ridge; posterior margin of T8 (excluding median emargination) rounded (Ballantyne & McLean 1970 Fig. 14) . . . . *torricelliensis* (Ballantyne)
MPP of V7 narrow, not expanded apically, not bearing hooks or fine lateral ridges as above; posterior margin of T8 (excluding median emargination) straight (Ballantyne 1987a Fig. 13). . . . . *flagrans* (Ballantyne)

Medeopteryx amilae (Satô) comb. nov.

Pteroptyx amilae Satô, 1976: 1. Ballantyne *et al*. 2011:10.

Holotype. Male. **PHILIPPINES**: 9.52N, 123.35E Cebu Island, Argao, 62 km S of Cebu City, 10.x.1968, (Yokosuka City Museum, Japan).

Diagnosis. With orange pronotum and dark brown elytra; without flashing data; very similar to *M. effulgens* and *M. fulminea*, (both of which have associated flashing data), distinguished from *M. effulgens* by the brown head, and from *M. fulminea* by its distribution in the Philippines.

Remarks. Previously it was considered that bent-winged fireflies without the MFC were restricted to New Guinea and northern Australia (Ballantyne, 1987a). *M. amilae* is the first species without the comb recorded west of the island of New Guinea.

The head colour between the eyes of the holotype as interpreted by LB is medium brown (Satô described it as yellow orange). This colour is characteristic of *M. fulminea* which is retained because it is based on Behaviour Voucher specimens where accurate light patterns are related to individual specimens. No such data is available for *M. amilae*.

Medeopteryx antennata (Olivier) comb. nov.

[Figs 154, 160]

Luciola antennata Olivier, 1885: 365.

Pteroptyx antennata (Olivier). Olivier, 1909a: 319. McDermott, 1966: 117. Ballantyne and McLean, 1970: 240. Ballantyne, 1987a: 127. Lloyd, 1973a: 994, 996, 998, 1001, 1003, 1005 (light production); 1973b: 268; 1978: 265 (light production); 1979, Fig. 7.

Pteroptyx antennatum Olivier, 1910b: 47; 1913b: 417. Ballantyne, 1987a: 127 (synonymy).

Lectotype. Male. **NEW GUINEA**: Fly River, designated by Ballantyne (1987a: 127) (MCSN).

Other specimens examined. NEW GUINEA: 143.00E, 9.00S, Western Pr., Ellangowan Island, Fly River, 11.xi.1922, A. McCulloch, male, 2 females (AMSA). Madang District, Alexishafen, Sek Bridge, xi.4.1969, J. Buck (SEK 23), mating pair*.

Diagnosis. 7–9mm long; orange pronotum, dark brown MS and elytra; FS orange or dark brown; FS 7–9 shorter than other FS; elytral apex broadly rounded; LO entire in V7; MPP of V7 short, broad, apically truncate and projecting moderately beyond the posterolateral corners. Distinguished from *M. similisantennata* by the antennal colour, shape of the MPP and outline of the deflexed elytral apices (Ballantyne 1987a Figs 3, 4).

Female (of mating pair) (Figs 154, 160). 8.0 mm long. Colour: as for male except for brown flagellar segments, abdominal ventrites pale brown, V5 paler across posterior margin, V6 entirely pale except for brown laterally reflexed margins and very narrowly brown posterior margin; V7 pale in anteromedian portion; abdominal tergites light brown except for tT7, 8 which are darker than rest. Abdomen (Fig. 154): V6 posterior margin with posterolateral corners acute, broadly excavated across posterior margin with small pointed projection in median line; V8 not indented in median line. Bursa (Fig. 160): two sets of separate plates with very small median oviduct sclerite.

Remarks. Olivier named this species for the distinctive orange FS, and brown scape and pedicel. A lectotype male and a female (Ballantyne & McLean, 1970; Ballantyne, 1987a), and a further male and two females listed above, are the only specimens LB has seen with the pale coloured FS, consistent with the original description. All are from the type locality of the Fly River. All other specimens assigned have brown FS. Ballantyne and McLean (1970:240, Fig. 5) described 2 males with brownish orange FS (from Milne Bay area in Eastern Papua, and River Tor in Indonesia Papua), as *Pteroptyx antennata*, and another 4 males (as "Species A", page 266) which conformed to *P. antennata* except for the uniformly dark FS. Ballantyne (1987a) designated a lectotype male from a syntype series from the type locality and assigned a further 23 males to the species and included Ballantyne and McLean's Species A; all conformed to the description of *antennata* in Ballantyne and McLean (1970) (i.e. all lacked paler coloured FS), and many had flashing data associated (Lloyd 1973a). When observed with the unaided eye the dark and shiny brown scape and pedicel, and dull lighter brown FS approach Olivier's original description.

Lloyd (1973a) described the two major flash patterns of the males and the ability of small groups of flying males to flash in "apparent synchrony." Lloyd (1973b) described and figured the "four modulation flicker"; Lloyd (1978) figured "one of two flicker patterns" and (1979) the flash pattern of Species F (assigned to *antennata* by Ballantyne (1987a).

Guérin-Méneville (1838) described *Luciola ruficollis* with black antennae, abdomen entirely yellow beneath and abdominal apex "trilobo". Ballantyne (1987a) considered *ruficollis* may have been based on *antennata* like specimens. *Luciola ruficollis* is not presently identified in collections of New Guinean *Luciola*.

At Alexishafen *Medeopteryx antennata* is sympatric with, and similar to *M. similisantennata*, with which it apparently shares the same pattern of light production. The similarities in light patterns suggest a form of mimicry.

Medeopteryx clipeata **sp. nov.**

[Figs 147–153]

Holotype. Male. **NEW GUINEA**: Ruka, 9 m, 12.viii.1964, H. Clissold, light trap (BPBM).

Paratypes (42). Same locality as holotype, 18 males. 8.51S, 143.11E, Western District, Oriomo River, 3 m, light trap, H. Clissold, 1.viii.1964, 6 males; 4.viii.1964, 2 males; 6.viii.1964, 14 males; 16.viii.1964, 2 males (BPBM).

Diagnosis. Pronotum orange, elytra dark brown; distinguished from all other *Medeopteryx* by the loss of the anteromedian area of LO in V7 (Fig. 147). Female and larva unknown.

Male. 6.5–7.0 mm long. Colour: pronotum, MS and MN orange; elytra dark brown (under direct microscopic examination the illumination makes the elytral pubescence appear golden thus masking the base elytral colour); head dark brown with a median triangular area on vertex dingy orange; labrum orange; antennae and palpi dark brown; ventral aspect of thorax and abdominal V2–4 and basal fourth of V5 light brown (ventral surface of metathorax sometimes dingy orange); legs orange except tibiae 1, and tarsi of all legs dark brown; V6 and 7 pale cream in area of LO, yellowish elsewhere; all tergites pale brown; dorsally reflexed margins of Vs cream. Pronotum: 1.0–1.2 mm long; 1.4–1.6 mm wide; subparallel sided; punctures small, shallow, separated by their width. Head: moderately depressed between eyes; GHW 1.2–1.3 mm; SIW 0.3 mm; ASD subequal to ASW. Antennae elongate, slender, FS 7–9 not obviously shorter than remaining FS. Elytron (Fig. 153): apex rounded. LO (Figs 147, 149, 151) : retracted from anteromedian area of V7 (the cuticular area extending from the MPP of V7 attaches in this area, as do longitudinal muscles visible through cuticle; Fig. 150). Abdomen: MPP projecting posteriorly a little beyond PLP and projecting ventrally (Fig. 147, 149, 151), terminating in fine paired projections. T8: ventral surface with lateral ridges and finely pointed, forwardly projecting flanges. Aedeagus: (Fig. 152) with apex of median lobe pointed, and bearing an acute ridge on dorsal surface level with the incurved tips of LL.

Remarks. The specific name *clipeata* (clipeatus, a um, Latin = bearing a shield) refers to the shield shaped area in V7 devoid of LO. This new species superficially resembles *M. antennata*. The functional significance of the modifications to V7 and the reduction in LO area are discussed subsequently.

Medeopteryx corusca **(Ballantyne) comb. nov.**

[Figs 139–142, 155, 161, 162]

Pteroptyx corusca Ballantyne, 1987a:1387, Fig. 10.

Holotype. Male. **NEW GUINEA:** Eastern Highlands Pr.: 145.22E, 6.02S, 4.7 miles east of Goroka (ANIC).

Other specimens examined. Listings extend Ballantyne (1987a). **NEW GUINEA**: 143.35E, 3.35S, Wewak, 2–20m, 13.x.1957, on palm, JLG, male (BPBM). 144.45E, 5.53S, Banz, west of Nondugl, 21.vii.1955, light trap, JLG, 1750m, male (BPBM). Banz, Waghi Valley, 1500m, vii.21.1955, light trap, JLG, 2 males (BPBM). 144.37E, 5.55S, Western Highlands, Kamang, near Minj, 1840m, 21.v.1966, JLG, male (BPBM). Western Highlands, Korn farm, 1560m, x.15.1958, light trap. JLG, male (BPBM). 145.22E, 6.02S, Korifeuga, 22 km SE Goroka, 1200m, 30.vii.1961, malaise trap, JLG, male (BPBM). 146.40E, 7.22S, Wau, Morobe Distr., 1200m, 30.vii.1961, malaise trap, JLG, male (BPBM). 146.55E, 8.16S, Tapini, 1000m, 9–12.vii.1968, Mena, 2 males (BPBM).147.13E, 7.52S, Morobe Pr., Garaina, 800m, 15–21.i.1968, J. & M. S., male (BPBM). 147.44E, 8.52S, Kokoda, iii.20.1956, JLG, light trap, 6 males, (1 male 400m), male 28–29.iii.1956, male at 400m, 14–16.xi.1965 (BPBM). Eastern Highlands, Simbu Pr., Chimbu district, Kundiu 5 mating pairs, 26–27.xi.1969; 9.xi.1969, sp. samp. #5 MP 'flasher'(1) (ANIC). Eastern Highlands, outside Goroka on Lae Road, across from Tech. College, mating pair (G383) (ANIC).

Diagnosis. 6–7.5 mm long; yellow pronotum, black MS and elytra; elytral apex rounded (Fig. 141); LOs entire in V7; abdomen with dimple and hump (Figs 139, 140, 142) (Ballantyne 1987a Fig. 10).

Female. 6.8–7.0 mm long. Colour: as for male – pronotum and MN yellow, MS dark brown in posterior 2/3 and dusky brown in anterior 1/3; elytra brown; ventral surface of body including head and legs brown except for pale yellow venter of prothorax and yellow coxae 1, pale light organ, and slightly darker brown posterolateral corners of V7; all abdominal tergites pale brown, T7 slightly darker in lateral third;T7, 8 slightly darker than preceding. Abdomen (Fig. 155): posterolateral corners of V6 rounded, V6 not excavated across posterior margin; posterior margin of V7 broadly, deeply and evenly excavated, with posterolateral corners acutely angled and pointed; V8 not indented in median line. Bursa (Figs 161, 162).

Remarks. Lloyd (1973a) listed all his species by number and his "P. (=*Pteroptyx*) species 17" was identified by Ballantyne as *P. cribellata*. These specimens were subsequently assigned to *P. corusca* (Ballantyne, 1987a), which was the only Highland species recorded. (The improbability of a highland species having been collected around 1890 was pointed out by John Buck and others, who considered that *P. cribellata* could not have been based on highland specimens.). This species is one of a complex of cryptic species, the '*cribellata* complex' of Ballantyne (1987a), who described a female of a mating pair (from Goroka) with lateral pronotal margins finely dark, but otherwise consistent with this description.

"The synchronised flash pattern appeared to be a single simple flash, but actually consisted of 2 modulations a preliminary dim one followed by a brighter one" (Lloyd, 1973a).

Medeopteryx cribellata (Olivier) comb. nov.

[Figs 143, 156, 163]

Luciola cribellata Olivier, 1892:1010.
Pteroptyx cribellata Olivier, 1909a:319. McDermott, 1966:117 (**partim**). Ballantyne & McLean, 1970:242 (**partim**). Lloyd, 1973b:268; 1973a:991; 1979:25. Ballantyne, 1987a: 133. Ballantyne in Calder, 1998:180.
Nec Hanson *et al.*, 1971:161; Hanson, 1978:2158; Haneda, 1966:4; Buck *et al.* 1981a:277, 1981b:287.
Pteroptyx cribellatum Olivier, 1910b:47; 1913b:417. Ballantyne & McLean, 1970: 242 (synonymy).
Pteroptyx cribratellum Pic, 1932:88. Ballantyne & McLean, 1970:243 (synonymy). Ballantyne in Calder 1998:180.
Nec *Luciola platygaster* Lea. Olivier, 1913b:417 (synonymy). Ballantyne & McLean, 1970: 243. Ballantyne in Calder, 1998:180.

Lectotype. Male. **NEW GUINEA**: 9.43S, 147.45E Central Province, Ighibirei, lectotype male of *Luciola cribellata*, designated by Ballantyne (1987a) (MCSN).

Other specimens examined. Unless otherwise indicated, specimens were collected by J., J. H., and M. Sedlacek, and are in BPBM. Listings extend Ballantyne (1987a). **NEW GUINEA**: 145.04E, 6.37S, Chimbu Pr., Karimui: 4.vi.1961, light trap, male, J. & M. Gressitt; 1080m, 14–15.vii.1963, male. 146.35E, 7.13S, Morobe Pr., Bulolo: 700m, 26.xi.1969, 4 males; 6.xi.1969, male; 900m, 6.xi. 1969, male; Bulolo, Vatut: 700–800m, 1–7.vi.1969, male; Bulolo River: 680m, 27.iii.1969, male; 700m, 26.xi.1969, male; 800–900m, 31.viii.1965, male; 850–900m, 24.viii. 1965, 2 males. 146.40E, 7.22S, Morobe Pr., Wau, Kujera: 1300m, 27.vi.1969, male, A. Mirza. Wau, Morobe District: 880–1050m, 8–9.ii.1963, male; 1050m, 11.xi.1961, male, 5.i.1961, male; 1100m, 29.viii.1961, male, 26.x.1961, 2 males; 1150–1600m, 9.xi.1968, male; 1200m: 27.i.1966, male; 13.viii.1961, light trap, male; 14.vii.1961, light trap, male; 5–13.iii.1964, M–V light trap, male, 8.v.1967, on *Amaranth*, no collector, male; 12–1300m, 22.x.1965, male; 1300m, 14.viii.1961, male; Oct 19, 1969, J. E. Lloyd (G381) male, female.

Wau, Morobe District, Mt Missim: 880–1050m, 8–9.ii.1963, 4 males; 900m, 22.ii.1965, 2 males. 147.44E, 8.52S, Kokoda, 380m, iii.20.1956, light trap, 2 males, JLG; 28–29.iii.1956, light trap, 2 males, JLG; 400m, 17–18.xi.1965, male. Madang District, Kar Kar Island, 'Mt H. I. Tree' 28.XI.1973, E. Ball Tube 21, 16 males 18 females (10 dissected) (ANIC).

AUSTRALIA, Queensland: Cape York Peninsula: Dividing Range, 15 km west King Billy Creek, 5–12. ii. 1976, G. B. Monteith, 3 males (synchronous flashing). (QMBA). 143.17E, 12.44S, Iron Range, Gordon's Creek, 8.viii.1983, B. Gillies, male (MUMA).

Diagnosis. Orange pronotum, dark brown elytra, rounded elytral apices (Fig. 143), dimple on V7 (Fig. 143 arrowed); distinguished from other similarly coloured species by the dimensions of the deflexed elytral apex (A, B, C are subequal) and the deep dimple on V7 (Ballantyne 1987a Fig. 7).

Female (Figs 156, 163) (Kar Kar Island specimens). 6.5–7.2 mm long. Colour: as for male except for dusky brown MS appearing slightly darker in posterior half (probably because of underlying mesothorax), pale LO in V6, and moderately dark brown V7, 8 and T7, 8 (V7 may bear irregular whitish patches along its anterior margin and the posterolateral corners of V7 may be darker brown than rest. Abdomen (Fig. 156): posterior margin of V6 not excavated, posterolateral corners rounded; posterior margin of V7 broadly, deeply and evenly excavated, with posterolateral corners acutely angled and pointed; V8 not indented in median line. Bursa plates (Fig. 163).

Remarks. The type locality of Ighibirei is in Central province on the Kemp Welch river (Helgen *et al.* 2008). In the absence of knowledge of this locality specimens were assigned to this species (see Ballantyne and McLean 1970; Ballantyne 1987a). Any reassessment of such specimens can only be made on morphological grounds.

In the absence of any flashing data, Ballantyne and McLean (1970) assigned a range of morphologically variable specimens to *Pteroptyx cribellata.* In 1970 LB had provided Lloyd with tentative determinations, and his species "P. 17" was thus identified in Lloyd (1973a) as *Pteroptyx cribellata.* Ballantyne (1987a) described a lectotype and considered that only two of Lloyd's (1973a) species, viz. species 17 and 20, conformed closely to *cribellata.* The flashing patterns of these two species are very similar. LB eliminated the possibility of Lloyd's species P. 17 with its highland distribution, being *cribellata* (Ballantyne, 1987a). Of the broad assemblage of specimens tentatively assigned to *cribellata* by Ballantyne and McLean (1970), and reassigned by Ballantyne (1987a), only specimens with lowland distribution were considered as possible *cribellata.*

Haneda (1966), Hanson (1978), and Hanson *et al.* (1971) refer to *Pteroptyx cribellata* from New Britain; the species is *Medeopteryx effulgens* (Ballantyne 1987a). Buck (1988:268) was not sympathetic to the need for such taxonomic changes, despite having heralded the possibility (Buck *et al.*, 1981a:278).

Olivier (1913b) synonymised *Luciola platygaster* Lea with *Pteroptyx cribellata* (Olivier). Ballantyne and Lambkin (2000) assigned *platygaster* to *Pteroptyx.*

Specimens listed here extend the range of *cribellata* and are tentatively assigned as no definitive information on light production is available.

Medeopteryx effulgens **(Ballantyne) comb. nov.**
[Figs 144, 157, 164]

Pteroptyx effulgens Ballantyne, 1987a: 141.
Pteroptyx cribellata Olivier misidentification. Hanson *et al.* (1971), Hanson (1978), Buck *et al.* (1981a, 1981b).

Holotype. Male. **NEW GUINEA**: 152.00E, 4.00S, New Britain, Gazelle Pen., 8.2 mi S Rabaul (ANIC).

Other specimens examined. Unless otherwise indicated specimens are in BPBM. Listings extend Ballantyne (1987a). **NEW GUINEA**, New Britain: Bismarck Archipelago: 152.0E, 4.20S, Vudal, SW of Keravat, 13.xii.1959, T. Maa, male. Gazelle Peninsula, 140m, 21–27.x.1962, malaise trap, JS, male; Gazelle Peninsula, Baipinrs: St Pauls, 350m, 4.ix.1955, light trap. JLG, male. 152.20E, 4.20S, Keravat, Lowl Agr. Exp. Sta., 3.vi.1965, 3 males, 2 females; 21.vii.1965, 2 males G. S. Dun; 15.vi.1954, J. Szent-Ivany, female, resting on cacao (Dept. Agriculture, Port Moresby). Keravat, 10.ii.1966, G Monteith, 13 males, 2 females (Tubes 231, 221, 223 UQIC); 60 m, ix.11.1955, JLG, 2 males, 31.viii.1955, male. Vunabakan, 180m, 10 km east of Keravat, 16–20.xi.1959, T. Maa, 6 males, female. Gazelle Peninsula, Malmalwan–Vunakanau, v.4.1956, light trap, 4 males, v–11–13–1956, male, JLG. 150.0E, 5.0S, Willaumez Peninsula, Volupai, 100m, iv.16.1956, light trap. JLG, male. Vunakanau, 350m, x.10.1957, 2 males, v.4.1956, JLG 2 males. 151–152.0E, 5.0–6.0S, Jacquinot Bay, Wunung Plantation, iv.30.1956, JLG, male. 152E, 2–5.0S, New Ireland: Lakuramau Plantation, east coast, 1.viii.1955, feeding on cacao foliage (adult was probably resting), J. Szent-Ivany, male (Dept. Agriculture, Port Moresby).

Diagnosis. 6.8–7.5mm long; orange yellow pronotum, MS and MP; head between eyes yellow; deflexed elytral apex pointed; LO entire in V7; abdomen with dimple and hump; distinguished from all but *M. fulminea* and *M. amilae* by the possession of pointed elytral apices, and from *fulminea* and *amilae* by the orange head, and apparent restriction of *effulgens* to New Britain (Ballantyne 1987a Fig. 8).

Female. 5.7–6.9 mm long. Colour: as for male except V5 sometimes paler brown than preceding ventrites, pale light orgn in V6, and the yellow semitransparent terminal two ventrites; basal abdominal tergites brown, T7, 8 paler brownish yellow than preceding ones. Abdomen (Fig. 157): posterior margin of V6 not excavated, posterolateral corners rounded; V7 broadly, moderately deeply and evenly excavated along posterior margin, with posterolateral corners acutely angled and pointed; V8 not indented in median line. Bursa (Fig. 164).

Remarks. Ballantyne (1987a) included only specimens with associated flashing data in the type series, and indicated that assignment of specimens without flashing data was tentative only. Because *effulgens* and *fulminea* are very similar, determination of the colour patterns (especially those of head, MS and the terminal tergites) is important. Ballantyne (1987a) encountered difficulty determining colour patterns in alcohol preserved specimens, which were apparently dead before being preserved. This difficulty is sometimes overcome by drying specimens before examination.

M. effulgens has an orange head with a dark triangular area on the vertex, and occur in New Britain. However Ballantyne (1987a) recorded one mating pair with an orange-headed male and black-headed female. No conclusions should be drawn from distributional records of specimens other than those of the type series. Type specimens of *effulgens* and *fulminea* are not sympatric, with *effulgens* restricted to New Britain while *fulminea* occurs on the New Guinea mainland. Although very similar morphologically, their light production is different.

Ballantyne and McLean's (1970) composite *Pteroptyx cribellata* included certain specimens with orange head; their Groups 1A, p. 244 and 1D, p. 244 were recorded from both New Guinea and New Britain, and the New Guinean specimens are tentative inclusions here.

In New Britain *M. effulgens* is sympatric with an orange-headed *Australoluciola pharusaurea* **sp. nov.** Lloyd (1973a) recorded 2 collecting sites "SW of Simpson Harbor, on Burma Road......The swarm trees were cocoas and palms at the roadside. Males flashed single, short flashes at a period of about 1.2 sec., frequently in bouts of about 6 flashes". Lloyd (1973a) described the "simple flashes" of both *M. effulgens* and *M. fulminea* and he listed them on p. 268 as species 15 and 16, and figured the flashes of the latter.

The species recorded as *Pteroptyx cribellata* in Hanson *et al.* (1971), Hanson (1978), Buck *et al.* (1981a, 1981b) from New Britain is *M. effulgens.*

Medeopteryx elucens (Ballantyne) comb. nov.

Pteroptyx elucens Ballantyne, 1987a: 147.

Holotype. Male. **NEW GUINEA:** 146.40E, 7.22S, 4 mi n Wau, elev. c 2800', near Kunai Creek, Lae Road (ANIC).

Other specimens examined. Listings extend Ballantyne (1987a). **NEW GUINEA**: 143.35E, 3.35S, Wewak, 2–20m, 13.x.1957, JLG, male. 146.35E, 7.13S, Bulolo, 1010m, 19.viii. 1956, male, light trap, EF. 146.40E, 7.22S, Wau, Morobe Dist., 1200m, male 29.vi.1961, at light, male 22–30.vi.1962, light trap. 146.55E, 8.16S, Tapini, 1000m, 9–12.vii.1968, 2 males, Mena. (BPBM).

Diagnosis. 6.5–7.2 mm long; pronotum and MN yellow, MS medium brown; head dark brown; elytral apices rounded; very similar to *M. corusca* and *M. cribellata*, from which it can be distinguished by the completely dark dorsal aspect of the abdomen, the outline of the median posterior projection of V7, the ventral surface of T8 including the shape of the flanges, and its simple single flash (the other 2 species have a bimodal flash) (Ballantyne 1987a Fig. 11)

Remarks. Lloyd (1973a) recorded it as "abundant at the Namie-Bulolo site near Wau" and sympatric with *M. effulgens, M. cribellata, M. sublustris,* and 3 *Luciola* species, and the male flash pattern "a single, short flash with a period of about 5.5 secs".

Medeopteryx flagrans (Ballantyne) comb. nov.
[Figs 146, 158]

Pteroptyx flagrans Ballantyne, 1987a:151.

Holotype. Male. **NEW GUINEA**: 144.58E, 5.59S, Chimbu District, Catherine Mission (ANIC).

Other specimens examined. Specimens are in BPBM unless otherwise indicated, and listings extend Ballantyne (1987a). **NEW GUINEA**: 145.53E, 5.54S, Above Kerowagi, 2300m, vii.6.1955, JLG, male. 144.37E. 5.55S, Minj, W Highlands, ix.8–13.1959, sweeping, T. Maa, 2 males, 2 females. 145.04E, 6.37S, Karimui, 1080m, 13.vii.1963, male. 146.40E, 7.22S, Wau, Morobe District, Mt Missim, 1100m, 17.i.1963, H. Clissold, male; 880–1050m, 8–9.ii.1963, male; 1450m, 20.iii.1974, on Urticaceae, JLG male. Wau, Bulolo River, 850–900m, 24.viii.1965, male; 1100–1200m, 25.ix.1968, male NK. Morobe Dist., Aseki, 1100m, 13.iv.1974, A. Hart, male. Feramin, 150–120m, 11–22.v.1959, WB, male. Chimbu District, Kundiu, Catherine Mission.26–29.XI.1969, 8 mating pairs; one MP #6, 13.XI.1969; 1 MP no spect. 8.XI.1969 (ANIC).

INDONESIA, West Irian (as New Guinea, Netherlands): 140.10E, 2.48S, Genjam, 40 km W of Hollandia, 100–200m, 1–10.iii. 1963, T. Maa, male. Guega, W. of Swart Valley, 1200m, 15.xi.1958, JLG, 2 males. Swart Valley, W side, 1400–2000m, xi.13.1958, male, JLG. Swart Valley, Karubaka, 1450m, xi.12.1958, male; 1300m, xi.7.1958, 2 males, 3 females, JLG.

Diagnosis. 6.1–7.1mm long; pronotum, MP yellow, MS dusky yellow, darker than pronotum; frons and labrum sometimes orange; elytral apices rounded (Fig. 146); LOs entire in V7; dimple and hump absent; distinguished from *M. torricelliensis* (Fig. 183) by its smaller size and the outline of the terminal abdomen; from *M. hanedai* by the uniformly orange pronotum, and *M. sublustris* by the smooth surface of the pronotum (see Fig. 184) (Ballantyne 1987a Fig. 12; Ballantyne & McLean 1970 Figs 14, 15).

Female (Fig. 158) (Kundiu specimens). 5.9–7.2 mm long. Colour: as for male except for dusky brown MS, pale LO in V6, and slightly paler brown V7, 8 which may be irregularly marked laterally in darker brown. Abdomen: posterior margin of V6 not medially emarginate, posterolateral corners rounded; posterior margin of V7 broadly, shallowly and evenly emarginated, posterolateral corners rounded; V8 not indented in median line. Bursa with two sets of wide plates.

Remarks. Ballantyne (1987a:152) described the flashing patterns of this species which earned it the common name of "flickerer" used by Lloyd, Buck, Hopkins and others.

Lloyd (1973a) described "3 common and distinctive luminescent patterns" and the female behaviour pattern, where "females are attracted to and land near flashing males. In other species (non *Pteroptyx*) studied in New Guinea and elsewhere, it is the males that are attracted to stationary luminescing females".

Medeopteryx fulminea (Ballantyne) comb. nov.
[Figs 145, 159]

Pteroptyx fulminea Ballantyne, 1987a:153.

Holotype. Male. **NEW GUINEA**: Morobe District, 2,800' (ANIC).

Other specimens examined. Collector is J. Sedlacek unless indicated otherwise, and specimens are in BPBM. Listings extend Ballantyne (1987a). Ball's tubes from Kar Kar Island (in ANIC) are identified by tube number and annotation as KK followed by a number; these can be related to field data records kept by Ball. Specimens * have lateral pronotal margins finely dark.

NEW GUINEA: 146.00E, 4.40S, Kar Kar Island, Namau, 0–200m, 9.viii.1968, NK, 11 males; 145.52E, 4.42S, Kurum, 0–100m, viii.1968, NK, male. Kar Kar Island, Eldon Ball, 22.xi.1973 3 males, 6 females (tube 11 KK2); 20.xi.1973 5 females (tube 13 KK1); 22.xi.1973 2 males, 5 females (tube 9 KK2); 23 Nov 1973 9 males, 1 female (Tube 20, KK2); 22 Nov 1973 5 males, 4 females (tube 25 KK5); 22 Nov 1973 5 males 4 females (tube 28 KK4)(ANIC). 147.51E, 6.35S, Finschhafen, 14.iv.1944 male, 21.iv.1944 male*, E. Ross; iv.1944, F. Skinner, male*. 146.53E, 6.43S, Bubia, near Lae, vii.22.1959, *Freycinetia*, male. 146.35E, 7.13S, Bulolo, 700m, 18.vi.1969, male, 6.xi.1969, male, 26.xi.1969, 4 males (2 males*), 31.xii.1969, male. Bulolo River, 680m, 2.ii.1969, male*, 23.iv.1969, male*, 8.v.1969, male*, 4.vi.1969, male*; 26.xi.1969, 2 males*; 1130m, 17.ix.1969, male*. Bulolo-Vatut, 7–800m, 1–7.vi.1969, male*. 146.40E, 7.22S, Wau, Morobe District, 1080m, 15.viii.1964, light trap, male*; 1100m, 2.ix. 1961, male*; 1150m, 11.vii.1971, (*Mallotus*), male; 1200m, 19–23.vi.1961, light trap, 2 males; 30.vii.1961, malaise trap, male; 10.vii.1961, male; 7.viii.1961, male; 14.viii.1961, light trap, male; 17.viii.1961, light trap, male*; 26–29.ix.1961, M-V light trap, male; 27.x.1961, 2 males; 15–22.xi.1961, 3 males; 19.xi.1961, 2 males (1 male *); 2.xii.1961, male; 15.xii.1961, male*; 18.xii.1961, 2 males*; 25.xii.1961, male; 28–30.vi.1962, light trap, male*; 23.i.1968, male; 22.iii.1969, on coffee, male*; 19.vii.1971, (*Mallotus*), 2 males; 6.vii.1973, on *Ficus* sp., male; 1200–1300m, 4.ii.1962, male, G. Monteith; 14–17.i.1963, male; 1600–1700m, 28.xii.1961, male. Wau, Hospital Creek, 1200m, 6.iv.1965, male. Wau, Mt Missim, 900m, 22.ii.1965, male*. 147.10E, 7.53S, Garaina, 800m, 15.i.1968, male*, 4.i.1968, male*, 830m, 13–15.i.1968, male*. 147.44E, 8.52S, Kokoda, 400m, 15–20.xi.1965, light trap.4 males; 18.xi.1966, male; 380m, iii.20.1956, light trap, JLG, 2 males. 147.07E, 9.30S, east of Port Moresby, Bisianumu, 500m, 8.vi.1955, primary forest, JLG, male. Daradae Plantation, 500m, 80 km N to Port Moresby, ix.4.1959, T. Maa, 21 males (1 male sweeping). Mamai Plantation, near Port Glasgow, i.1965, 30–60m, P. Shanahan, male.

INDONESIA, West Irian (as New Guinea, Netherlands): 139.00E, 2.00S, River Tor, mouth, 4 km E of Hol Maffen, 2–5.vii.1959, light trap, T. Maa, male*. 140.39E, 2.37S, Hollandia area, W Sentani, Cyclops Mts, 50–100m, 22–24.vi.1959, light trap, JLG and T. Maa, male. Hollandia, 13.iii.1960, T. Maa, male.

Diagnosis. 5.5–6.8 mm long; pronotum yellow with narrowly dark lateral margins; MP yellow, MS dark brown; head between eyes brown; deflexed elytral apex pointed (Fig. 145; Ballantyne 1987a Fig. 9); LOs entire in V7 (Fig. 145); most similar to *M. amilae* and *M. effulgens,* distinguished from the former by its patterns of light production and distribution in eastern New Guinea, and from the latter by light patterns, head colour, and occurrence in mainland New Guinea.

Female (Fig. 159; Kar Kar Island specimens). 6.3–7.2 mm long. Colour: as for male with dark MS; pale LO in V6; V7, 8 not as dark as preceding ventrites, V7 may have pale markings irregularly scattered in anterior section. Bursa plates like those of *M. cribellata*: (e.g. Fig. 163).

Remarks. Ballantyne (1987a) chose the specific name to emphasize the pattern of light production, and the common name of "flasher" given by Buck and others. *M. effulgens* and *M. fulminea* may be restricted in distribution i.e. *effulgens* to New Britain and *fulminea* to mainland New Guinea. Ballantyne's (1987a) decision to erect 2 species was a purely taxonomic one. Ballantyne (1987a) described two exceptions in the New Britain population of *M. effulgens* without orange heads; of specimens recorded here the dark headed Lindenhafen male has MS dusky and T8 dark; the Keravat male has MS and T8 pale. Ballantyne (1987a) recorded two elytral apex types for specimens assigned to fulminea– viz. elytral apices pointed (Fig. 9g) and rounded (Fig. 9j), but keyed the species with elytral apices pointed. Specimens from Kar Kar Island have elytral apices more broadly rounded, and their assignment here without any information on flashing patterns is thus tentative only.

Lloyd (1973a) recorded this species from "Bulolo River near Wau....near Lae at the Markham River Bridge...and at Alexishafen at the Biges River Bridge". It occurred alongside *M. pupilla* and *M. antennata* at Alexishafen, and *M. elucens* at Wau (Ballantyne 1987a, p. 156); it emits "single short flashes at periods of 1 to 1.9 sec " (Lloyd 1973a). At similar temperatures the interval is 1.2–1.3 seconds for both *fulminea* and *effulgens.* The single male in "Species F" (Ballantyne & McLean, 1970) is assigned to *M. fulminea.*

Medeopteryx fulminea was erroneously recorded as "P. sp. 3" under "P. 19. *Pteroptyx antennata"* by Lloyd (1973a:1001) (Ballantyne, 1987a).

Medeopteryx hanedai (Ballantyne) comb. nov.

Pteroptyx hanedai Ballantyne, in Ballantyne & McLean, 1970:259.

Holotype. Male. **NEW GUINEA**: 144.44E, 5,51S Star Mountains, Sibil Valley (BPBM).

Other specimens examined. NEW GUINEA: 143.00E, 9.00S, Western Pr., Fly River, Losobip, 400–600 m, viii. 1969, JS, male, 2 females (BPBM).

Diagnosis. 5.9–6.2 mm long; distinguished from all other *Medeopteryx* by the median dark marking on the pronotum. (Characters of terminal abdomen not determined).

Remarks. *Luciola aspera* Olivier, described from a female, has median dark pronotal markings similar to *M.*

hanedai; however males without deflexed elytral apices are assigned to *aspera* which is transferred to *Australoluciola* **gen. nov.**

The Fly River male is the only representative of this species from other than the Sibil Mountains and the specimens may not be conspecific.

Medeopteryx platygaster (Lea) comb. nov.

Luciola platygaster Lea, 1909:110. Olivier, 1910b:45.
Pteroptyx platygaster (Lea). Ballantyne & Lambkin 2000: 69.
Nec *Pteroptyx cribellata* Olivier. Olivier, 1913b:417 (synonymy). McDermott, 1966:117. Ballantyne & McLean, 1970:242. Ballantyne, 1987a:133. Ballantyne in Calder, 1998:180.

Lectotype. Male. **AUSTRALIA.** Cairns, lectotype male of *Luciola platygaster* Lea, designated by Ballantyne & McLean (1970) (SAMA).

Diagnosis. An Australian *Medeopteryx* with orange pronotum, dark brown elytra, dimple and hump on V7, and narrowly deflexed elytral apex (Ballantyne & Lambkin 2000 Fig. 20). Female macropterous, larva unknown.

Remarks. Ballantyne and Lambkin (2000) revealed two species of *Pteroptyx* (now *Medeopteryx*) in Australia, distinguished by the form of the deflexed elytral apex. The females recorded from Iron Range in Ballantyne and Lambkin (2000:69) are probably females of *M. cribellata*.

Medeopteryx pupilla (Olivier)
[Figs 168–176]

Luciola pupilla Olivier, 1892:1011; 1902:72.
Pteroptyx pupilla (Olivier). McDermott, 1966:117.
Luciola (Luciola) pupilla Olivier. Ballantyne & McLean, 1970:237, 268. Nec Ballantyne, 1987a:164, 165, 167; Ballantyne, 1987b:177, 178, 185.

Lectotype. Male designated here. **NEW GUINEA**: 9.43S 147.45E Central Pr., Ighibirei (MCSN).

Other Specimens examined. NEW GUINEA: 5.14S, 145.45E, Madang Dist., Sek Harbor, 10 mi n Madang, Oct. 5, 1969, J.E. Lloyd, 2 males (G148, 141). (JELC). Mt Lamington District Northern Division, C. McNamara 6 males (1 male v.1927) (AMSA).

Diagnosis. One of two *Medeopteryx* with trisinuate V7 but without deflexed elytral apices; distinguished most from *M. similispupillae* by the pale terminal abdominal tergites (Fig. 170) and the broader ML (that of *similispupillae* is very narrow; Fig. 182).

Male. 5.3 (lectotype)–7.7 mm long. Colour (Fig. 168): pronotum dingy orange (finely dark margined in G141); MS dingy orange, marked in brown in anterior half; MN cream; elytra uniformly very dark brown, reddish brown with narrowly pale margins in one Mt Lamington male; head between eyes, antennae and palpi almost black (head of G148 appearing paler brown as semitransparent cuticle reveals underlying fat body); entire ventral surface of thorax, all of legs 1–3 dark brown (coxae and base of femora of legs 1, 2 orange in one Mt Lamington male); basal abdominal ventrites dark brown; V5–7 dirty white (1/4 to ½ of posterior area of V5 pale in Mt Lamington males; T2–6 yellow (lectotype), brownish in Mt Lamington males, semitransparent, T7–8 white, semitransparent. Pronotum: 1.3 (lectotype)–2.2 mm wide, 1.0 (lectotype)–1.4 mm long, W/L = 1.4–1.7; punctures shallow, contiguous across anterior and lateral margins, separated by up to their width over central area of disc; midanterior margin broadly rounded, moderately projecting beyond rounded anterolateral corners, with lateral margins subparallel, converging slightly in anterior and posterior third in lectotype; lateral margins divergent slightly posteriorly, with anterolateral and posterolateral corners angulate in Mt Lamington males. Head: GHW 1.1(lectotype)–1.8 mm, SIW 0.2 mm; ASD slightly < ASW. FS elongate, slender, subequal. Abdomen (Figs 169, 170, 175, 176): LOs occupying all of V6 and 7 except for narrow posterior margin of 7; MPP moderately broad, longer than wide, apically truncate (lectotype) or slightly emarginated, longer and wider than PLP, T8 with broad short rounded flanges in lectotype; flanges about as long as wide and apically truncate in Mt Lamington males (Fig.

175). Aedeagus: (Figs 171–173) ML expanded, and may appear concave in posterior half, 0.7 as wide as LL across narrowest portion of ML; LL inturned at inner apex.

Remarks. Confusion in the literature over the identity of *Luciola pupilla* is resolved by designation of a lectotype (first in a syntype series). McDermott (1966) incorrectly assigned *pupilla* to *Pteroptyx.*

LB tentatively identified Lloyd's (1973a) *Luciola* species 11 as *Luciola pupilla* and abdominal modifications were described (Ballantyne, 1987a, b). This study has revealed two species with similar V7, viz. *M. pupilla* and *M. similispupillae* **sp. nov.**

It is now possible to determine an approximate location for "Ighibirei" which is also the type locality of *Medeopteryx cribellata* (Olivier). Helgen *et al.* (2008) referred to Loria's collecting locality as either "on the Kemp Welch river some little way inland "or " just inland from the mouth of the Wanigela River". The elevation is unknown.

Lloyd's field records for specimen G148 read "slow double pulse signal, one second interval".

Medeopteryx similisantennata (Ballantyne) comb. nov.

Pteroptyx similisantennata Ballantyne, 1987a:158.

Holotype. Male. **NEW GUINEA**: 145–146.00E, 4–6.00S, Madang District, Alexishafen, at bridge (ANIC).

Diagnosis. Moderate sized (7.5–8.9 mm long); pronotum, MS and MN orange; elytra dark brown; LO entire in V7; dimple and hump absent; very similar to *Medeopteryx antennata* (Olivier), distinguished by the outline of the terminal abdomen and elytral apex and the uniformly dark antennae (Ballantyne 1987a Figs 3, 4).

Remarks. The specimens included by Ballantyne (1987b:159) in the type series of this species were initially included by Lloyd (1973a) in *Pteroptyx* (now *Medeopteryx*) *antennata* on the basis of their flashing data, and similarities with that species are discussed elsewhere.

Medeopteryx similispupillae sp. nov.

[Figs 164–167, 177–182)

Holotype. Male. **NEW GUINEA**: Madang District, Alexishafen at bridge, 10.x.1969, (G206) J E Lloyd (ANIC).

Paratypes (68) **NEW GUINEA**: Madang District, Alexishafen, at bridge, 1969, J.E. Lloyd, Oct. 9 3 males (G184, 193, 198*); Oct. 10 3 males (G204, 211, 215); Oct. 12 4 males (G218, 219, 222*, 224); x/9/1969, SEK 12, J Buck male (ANIC). Madang District, Sek Harbor, 10 mi N Madang; Oct. 7 male (G174); Oct. 29 male (G448).(JELC). All but * have associated flashing data.

The following ethanol preserved paratypes have associated flashing data with labels quoted exactly as written to permit association with Buck's field records (KK= Kar Kar Island followed by tube number). Collector is J. Buck and specimens are in ANIC unless otherwise indicated

NEW GUINEA: 4.40S, 146.00E, Kar Kar Island: 2 males, xi/II/1969, KK/1; male, female xi/13/1969 KK#1; male xi/14/1969 phase shift, bat house, KK/1; male, xi/14/1969, phase shift bat house, KK/2; male, xi/15/1969 phase shift bat house, KK/3; male, xi/15/1969 phase shift, bat house, KK/4; mating pair xi/11/1969 KK/4; male, xi/11/1969 phase shift, bat house, KK/5; male, xi/15/1969 phase shift, bat house KK/6; male, xi/16/1969 phase shift, bat house, KK/7; male, xi/15/1969 phase shift, bat house KK/8; male, xi/16/1969, phase shift, bat house KK/9*; 2 males, xi/11/69 KK/9*; male, xi/11/1969, KK/11; male, xi/11/1969 KK/12*; male, xi/11/1969, KK/13*; 2 males, xi/11/1969, KK/14*; male, female, xi/11/1969, KK/15; 4 males, xi/11/1969 KK/16; male, xi/11/1969 KK/16; 2 males, xi/11/1969 KK/16; 4 males, xi/11/1969, KK/16; male, xi/11/1969 KK/16; male, female Kar Kar morgue, xi/11/1969, KK/21; male, X/23/1969; male, xi/11/1969 used by Eldon Ball Tube KK/E41; male, xi/11/1969. Collector Eldon Ball: 2 males, 22 Nov. 1973 KK/1–1,1–21 Tube 18; male, Tube 5A (no other data); male, (used for temperature coefficient work), Tube Ball 4; 3 males, 22 Nov 1973, KK–3, 1–23, Tube 8; 3 males, specimens #2, #6 and #8 respectively, labelled Kar Kar, near Kurum school, to accompany tapes 1A & 1B of 25/xi/1973. (ANIC).

Code name. *Luciola* 11 (Lloyd, 1973a).

Diagnosis. One of two species of *Medeopteryx* with trisinuate V7 but without deflexed elytral apices; most obviously distinguished from the similar *M. pupilla* by the dark brown T6–8 (those of *pupilla* are pale).

Male. 6.5–7.3 mm long; Colour (Fig. 177–179) pronotum bright clear orange, fat body evenly distributed beneath; MN cream; MS transparent, orange in anterior half, brown in posterior half in holotype, orange in G204, dark brown in G184, 193, 218, 219, 222, 224; elytra dark brown, (lateral margin may appear paler because of golden hairs); head between eyes with a triangular very dark brown area on vertex, remainder medium brown; median fine dark sulcus apparent through posterior dark triangle on head; labrum transparent, dingy orange; apices of palpi dark brown; antennae dark brown (as dark as vertex), scape and pedicel largely glabrous, appearing slightly darker than hair covered FS or much darker in G193, 184; ventral surface of pro and mesothorax, coxae 1 and 2 and bases of femora 1 and 2 orange; rest of legs 1 and 2 brown; all of metathorax and legs 3 brown (except for orange trochanters); basal abdominal ventrites brown, V5 with very narrow cream band across midposterior margin; V6 and 7 creamy yellow; all tergites, and dorsally reflexed lateral margins of ventrites, brown (Fig. 179). Pronotum: 1.3–1.6 mm long, 1.3–2 mm wide, W/L = 1.2; punctures small, shallow, irregularly distributed, contiguous or separated by up to their width; midanterior margin rounded, projecting moderately beyond acute anterolateral corners; lateral margins converging in anterior and posterior areas; midposterior margin indented. Head: GHW 1.5–1.6 mm; SIW 0.3–0.4 mm; ASD = ASW. LOs: occupying V6 and 7 entirely except for narrow posterior band of 7; MPP of V7 moderately broad, apically truncate (Fig. 178) projecting a little beyond the broadly rounded LPP, and separated from them by moderately deep excavations; dorsal face of V7 bearing 2 elevated cuticular strips; T8: median posterior margin emarginated (Fig. 179); with lateral ridges and flanges similar to those of *M. pupilla*. Aedeagus: (Figs 180–182): elongate, slender; ML narrowed in middle third, ¼ as wide as LL at this point.

Female. 6.3–7.2 mm long; coloured as for *M. pupilla* and not further distinguished here.

Remarks. This species was initially identified by LB as *Luciola pupilla* and references to *L. pupilla* in Ballantyne (1987a:164, 165, 167, Fig. 14k; 1987b:177, 185), Buck and Buck (1978:486, 487), and Hanson (1978:2158) are to this species (See Table 1). Lloyd (1973a) described the flash pattern "Males flew slowly around and through the bushes and trees, emitting single, short flashes at periods of ca 1 sec".

Medeopteryx sublustris (Ballantyne) comb. nov.

[Fig. 184]

Pteroptyx sublustris Ballantyne, 1987a:160.

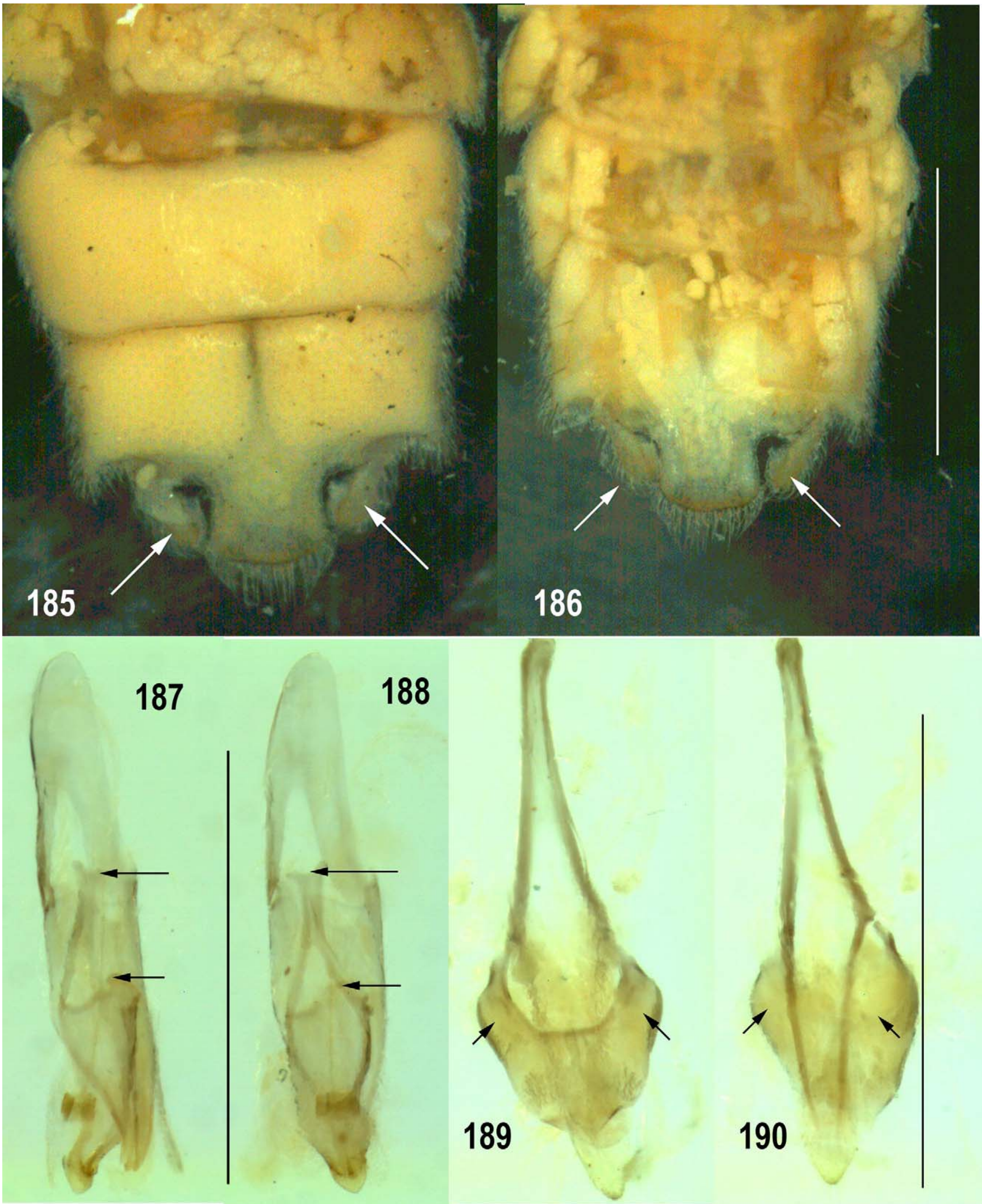
Holotype. Male. **NEW GUINEA**: 146.40E, 7.22S, Morobe district, 4 miles north of Wau, 2800', near Kunai Creek, Lae Road, xi.12.1969, J. Lloyd (ANIC).

Other specimens examined (listings extend Ballantyne 1987a)**. NEW GUINEA**: 146.53E, 6.43S, Bubia, Markham valley, 50m, 20.ix.1955, JLG, male. 147.00E, 6.45S, Lae, 20m, 19.vii.1964, JS, male. 146.35E, 7.13S, Bulolo, 700m, 26.xi.1969, JS, male. Bulolo River, 680m, 8.v.1969, JS, male. Sum-Sum, 580m, 64 km north of Wau, 15.ii.1963, H. Clissold, male. 147.10E, 7.53S, Garaina, 830m, 13–15.i.1968, JS, male. 148.15E, 8.45S, Popondetta, 23.ii.1966, G Monteith, male, 4 females (Tube 240, UQIC). 147.44E, 8.52S, Kokoda, 400m, JS, 15–20.xi.1966 male, 18.ix.1966, male. Kokoda-Pitoki, 450m, iii.24.1956, JLG, male. (BPBM).

Diagnosis. 6.5–7.3 mm long; pronotum orange, MS yellow, MN brown; without dimple and hump on V7; distinguished from all other *Medeopteryx* by the elaborate pronotal sculpturing (Fig. 184) (Ballantyne 1987a Fig. 12).

Remarks. The specific name characterises the flash pattern, where, to the naked eye, the second component of the double flash is not visible (sublustris = gleaming faintly, glimmering). "The 2 peaks are nearly completely separate and the 1st is about twice the intensity of the 2nd" (Lloyd, 1973a). This species was not at first recognized by Lloyd in the field.

Olivier (1909a) described *Luciola foveicollis* from New Guinea with distinctive pronotal sculpturing and colour pattern similar to this species. However *Luciola foveicollis* (assigned herein to *Australoluciola* **gen. nov.** and redescribed) lacks the deflexed elytral apex and the pronotal sculpturing of the holotype is not to LB's eye at all unusual, and quite unlike the distinctive pattern described for *sublustris.*



FIGURES 185–190. *Poluninius selangoriensis* **gen.** *et* **sp. nov.** Holotype male (ANIC). 185, 186 abdomen, ventral (185) and dorsal (fleshy lobes of V7 arrowed; 186 with T8 dissected; 187, 188 aedeagus left lateral (187) and ventral (top arrow is anterior margin of ML; bottom arrow is anterior margin of LL on dorsal surface; 189, 190 aedeagal sheath dorsal (189) and ventral (paraprocts arrowed). These figures share scale lines: 185, 186; 187, 188; 189, 190.

FIGURES 191–199. *Pteroptyx bearni* (type male 191–195 MNHN; Pingan Pingan male 195–196 FRIM; Kalabakan River male 198, 199 ANIC). 191 dorsal at top, labels beneath; 192 head and pronotum;193 ventral part of abdomen and right deflexed elytral apex; 194–196, 198, 199 abdomen, 194, 196, 198 ventral; 195, 199 dorsal; 197 dorsal. Figure legends: T7 tergite 7; T8 tergite 8. These figures share scale lines: 194, 195; 198, 199.

Medeopteryx tarsalis (Olivier) comb. nov.

Luciola tarsalis Olivier, 1885: 360; 1902:72.
Pteroptyx tarsalis (Olivier). Olivier, 1909b:319. McDermott, 1966:117. Ballantyne & McLean, 1970:253.
Pteroptyx tarsale Olivier, 1910b:48; 1913b:417. Ballantyne & McLean, 1970:253 (synonymy).

Holotype. Male. **NEW GUINEA**: 143.00E, 9.00S, Western Pr., Fly River (MCSN).

Other specimens examined. NEW GUINEA: New Ireland: 150.48E, 2.34S, Kavieng, 11.ii.1966, G. Monteith, 2 males, 8 females (Tube 222 UQIC). **NEW GUINEA**: 143.00E, 9.00S, Western Pr., Sturt Is., Fly River, 5.x. 1936, male, 2 females; 7.x. 1936, 2 males, 4 females; 8.x. 1936, 2 males, 3 females; 14–16.x. 1936, 15 males, 18 females (AMNH). Mediri, 60 miles up Fly River, 8.xi.1922, A. McCulloch, male, 2 females (AMSA).

Diagnosis. 6.2–9.1 mm long; dorsally yellow with elytral apices dark brown: the apical brown area may extend anteriorly in strips of decreasing width, sometimes reaching humeral angles; distinguished from all other New Guinean *Medeopteryx* by its dorsal colouration.

Remarks. This species is only known from mainland New Guinea at the Fly River, and on New Ireland. There are no details of light production and the two populations may not be conspecific.

The pale dorsal colouration with dark tipped elytra which are sometimes dark margined probably provides some protective advantage. To the unaided eye the outline of the lateral margin of the body is totally disrupted.

Medeopteryx torricelliensis (Ballantyne) comb. nov.
[Fig. 183]

Pteroptyx torricelliensis Ballantyne, in Ballantyne & McLean, 1970:258.

Holotype. Male. **NEW GUINEA**: West Sepik Pr., 3.23S, 142.14E. Torricelli Mountains, Mokai Village, 750m, i.1.1959 (BPBM).

Diagnosis. Moderately large (10–11mm long); pronotum and MS reddish orange, MN brown medially, orange laterally; elytra black; most similar to *Medeopteryx antennata,* distinguished by the uniformly dark antennae, the nature of the posterior margin of V7 (Ballantyne & McLean 1970 Fig. 14), and its restricted distribution.

Remarks. This distinctive species is known only from the two specimens originally described and an additional specimen listed here.

Pacifica gen. nov.

Type species. *Pygatyphella salomonis* (Olivier)

Diagnosis. Ballantyne and Lambkin (2009) distinguished a group of five species within *Pygatyphella* (Ballantyne) as "*Pygatyphella* B" and this difference is formalised here with the erection of *Pacifica* **gen. nov.,** which differs from *Pygatyphella* (Ballantyne) as follows: four species with dorsal colouration of orange pronotum (sometimes with median dark mark), and dark brown elytra which may be pale margined; *Pac. russellia* is pale dorsally; pronotum never with angulate convergence along lateral margins, or small depression present just anterior to corner; with irregularities at rounded obtuse posterolateral corners, not projecting strongly if at all beyond median posterior margin; no interstitial lines well-defined; elytral margins convex-sided; posterior area of V7 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 continues along the ventral surface of the MPP as a ridge (e.g. Ballantyne & Lambkin 2009 Figs 342–349, especially Fig. 358); ventral surface of T8 usually with a curved, slightly off–centre ridge close to posterior margin; T8 outlines in *Pac. limbatipennis*, *limbatifusca* and *salomonis* characterised (Ballantyne & Lambkin 2009 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.

Male. Pronotum: dorsal surface without irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense; wider across posterior area than rest (C>A, B); 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; indentation at mid-point absent; without sinuousity in either horizontal or vertical plane; indentation in lateral margin near posterolateral corner absent; irregularities at corner present; posterolateral corners rounded obtuse, projecting as far as, or beyond median posterior margin, separated from it by shallow emargination.

Hypomera: closed; median area not elevated vertically; anterior area not flat to side of head; posterior area widely and strongly flattened and strongly adpressed; pronotal width/ GHW 1.6.

Elytron: punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and sutural ridge extend beyond mid-point, do not extend as a ridge around apex and neither is expanded in apical half; 0 interstitial lines; 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 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, not well-defined; without median elevation; posterolateral eye excavation not strongly developed and not visible in resting head position; antennal sockets on head between eyes, separated by less than 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 labial palpomere non–lunate, strongly flattened, in the shape of a wide triangle, 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: inner tarsal claw not split; without MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen: without 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 half of V7, entire LO reaching to sides or not, not reaching to posterior margin; neither anterior nor posterior margin of entire LO in V7 medially emarginated; posterior half of V7 arched with transverse muscle impressions usually visible in this area; posterolateral corners not produced, rounded; LO present in V6, occupying almost all V6. MPP present, symmetrical, apex symmetrical or not, and rounded, squarely truncate, or obliquely truncate; MPP with a narrow to wide and elongate dorsal ridge slightly to left of the median line; L=W, not strongly inclined dorsally; not engulfed by the apex of T8; V7 without median carina, median longitudinal trough, anteromedian depression on face of LO, PLP, incurving lobes or pointed projections, median ‘dimple’, or reflexed lobes. T7 without prolonged posterolateral corners. T8 strongly sclerotised, not subparallel-sided, margins converge gently towards posterior end; symmetrical, W=L or L>W of visible posterior portion, which does not narrow abruptly; without prolonged posterolateral corners, median posterior emargination, median posterior projections, not inclined ventrally nor engulfing the posterior margin of V7 nor the MPP; T8 not extending conspicuously beyond posterior margin of V7 horizontally; T8 ventral surface without flanges, lateral depressed troughs; median longitudinal trough absent; median posterior ridge present, usually curved, may be straight (*plagiata*); concealed anterolateral arms of T8 present, not laterally emarginated before their origins, narrow, usually as long as visible posterior portion and expanded dorsoventrally; apices without bifurcation of inner margin; bases with ventrally directed pieces present.

Aedeagal sheath: never > 4 times as long as wide; without paraprocts; asymmetrical in posterior area with sheath sternite subparallel-sided for a third its length past articulation with sheath tergite, and then emarginated on right side; sternite not angulate on L or R sides; posterior margin entire, rounded, not emarginated on either side; anterior half of sternite broad, apically rounded; tergite without lateral arms extending widely anteriorly beside sheath sternite; tergite not subdivided, without projecting pieces along posterior margin of T9; anterior margin of tergite without transverse band.

Aedeagus: L/W < 3/1; LL without lateral appendages, visible from beneath beside ML; LL/ML wide to moderate; 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 or narrower than that of ML; LL apices not expanded horizontally; dorsal base of LL symmetrical, not excavated, median margin broadly rounded; LL without lateral hairy appendages; inner margins without slender leaf-like projection; ML symmetrical, with paired lateral teeth.

Female. Macropterous and assumed capable of flight. Pronotum shaped as for male; punctation moderate to dense; pronotum > humeral width; irregularities near posterolateral corner present. Elytral punctation neither as large as that of pronotum nor evenly spaced, punctation dense. Head not strongly reduced but can be retracted within prothoracic cavity, and antennae on head between eyes. Elytra with no interstitial lines; elytral carina absent. No legs or parts thereof swollen and /or curved. LO in V6 only, without any elevations or depressions or ridges on V7 .

Larva not associated.

List of species of *Pacifica* gen. nov.

- *limbatifusca* (Ballantyne) **comb. nov.**
- *limbatipennis* (Pic) **comb. nov.**
- *plagiata* (Blanchard) **comb. nov.**
- *russellia* (Ballantyne) **comb. nov.**
- *salomonis* (Olivier) **comb. nov.**

Key to species of *Pacifica* gen. nov.

1. Dorsal surface pale brownish yellow (Ballantyne & Lambkin 2009 Figs 405, 406) . . . .*russellia* (Ballantyne) **comb. nov.**
   Elytra always very dark brown, sometimes with paler margins (Ballantyne & Lambkin 2009 Figs 329–337, 340, 397, 417, 418–420) 2
2. Elytra dark brown, no paler margins 3
   Elytra always with paler margins (either lateral, apical or sutural or a combination of these) 4
3. Pronotum orange with no dark markings (Ballantyne & Lambkin 2009 Figs 417, 418) . . . .*salomonis* (Olivier) **comb. nov.**
   Pronotum orange with darker median markings (Ballantyne & Lambkin 2009 Fig. 397) . . . . .*plagiata* (Blanchard) **comb. nov.**
4. Pronotum pale with no median darker marking . . . . *limbatipennis* (Pic) **comb. nov.**
   Pronotum orange with median darker markings (Ballantyne & Lambkin 2009 Figs 329, 338) . . . . *limbatifusca* (Ballantyne) **comb. nov.**

Pacifica limbatifusca (Ballantyne) comb. nov.
(Ballantyne & Lambkin 2009 Figs 329, 338, 341, 362, 363, 370, 371)

Pygatyphella limbatifusca Ballantyne. Ballantyne & Lambkin 2009: 88.

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

Diagnosis. Part of Ballantyne and Lambkin's 2009 *Pygatyphella* B complex; very similar to *Pacifica 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.

Pacifica limbatipennis (Pic) comb. nov.
(Ballantyne and Lambkin 2009 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.
Pygatyphella limbatipennis (Pic). Ballantyne & Lambkin 2009: 90.

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).

Diagnosis. One of the *Pygatyphella* B complex of Ballantyne and Lambkin (2009); dorsal colouration orange pronotum with dark brown elytra which are pale margined along their lateral margins; most similar to *Pac. limbatifusca* (Ballantyne), distinguished by the absence of small paired dark markings on the pronotum, the very dark brown elytra and the narrower lateral pale band. Ballantyne and Lambkin (2009) distinguished this from other similarly coloured species on page 69 and from *Pygat. salomonis* in Tables 8, 9.

Pacifica plagiata (Blanchard) comb. nov.

(Ballantyne and Lambkin 2009 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. Synonymy.
Luciola (Luciola) caledonica Bourgeois. McDermott, 1966:100. Synonymy.
Luciola (*Luciola*) *plagiata* Blanchard. McDermott, 1966: 111. Synonymy.
Pygatyphella plagiata (Blanchard). Ballantyne & Lambkin 2009: 97.

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 specimens unknown.

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 V7 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.

Pacifica russellia (Ballantyne) comb. nov.

(Ballantyne & Lambkin 2009 Figs 405–416)

Pygatyphella russellia Ballantyne. Ballantyne & Lambkin 2009: 99.

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

Diagnosis. The only species Ballantyne and Lambkin (2009) identified in the *Pygatyphella* Group B complex with pale dorsal colouration. Known from 2 specimens.

Pacifica salomonis (Olivier) comb. nov.

Atyphella salomonis Olivier, 1911a:172.
Pygatyphella salomonis (Olivier). (Ballantyne & Lambkin 2009 Figs 417–439)
Nec *Atyphella salomonis* var. *limbatipennis* Pic, 1911:165. Ballantyne & Lambkin 2009: 100.
Nec *Luciola (Luciola) salomonis* var. *limbatipennis* Pic. McDermott, 1966:112. Ballantyne & Lambkin 2009: 100.

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

Diagnosis. Distinguished from other similarly coloured Solomon Island species by the retracted LO in V7, the arched posterior area of V7. Distinguished from *Pac. limbatipennis* by the pale lateral elytral margins, and narrower and apically pointed teeth on the ML in the latter (see Ballantyne & Lambkin 2009, Tables 8, 9 for comparisons).

Poluninius gen. nov.

[Figs 185–190]

Type species: *Poluninius selangoriensis* **sp. nov.** monotypic.

Diagnosis. *Poluninius* **gen. nov.** is an oriental genus belonging in a group of 7 genera characterized by: an elongate slender aedeagus with LL concealed behind the median lobe when viewed from beneath, pronotal width less than width across elytral humeri, parallel-sided elytra, aedeagal sheath elongate slender, widest across the middle, with posterior half of sternite tapering evenly on both sides towards a narrow entire apex. Males are distinguished from *Australoluciola* **gen. nov.** which has an entire LO in V7 by the bipartite V7 LO; from *Colophotia* in lacking both a median carina on V7, and expanded and oblique PLP; from *Pteroptyx* in lacking deflexed elytral apices; from *Trisinuata* **gen. nov.** by the presence of lobes along V7 posterior margin and aedeagal sheath paraprocts; from most *Medeopteryx* **gen. nov.** in lacking deflexed elytral apices. Similar to *Pyrophanes* with lobes along V7 posterior margin, differing in lacking the MFC, and lateral ventral troughs of T8 bearing spines and hairs. It differs from *Luciola indica* in lacking the bulbous median lobe and in possessing bulbous projections along V7 posterior margin. Dorsal colour pattern of yellowish pronotum and elytra with apical brown area is common to many species in SE Asia (McDermott 1966).

Male. Pronotum: dorsal surface without irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense; anterior margin not explanate; subparallel-sided, margins straight (A=B=C); width < humeral width; anterolateral corners rounded obtuse; lateral margins without indentation at mid-point, or sinuousity in either horizontal or vertical plane; without indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners angulate, less than 90 and inclined obliquely to the median line; posterolateral corners not projecting as far as median posterior margin and separated from it by scarce emarginations.

Hypomera: closed; median area not elevated in vertical direction; median area more widely flattened than elsewhere; pronotal width/ GHW 1.2.

Elytron: punctation not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed; epipleuron and sutural ridge extend beyond mid-point, almost to apex but not as ridge around apex, neither thickened in apical half; no interstitial lines; elytral carina absent; in horizontal specimen viewed from below epipleuron at elytral base wide, covering humerus; viewed from above the anterior margin of the 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, without median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous, ASD subequal 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 labial palpomere strongly flattened, shaped like narrow triangle (narrowest at base and L 2–3 X W), with inner edge entire, and less than half as long as apical maxillary palpomere. Antennae 11 segmented; length>GHW to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel.

Legs: inner tarsal claw not split; without MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen: (Figs 185, 186; Fu *et al.* 2012b Figs 13–15) without cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior; LO in V7 bipartite with inner margins almost contiguous, occupying most of V7, and reaching to sides and into the short PLP; LO present in V6, occupying almost all V6. MPP present, symmetrical, apex rounded and shallowly emarginate, not laterally compressed, short, longer and wider than PLP, not inclined dorsally nor engulfed by T8 apex, without dorsal ridge, median longitudinal trough. V7 posterior margin trisinuate with incurving apically bulbous lobes and pointed projections in the emarginations between MPP and PLP; V7 without median carina, median longitudinal trough, anteromedian depression on face of LO, median 'dimple', or reflexed lobes; PLP short slightly produced and narrow, much narrower and shorter than MPP. T7 without prolonged anterolateral corners. T8 well sclerotised, symmetrical, W=L, visible posterior area not narrowing abruptly, median posterior margin shallowly and narrowly emarginate; widest across middle with lateral margins tapering evenly in both an anterior and posterior direction; without prolonged posterolateral corners, 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 with well developed median longitudinal trough, margined by well defined symmetrical ridges; anterior end of ridges not produced, rounded in outline; without lateral depressed troughs, asymmetrical projections, median posterior ridge; concealed anterolateral arms of T8 slightly shorter than visible posterior portion of T8, not laterally emarginated before their origins, not expanded dorsoventrally, expanded only in horizontal plane; without bifurcation of inner margin and ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath (Figs 189, 190): approx. 3 times as long as wide; with bulbous paraprocts; symmetrical in posterior area where sheath sternite tapers evenly to a narrow rounded apex; anterior half of sternite relatively narrow, apically rounded; tergite without lateral arms extending anteriorly at sides of sheath sternite; tergite without projecting pieces along posterior margin of T9, anterior margin without transverse band.

Aedeagus (Figs 187, 188): L/W 5/1; LL not visible from beneath at sides of ML, LL/ML narrow; LL of equal length, slightly shorter than ML, contiguous along inner dorsal margins; separated longitudinally by 1/3 their length; LL base width not = LL apex width which is much narrower than that of ML; LL apices not expanded in horizontal plane; LL without lateral appendages; dorsal base of LL symmetrical, not excavated (arrowed in Figs 187, 188); LL without lateral hairy appendages along their outer ventral margins, not produced preapically nor narrowly on inner apical margin, apices of LL not inturned, nor out–turned; without projection on left LL; inner margins without slender leaf-like projection; ML symmetrical, with anterior prolongation long and narrow (anterior end arrowed in Figs 187, 188); without paired lateral teeth and tooth to left side, not strongly arched, apex not shaped like arrowhead, not bulbous, not inclined ventrally; BP much longer than wide, not strongly sclerotised, not hooded, not strongly emarginated along anterior margin.

Female, Larva not associated.

Etymology. *Poluninius* (masculine) is a noun latinised from the surname of the late Ivan Polunin who collected the few species of this unusual genus, and is named in his honour.

Poluninius selangoriensis sp. nov.

[Figs 185–190]

Type. Male. **MALAYSIA**: Selangor, I. Polunin (ANIC).

Paratypes (3). Two males same data as holotype (ANIC). Kg Kuantan village orchard, DZA outside, coll Kat, male (FRIM).

Diagnosis. The only species of *Poluninius*, distinguished by its pale dorsal colouration and the fleshy lobes on V7.

Male. 5.1–5.5 mm long. Colour: Dorsal surface of pronotum and elytra pale yellowish brown with narrow black areas at the tips of the elytra; Selangor specimens preserved in 70% ethanol appear semitransparent, with elytra are slightly darker than the pronotum because of underlying hind wings; head between eyes dark brown; maxillary palpi mid brown; apical labial palpomere mid brown, remainder yellowish; ventral surface of thorax and legs orange yellow except for brown tibiae and tarsi of legs 1, and brown tarsi of legs 2, 3; dorsal and ventral surface of abdomen very pale yellowish, except for white LOs in V6, 7.

Pronotum 1.0–1.1 mm long; 1.4–1.5 mm wide; W/L 1.4. Elytra 5.1–5.5 mm long. GHW 1.2 mm; SIW 0.2 mm.

Etymology. The type locality is latinised, genitive case to reflect the origins of this species.

Pteroptyx s. str. Olivier

Pteroptyx Olivier, 1902:72; 1907:55; 1909a:319; 1909b:lxxxii; 1910b:47; 1911b:16; 1913a:58. Olivier & Pic, 1909:139. McDermott, 1959:10 (**partim**); 1964:46 (**partim**); 1966:117 (**partim**). Ballantyne & McLean, 1970:223 (**partim)**. Ballantyne, 1987a:117; 1987b:171; 2001:51. Ballantyne *et al.* 2011:8 (partim).

Nec Ballantyne in Calder 1998:180.

Type species. Olivier (1902) described *Pteroptyx* from 2 species viz. *Luciola testacea* Motsch. and *Luciola malaccae* Gorham. Lucas (1920) designated *Luciola testacea* as the type species of *Pteroptyx* (see Ballantyne in Calder 1998:179). Ballantyne and McLean (1970) were of the opinion, from an examination of a black and white photograph of the type species, that *Luciola testacea* lacked deflexed elytral apices and its taxonomic position is uncertain, and considered that *Luciola malaccae* should be advanced to the International Commission for Zoological Nomenclature for consideration as the type species of *Pteroptyx* **s. str.** This matter has been held in abeyance until a phylogenetic analysis established the position of all species with deflexed elytral apices.

Diagnosis. *Pteroptyx* **s. str.** is an oriental genus that belongs in a group of 7 genera with males characterized by: an elongate slender aedeagus with apices of LL concealed behind the median lobe when viewed from beneath, pronotal width less than width across elytral humeri, parallel-sided elytra, aedeagal sheath elongate slender, widest across middle, with posterior half of sternite not emarginate on either side, and tapering evenly towards a narrow entire apex. Males of *Pteroptyx* **s. str.** have a MFC, deflexed elytral apices, aedeagal sheath with bulbous paraprocts and bipartite LOs in V7. Males are distinguished from *Australoluciola* which has entire LOs in V7 and lacks the MFC; from *Colophotia* in lacking a median carina on V7, expanded and oblique PLP and elongate slender aedeagal sheath; from *Pyrophanes* and *Poluninius* **gen. nov.** which lack deflexed elytral apices; from *Trisinuata* **gen. nov.** and *Medeopteryx* **gen. n** which lack the MFC and bulbous aedeagal sheath paraprocts. It differs from *Luciola indica* in lacking the bulbous median lobe and non deflexed elytral apices. Two presently undescribed species were identified in this analysis (Fig. 3 Node 15 blue numbers 5, 6) (one without deflexed elytral apices; Ballantyne in prep.).

List of species of *Pteroptyx* s. str.

- *asymmetria* Ballantyne
- *bearni* Olivier
- *decolor* Olivier
- *gelasina* Ballantyne
- *maipo* Ballantyne
- *malaccae* Olivier
- *macdermotti* McLean
- *masatakai* Kawashima
- *sulawesiensis* Kawashima
- *tener* Olivier
- *truncata* Ballantyne
- *valida* Olivier

Key to species of *Pteroptyx* from SE Asia using males

Modified slightly from, and with figure references to, Ballantyne *et al.* (2011). Interpretation of colour patterns in the elytra in ethanol preserved specimens where the underlying dark hind wing becomes visible may be difficult. Ballantyne (2008) suggested pulling the elytron aside and allowing it to dry.

1. V7 with slender incurving hair bearing lobes along its posterior margin between PLP and MPP (arrowed in Ballantyne *et al.* 2011 Figs 9, 10); LOs in V7 restricted to very small anterolateral plaques; PLP of V7 narrowed and considerably produced beyond the posterior margin of the MPP; T8 prolonged apically beyond MPP with margins converging posteriorly (Ballantyne *et al.* 2011 Figs 9, 10) . . . .*macdermotti* McLean
- V7 without slender incurving hair bearing lobes along its posterior margin between PLP and MPP; LOs in V7 never restricted to very small anterolateral plaques; if posterolateral processes of V7 narrowed then not produced far beyond the posterior margin of MPP if at all; T8 not as above 2

2. T8 bearing slender elongate lobes along its posterior margin to either side of the posterior median emargination (Ballantyne *et al.* 2011 Figs 7, 13); flanges on ventral surface of T8 absent; basitarsus of legs 2 often excavated in its inner margin (Ballantyne *et al.* 2011 Fig. 11) 3
- T8 without slender elongate lobes along its posterior margin to either side of the median posterior emargination (e.g. Ballantyne *et al.* 2011 Figs 8, 17, 19, 24); flanges may be present on ventral surface of T8. 6

3. Posterior margin of T8 strongly asymmetrical especially when viewed from above; posterior margin of T7 broadly, shallowly and evenly emarginate; elytral apices broadly rounded (C > A or B); all FS simple; posterolateral corners of V7 produced and rounded; MPP with short narrow paired hooks with apices inclining inwards (Ballantyne 2001 Figs 1–3) . . . . *asymmetria* Ballantyne
Posterior margin of T8 symmetrical or nearly so (Ballantyne *et al.* 2011 Figs 7, 19, 24); any asymmetry is in the paired lobes arising at each side of the MPP, and not an asymmetry of the entire posterior margin; posterior margin of T7 either scarcely emarginated and slightly bisinuate, or moderately deeply emarginated with acute posterolateral corners and straight anterior margin; elytral apices rounded or margin B obliquely truncate; FS1 slightly expanded in median area in *decolor*; posterolateral corners of V7 produced and rounded, or not produced and angulate; posterior margin of T8 deeply emarginated in middle area with posterolateral corners produced and rounded, or barely and very narrowly emarginated in median line only 4
4. Posterolateral processes of V7 angulate, not or scarcely produced posteriorly (Ballantyne *et al.* 2011 Figs 7, 12); posterior margin of V7 between PLP and MPP slightly sinuate; posterior margin of T7 with narrowed angulate corners and a small shallow median emargination (margin appears trisinuate); elytral apices obliquely truncate across most of their anterior (outer) margin (C); aedeagus dimensions B/A 0.6. . . . . *tener* Olivier
Posterolateral processes of V7 rounded obtuse, and produced posteriorly; posterior margin of V7 between PLP and MPP with moderately deep and rounded emarginations; posterior margin of T7 deeply emarginated in middle area with posterolateral corners produced and rounded; posterior margin of T7 not appearing trisinuate; elytral apices C rounded or truncate; aedeagus dimensions B/A > 0.6 5
5. Dorsal surface entirely pale coloured (dark markings at tip of elytra may be present); pronotum without any pink markings; head and anterior margin of scape pale yellow with labrum dark brown; elytral apices rounded; projections on either side of median emargination of T8 relatively broad and apically rounded; aedeagus dimensions B/A 0.75 . . . . *decolor* Olivier
Elytra pale brown, semitransparent, with lateral margin paler than rest and pronotum often deep pinkish orange; if elytra pale then at least base and apex brown; head pale brown, with labrum slightly darker; elytral apex B obliquely truncate (Figs); projections to either side of median emargination of T8 slender and apically pointed; aedeagus dimensions B/A 0.85 . . . . *bearni* Olivier
6. Deflexed elytral apex shortened (wider than long) (Ballantyne *et al.* 2011 Fig. 23); tibiae 3 not expanded; basitarsi 3 not swollen; fine ventrally directed flanges on ventral surface of T8 absent; PLP separated from MPP by moderately deep circular emarginations (Ballantyne *et al.* 2011 Fig. 18); apices of PLP broad, flat, slightly obliquely truncate; posterior margin of T7 not emarginated and posterolateral corners not produced; lateral margins of T8 rounded . . . . *truncata* Ballantyne
Deflexed elytral apex not shortened (i.e. about as wide as long); tibiae 3 often expanded at apex and basitarsi 3 may be swollen (Ballantyne *et al.* 2011 Fig. 26); fine ventrally directed flanges may be present on the ventral surface of T8 (Ballantyne *et al.* 2011 Fig. 17); PLP separated from MPP by moderately deep circular emarginations or not; apices of PLP sometimes flat, slightly obliquely truncate; posterior margin of T7 usually emarginated and posterolateral corners produced; lateral margins of T8 rounded or straight and converging anteriorly. 7
7. Posterior end of elytra dimpled (Ballantyne *et al.* 2011 Figs 20, 21); wide deep emarginations separating elongate narrow PLP from MPP; apices of PLP narrow and rounded; posterolateral corners of T8 angulate and lateral margins converge anteriorly; posterolateral corners of T7 narrowed and may project and are often visible from beneath in the emarginations between PLP and MPP (Ballantyne *et al.* 2011 Fig. 19). . . . . *gelasina* Ballantyne
Posterior end of elytra not dimpled; either wide emarginations separating elongate PLP from MPP, or emarginations scarce; apices of PLP often slightly oblique, or PLP broadly rounded and scarcely produced; posterolateral corners of T8 angulate and lateral margins converge anteriorly or corners and lateral margins rounded; posterolateral corners of T7 not usually visible from beneath in the emarginations between PLP and MPP 8
8. Posterolateral corners of V7 rounded or angulate, scarcely produced; MPP of V7 broad and apex almost squarely truncate or slightly rounded in ventral view and perpendicular to horizontal plane; median dorsal surface of MPP may be narrowly prolonged and apically emarginated. 9
PLP of V7 elongate, longer than wide, produced and apically obliquely truncated; MPP of V7 narrower and apex emarginated (emargination visible from beneath); median dorsal surface of MPP not developed (Ballantyne *et al.* 2011 Figs 24, 25) . . . . *masatakai* Kawashima, *malaccae* (Gorham)[1]
9. Dorsal surface of MPP of V7 strongly prolonged and apically narrowly emarginated . . . . *sulawesiensis* Kawashima; *valida* Olivier *sensu* Ballantyne (2001 Group 2:81)[2]
Dorsal surface of MPP either without a median posterior projection or with a slight projection 10
10. Elytral apices strongly deflexed (Ballantyne *et al.* 2011 Fig. 32); posterior margin of outer area of elytral apex grooved; LO in V7 well separated in the middle (Ballantyne *et al.* 2011 Figs 27, 31) . . . . *valida* Olivier *sensu* Ballantyne (2001) Groups 1, 3[3]
Elytral apices not strongly deflexed (Ballantyne *et al.* 2011 Fig. 2); posterior margin of outer area of elytral apex not grooved; LO in V7 contiguous in the middle (Ballantyne *et al.* 2011 Fig. 2) *maipo* Ballantyne

Footnotes 1. These species are not further distinguished here; Ballantyne (2001) identified *malaccae* in four distinct morphological groups from peninsular Malaysia, Sarawak, Thailand and Indonesia (Borneo); Kawashima (2003) did not align *masatakai* with any of these groups and *malaccae* and *masatakai* are distinguished here by the occurrence of *masatakai* on the island of Sulawesi. 2. Ballantyne (2001) distinguished a group of specimens of *valida* from peninsular Malaysia at Selangor, Sarawak and Indonesia (Bali) with a median posterior projection of the dorsal surface of MPP. 3. Ballantyne (2001) distinguished a single specimen from peninsular Malaysia as group 3.

Remarks. Two species of flashing fireflies in Malaysia both belonging to the genus *Pteroptyx* Olivier are similar, and their inconsistent identification in various publications, (not least those of the first author), is addressed and resolved here. The species are *Pteroptyx tener* Olivier, a mass synchronising species that is the basis for the tourist development involving firefly watching on the Selangor River in Western peninsular Malaysia, and *Pteroptyx bearni* Olivier, a non synchronising species sometimes found in the same habitats as *tener.* The problems in identification have arisen primarily because *Pteroptyx bearni* was first redescribed without examination or description of a type, which was not located in the initial investigations (Ballantyne & McLean 1970). Subsequent publications, including depictions of this species on Malaysian stamps, assumed this characterisation to be definitive and are discussed below.

Ballantyne located in the Pic collection from the Natural History Museum Paris a single specimen which can be regarded as a surviving syntype of *P. bearni* and it is described here, and issues covering identifications of this species and *P. tener* are addressed.

Pteroptyx bearni Olivier

[Figs 191–201, 204, 205]

Pteroptyx Bearni Olivier in Olivier and Pic, 1909:139; 1910:47.

Pteroptyx bearni Olivier. McDermott 1966:117. Ballantyne & McLean 1970:241 (**Partim**). Ballantyne 2001:62 (**Partim**). Ohba &Wong 2012: .

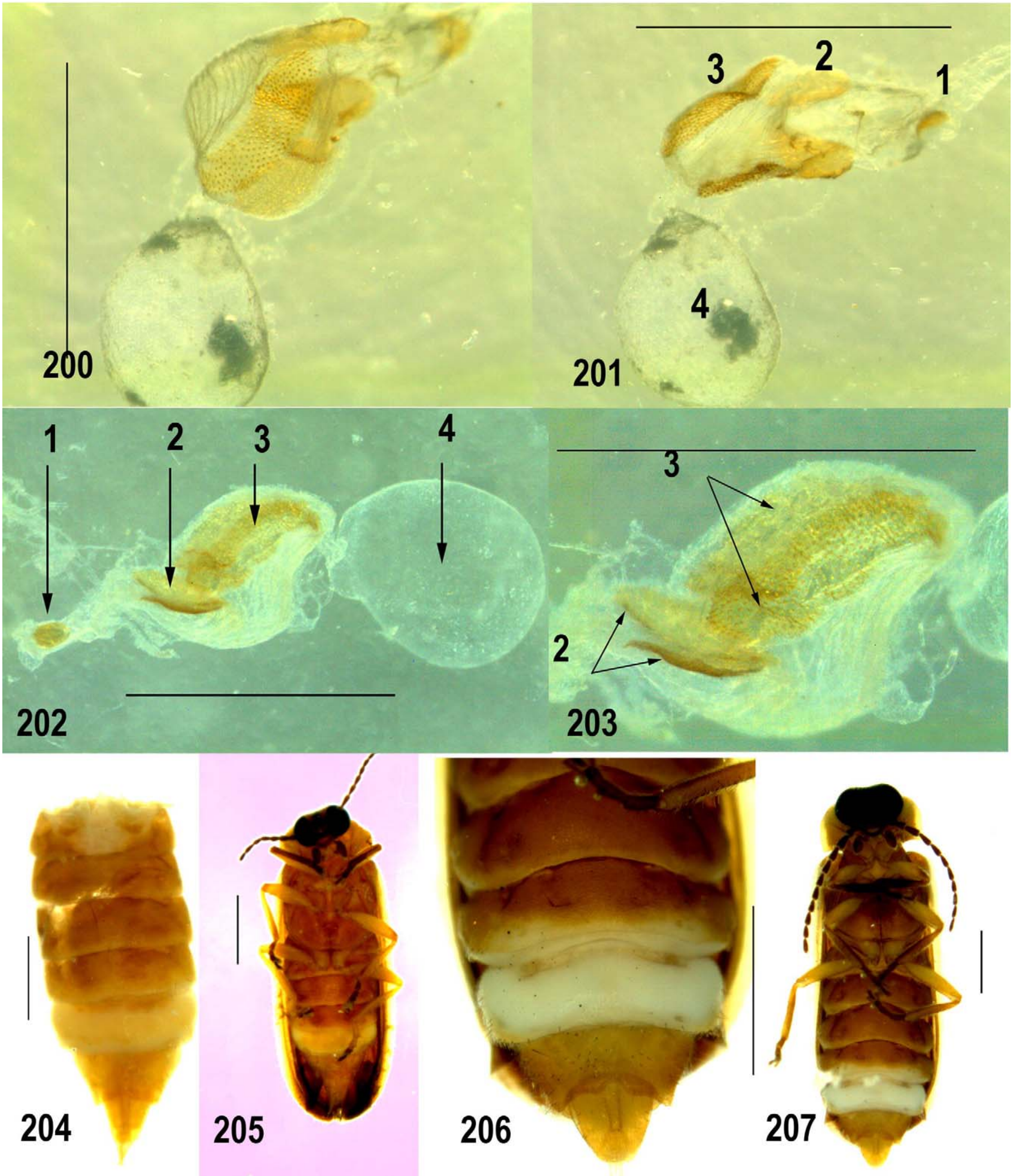
Pteroptyx similis Ballantyne. Ballantyne 2001:62. Mahadimenakbar, Hairul & Mazidi (2007):1. (**New synonymy**).

Lectotype. Male. **SINGAPORE:** Labelled 1. Handwritten: *Pteroptyx bearni* E. Ol. n. sp. (Olivier vidit) 2. Red printed label: TYPE. 3. Handwritten: type. 4. Symbol. 5. Printed: Coll. Ctesse de bearn Croisvere du “Nirvana” Singapore E. Cordier 7.iv.1908 (MNHN).

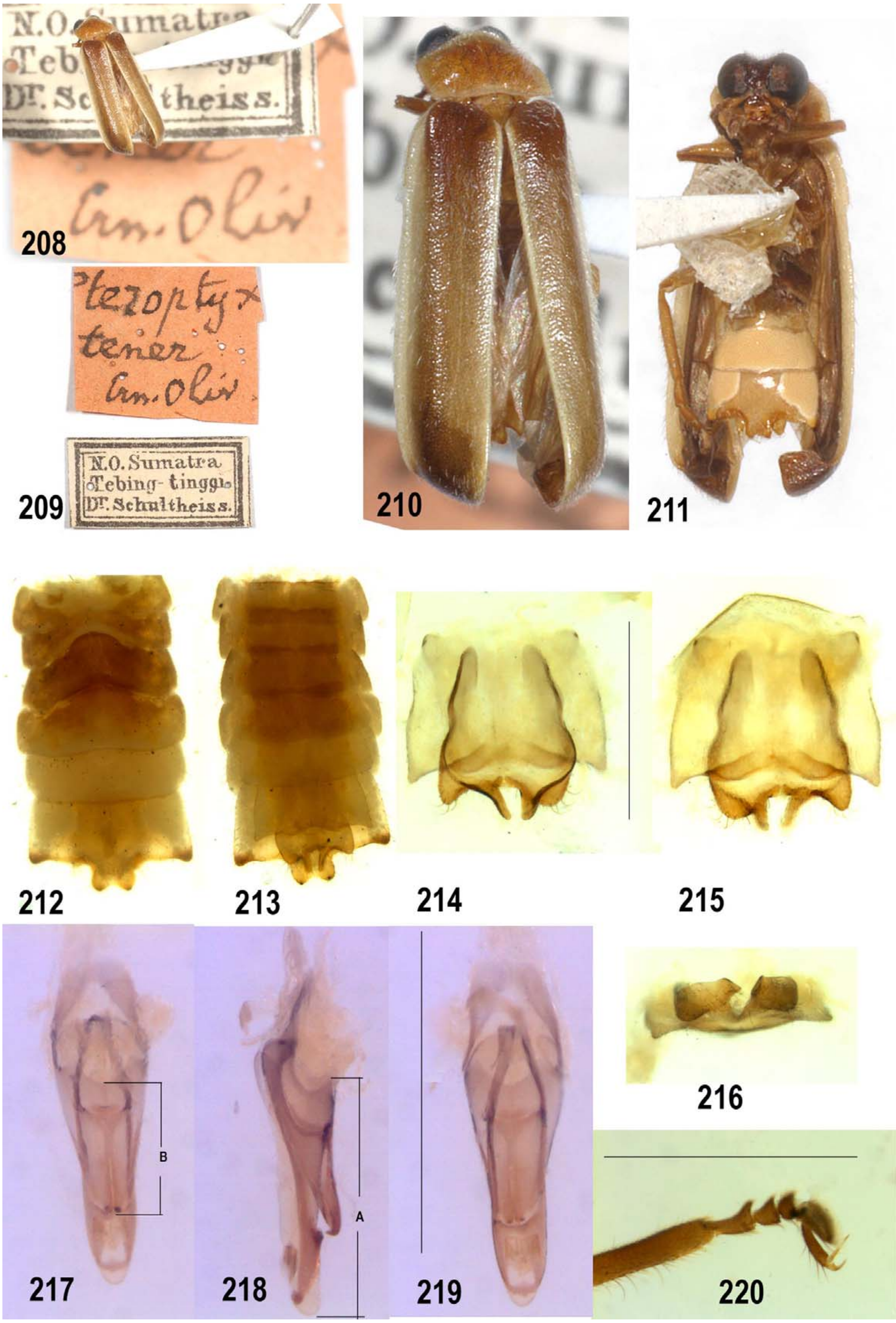
Other specimens examined. MALAYSIA: Kalabakan River, 2.vii.1972, I. Polunin, 10 males, 7 females (ANIC). Pingan Pingan, 20.vi.2009, Vito, male (FRIM).

Diagnosis. Belonging to a group of four species of *Pteroptyx* **s. str.** in which T8 has elongate lobes beside the median posterior emargination; most obviously distinguished from *asymmetria* and *tener* by the shape of the terminal abdominal tergites (in *asymmetria* T7 is not medially emarginated, and T8 is asymmetrical; in *tener* T7 is shallowly emarginated and slightly sinuous with posterolateral corners narrowed, and T8 is symmetrical); similar to *P. decolor* which is not well characterised in collections, differing in the dorsal colour pattern (*P. decolor* is entirely pale coloured dorsally).

Lectotype male. 5.5 mm long; *Colour* (Figs 191, 192, 194, 195): pronotum (Fig. 192) orange yellow (fat body retracted along both anterior and posterior margins); MS and MN pale brownish; elytra semitransparent, light brown with narrowly pale lateral margin not extending around apex; head, antennae and palpi very dark brown; ventral thorax and legs brownish orange except for dark brown tibiae and tarsi 1, dark brown tarsi 2 and dark brown 4th and 5th tarsomeres of legs 3; ventral thoracic colour (especially that of metathorax) partly obscured by dark dehydrated thoracic muscles visible beneath cuticle; basal abdominal ventrites whitish-yellow (underlying fat body visible beneath semitransparent cuticle contributes to colour); LO (Fig. 194) in V6, 7 yellowish white with very white margins; remainder of V7 orange; abdominal tergites (Fig. 195) orange, cuticle semitransparent and colour obscured by underlying white fat body; dorsal aspect of apices of PLP narrowly brown (Fig. 195). Pronotum (Fig. 192): 0.9 mm long; 1.5 mm wide; W/L=1.6; median anterior margin rounded scarcely projecting beyond obtusely rounded anterolateral corners; lateral margins slightly convex sided (i.e. B>A, C); median posterior margin rounded, projecting beyond angulate obtuse posterolateral corners, and separated from them by shallow emarginations; depressed area visible in median area of disc probably post-mortem artefact. Elytra: parallel sided; deflexed apex truncate with inner corner rounded (Fig. 193). Head: GHW 1.1 mm; SIW 0.3mm; ASD subequal to ASW; apical labial palpomere slightly longer than wide and ½ as long as apical maxillary palpomere. Antennae incomplete; FS1 elongate slender as long as scape. Legs: MFC sparse, may have up to 5 teeth (teeth appear to be missing).Abdomen (Figs 194, 195): posterior margin of V7 with broad MPP which is apically shallowly emarginated, and bearing tiny hooks on the dorsal surface of the posterolateral corners; MPP projecting posteriorly just beyond narrowed apices of PLP; LOs in V7 separated in middle by their width and occupying less than half the area of V7; posterior margin of T7 deeply and widely emarginated with posterolateral corners narrowing and apically acute; lateral margins of visible portion of T8 rounded, median posterior margin emarginated, emargination bounded laterally by narrowed apically pointed projections. Aedeagal complex not dissected from this unique specimen. Based on Ballantyne and McLean (1970), Ballantyne (2001), the aedeagal index (B/A) for *bearni* is 0.85 and 0.6 for *P. tener.*



FIGURES 200–207. *Pteroptyx* spp. Females. 200–201, 204, 205 *Pteroptyx bearni* female Kalabakan river (ANIC). 202, 203, 206, 207 *Pteroptyx tener* bred female (ANIC). 200–203 bursa (200, 202, 203 lateral; 201 ventral); 204, 206 abdomen ventral; 205, 207 whole body ventral. Figure legends: 1 median oviduct plate; 2 posterior bursa plate; 3 anterior bursa plate; 4 spermatophore digesting gland.



FIGURES 208–220. *Pteroptyx tener* male. 208–211 type (MNHN); 212–213, 220 Sarawak Limbang (ANIC); 214–219 Kota Tinggi (ANIC). 208, 210 dorsal; 209 labels; 211 ventral; 212, 213 abdomen, ventral (212) and dorsal; 214–216 tergite 8 cleared in cold KOH, ventral (214), dorsal (215) and from behind with ventral surface uppermost; 217–219 aedeagus dorsal (217), left lateral (218), and ventral; 220 tarsus leg 1 showing excavated basitarsus 1. Figure legends: A distance from base of LL to apex of ML measured along dorsal surface; B distance from base of LL to apex of LL measured dorsally. These figures share scale lines: 214–216; 217–219.

Female (Figs 200, 201, 204, 205)**:** (Kalabakan River specimens). 4.8–6.3 mm long. Colour: as for male except for pale LO in V6 only, and pale yellow slightly transparent V7, 8; no pink colouration in pronotum or fat body discerned. Bursa: anterior plates appearing indented along margins, probably postmortem effect (Figs 200, 201).

Discussion. Ballantyne (2001) distinguished *P. similis* from both *P. decolor* and *P. tener*, but not from *P. bearni* which had not been adequately characterised in Ballantyne and McLean (1970). Tergite 8 was not dissected and Ballantyne and McLean's Figure 6d shows T7 outline consistent with that of *bearni* as described here, but T8 is depicted without lobes to either side of the median emargination. Ballantyne (2001; Fig. 18) depicted a male from Paya Paloh apparently lacking these lobes on T8 and its identity has not been confirmed.

Ohba and Wong (2012) indicated incorrectly that the morphological features of this and *P. tener* were very similar except for the orange colour in the pronotum.

In the field the distinctive pinkish –orange pronotum and darker elytra enable quick and usually accurate identification of *P. bearni* (Wong pers com.), especially if light patterns are observed (e.g. Fig. 197). Ballantyne (in prep.) observed difficulties interpreting pronotal colour in ethanol preserved specimens, where the pink colour may have leached out. Its occurrence may be variable, since pinned specimens from the same locality also vary in pronotal colour. The pink colour in the fat body is usually found elsewhere apart from the pronotum, and can be seen especially in the dorsal abdomen, where the cuticle is paler and semitransparent (e.g. Fig. 197). Specimens of *P asymmetria* from Perak and Selangor (FRIM) also have pinkish colour in the pronotum (Ballantyne obs.).

In one Kalabakan River specimen the posterior margin of V7 is arched dorsally such that MPP not visible and projections of T8 are visible from beneath (Figs 198, 199).

P. bearni is non-synchronous, and is usually found downstream from the synchronously flashing *P. tener* in the more saline waters, but occasionally, probably due to tidal inflows, their habitats may overlap (Ohba and Wong 2012).

Pteroptyx tener Olivier
[Figs 202, 203, 206, 207, 209–220]

Pteroptyx tener Olivier, 1907:181; 1910:48. Ballantyne & McLean, 1970:254. Case, 1984:212; Lloyd, 1984:59. McDermott, 1966:117. Ballantyne, 1987a:120. Ballantyne & Menayah, 2000:323. Ohba & Wong, 2004:1; 2012:in press . Zaidi *et al.*, 2005:282. Dawood *et al.* 2007:1. Wan Jusoh *et al.*, 2010:56.

Holotype. Male. **INDONESIA**. Labelled 1. Pink handwritten *Pteroptyx tener* Ern Oliv.; 2. Printed N. O. Sumatra Tebing-Tinggi Dr Schultheiss (MNHN).

Other specimens examined. **MALAYSIA**: Selangor, Kampung Kuantan, bred from eggs March–June 2000 by Rasainthiran Menayah, 10 females (ANIC).

Diagnosis. Belonging to a group of four species of *Pteroptyx* **s. str.** in which T8 has elongate lobes beside the median posterior emargination (Figs 208–220); distinguished from *asymmetria* by the symmetrical T8 (that of *asymmetria* is asymmetrical), from *bearni* and *decolor* by the deep emargination of T7 (Figs 212–215; that of *tener* is slightly emarginate and the posterior margin of T7 sinuate; superficially similar to *P. decolor* which is not well characterised in collections, differing in the dorsal colour pattern (*P. decolor* is entirely pale coloured dorsally).

Female (Figs 206, 207). As described and figured in Ballantyne and Menayah (2000; Fig. 1e). Bursa: (Figs 202, 203) median oviduct plate small oval.

Remarks. Ballantyne and McLean (1970 Plate 1 c, d) figured the specimen depicted here but apparently did not recognise it as a type. The species characterisations given in Ballantyne and McLean (1970), Ballantyne and Menayah (2000), Ballantyne (2001), and Ballantyne *et al.* (2011), as well as Figures 208–220 here, amply describe this species.

Ohba and Wong's (2004) characterisation of this species is confusing. They describe the antenna with "13 thin flagellums" (the antennae are composed of scape, pedicel and 9 flagellar segments); the male light organs as occurring on the 4th 5th and 6th abdominal segments (they occur on V6 and 7 only); the female legs as the same as the males (only the male has the MFC). There is a suggestion of a possible copulation clamp e.g. (page 17) "male inserted its apex of elytra that is bent inside (LB = deflexed portion) under the female elytra and lifted the abdominal segment of the female with the hook of the elytra" (LB—the deflexed elytral apices press down on the top of the female abdomen; it is the MPP of V7 that presses upwards); (page 18) "The hook of the elytra of the male has the function to clamp securely onto the female abdominal segments when copulating with the female" (LB—the deflexed elytra apex is only part of the copulation clamp). Ohba and Wong (2012) incorrectly indicated that the morphology of this species and that of *P. bearni* was very similar.

Pygoluciola Wittmer

Pygoluciola Wittmer, 1939:21. Ballantyne & Lambkin, 2006:22; 2009: 21. Ballantyne 2008: 1. Fu *et* Ballantyne, 2008:1.
Luciola (*Pygoluciola*) (Wittmer). McDermott, 1966:115; Ballantyne, 1968:119; Ballantyne & McLean, 1970:233; Ballantyne & Lambkin, 2000: 82, 2001:363.

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

Diagnosis. Fu and Ballantyne (2008) gave a revised generic description which included species where the terminal abdominal segments were not prolonged, and characterised the two differing male forms included in the genus here**.** In one, consistent with *Pygoluciola sensu* Wittmer (1939) the median posterior margin of both V7 and T8 narrow and strongly incline either dorsally (V7) or ventrally (T8), often overlapping each other in dried specimens. In the second (* in list below) V7 has no posterior projection, while T8 may narrow very slightly and can be narrowly downturned. Both forms have a distinctive genital complex: aedeagus with LL considerably longer than ML and membranous in apical half; basal portion well sclerotised; aedeagal sheath with narrow elongate anterior portion of sheath sternite and expanded posterior area; lateral arms of tergite clearly visible at sides. Female: macropterous and assumed capable of flight. Larva not associated.

This analysis includes an as yet undescribed species of *Pygoluciola* (Fig.4 Node 50 blue number 21) which lacks the pronounced terminal abdomen modifications of *Pygoluciola sensu* Wittmer.

List of species of *Pygoluciola* Wittmer

* = Species without prolongations of terminal abdominal segments in the male

- *cowleyi* (Blackburn) **comb. n.** *
- *guigliae* (Ballantyne)
- *hamulata* (Olivier)
- *kinabalua* (Ballantyne & Lambkin)
- *qingyu* Fu *et* Ballantyne *
- *satoi* Ballantyne
- *stylifer* Wittmer
- *wittmeri* (Ballantyne)

Key to species of *Pygoluciola* using males

Modified and expanded from Ballantyne (2008)

1. Median posterior margin of V7 rounded, not narrowly prolonged; median posterior margin of T8 not prolonged 2
Median posterior margin of V7 narrowly prolonged and curving dorsally; median posterior margin of T8 prolonged narrowly and curving ventrally (Ballantyne & Lambkin 2006 Figs 18–27) 3

2. SE Asian species; black elytra and pinkish pronotum with median dark markings (Fu & Ballantyne 2008 Fig. 13) . . . . *qingyu* Fu *et* Ballantyne
Known only from N. Australia; elytra light brownish with paler margins; pronotum yellowish with extensive median dark markings; eyes with a strong posterolateral excavation visible when resting head withdrawn (Ballantyne & Lambkin 2009 Fig. 493) . . . . *cowleyi* (Blackburn**) comb. nov.**

3. All tibiae curved; lateral margins of elytra tapering posteriorly (Ballantyne & Lambkin, 2006, Fig. 6) 4
– No tibiae curved; lateral margins of elytra usually sub-parallel-sided 5

4. Apex of median posterior projection of T8 no wider than rest and rounded, not emarginate; lateral margins of pronotum slightly sinuate (Ballantyne & Lambkin, 2006 Figs 1, 19, 21) . . . . *guigliae* Ballantyne
– Apex of median posterior projection of T8 wider than rest and medianly emarginate; lateral margins of pronotum not slightly sinuate (Ballantyne & Lambkin, 2006 Figs 4, 25) . . . . *stylifer* Wittmer

5 Median posterior projection of abdominal V7 bifurcate at apex (Ballantyne & Lambkin, 2006 Figs 18, 26) 6
– Median posterior projection of abdominal V7 not bifurcate at apex 7

6 Apex of median posterior projection of abdominal V7 deeply emarginate, laterally ensheathing the downturned apex of T8 and projecting laterally beside it (Ballantyne & Lambkin, 2006 Figs 18, 26 . . . . *wittmeri* (Ballantyne)

– Apex of median posterior projection of abdominal V7 shallowly emarginate, not laterally ensheathing the downturned apex of T8 and not projecting beside it (Ballantyne & Lambkin, 2001 Figs 5, 10) . . . . *kinabalua* (Ballantyne & Lambkin)

7 MPP of V7 elongate slender, ventral surface shallowly depressed along its length, and bearing on its median dorsal surface two slender teeth; posterior apex of MPP not differentiated; lateral margins of T8 downturned (Ballantyne 2008 Figs 3–9) . . . . *satoi* Ballantyne

– MPP of V7 shorter, about as wide as long, ventral surface not shallowly depressed along its length, and not bearing dorsal teeth; posterior apex (face) of MPP differentiated and shallowly depressed; lateral margins of T8 not downturned . . . . *hamulata* (Olivier)

Key to species of *Pygoluciola* using females

Modified from Ballantyne (2008)

1 All tibiae curved . . . . *guigliae* (Ballantyne)

– No tibiae curved 2

2. Posterior margin of V7 deeply emarginate; bearing a small ridge anterior to . . . median area of deepest emargination; V8 with anteromedian prolongation not any more sclerotised than remainder of V8; T7 with anteromedian area rounded and elevated, lateral areas not flattened (Ballantyne & Lambkin 2001 Figs 1–19) . . . . *kinabalua* (Ballantyne & Lambkin)

– Posterior margin of V7 without an anteromedian ridge; V8 with anteromedian prolongation well sclerotised and visibly separated from remainder of V7; T7 without a rounded and elevated anteromedian area, with lateral areas flattened 3

3 Posterolateral areas of V7 irregularly expanded (Ballantyne 2008 Fig. 7). . . . . *satoi* Ballantyne

– Posterolateral areas of V7 not expanded . . . . *wittmeri* (Ballantyne)

Pygoluciola cowleyi (Blackburn) comb. nov.

Luciola Cowleyi Blackburn, 1897:34. Olivier, 1902:76; 1907:51. Lea, 1909:108; 1921a:197.
Luciola (Luciola) cowleyi Blackburn. McDermott, 1966:102. Ballantyne, 1968:125. Ballantyne in Calder 1998:178. Ballantyne & Lambkin 2000:58; 2009:22.
Luciola cowleyi Blackburn. Fu *et al*. 2012a :6.
Luciola quadricostata Pic, 1938:3. Ballantyne, 1968:125 (Synonymy).

Holotype. Male. *Luciola Cowleyi* Blackburn Australia, North Queensland: (NHML).

Holotype. Male. *Luciola quadricostata* Pic North Australia (Natural History Museum, Basel).

Other specimens examined. AUSTRALIA: Northern Territory: 12.27S, 130.50E, Darwin, male W. K. Hunt (UQIC), 11 males (SAMA), male (QMBA), 2 males (MUMA), 2 males, G. F. Hill (UQIC), 4 males G. F. Hill (ANIC), 6 males, G. F. Hill (SAMA); 14 males, 5 larvae, 11–12.ii.1945, B. Malkin (USNM); male, iii.1943, N. R Laird (ANIC). 12.33S, 131.02E, Virginia near Darwin, S M Gregg 24 males (Jan–March 1998; one male taken in Feb at light); 12 males (Feb and Dec 1999; 8 males taken in Feb at light; male taken in Dec at light); 2 males (March 2000, at light); 4 males (Feb and Dec 2001; one Dec male and 3 Feb. males taken at light) (MAGNT). 13.45S, 138.41E, Daly River Mission, 2 males, 14.i.1974, at light, J. F. Hutchinson (ANIC).

Diagnosis. Males small (5–5.5 mm long), pale brown, head deeply excavated between eyes; eyes very large, almost contiguous ventrally and bearing posterolateral excavations; inner two interstitial lines closest to sutural ridge well defined, outermost line nearest lateral margin moderately defined, second line in from lateral margin poorly defined; apical labial palpomere small, ovoid, entire; antennal length slightly less than GHW; labrum small, about as wide as long. Ventral surface of T8 without flanges and ridges. Aedeagus with a very short median lobe and broad hair bearing LL. Ballantyne (1968) redescribed and figured males and Ballantyne & Lambkin (2000) gave a short diagnosis.

Female. Not associated.

Larva. Larvae are associated by label data only. 8 mm long; dorsal surface very shiny, brown; without laterally explanate tergal margins; dorsal surface covered with short brown spines (all terga but the last bear 4 short rounded projections across their posterior margin).

FIGURES 221–227. *Pyrophanes* spp. 221, 222 *P. appendiculata* (slides, USNM). 223, 224 *Luciola venusta* type male (MNHN). 225, 226 *P. quadrimaculata* type female (MNHN). 227 *Luciola semilimbata* type female (MNHN). 221 male, 222 female abdomens; 223, 225 dorsal; 224 ventral; 226 type labels. Figure legends: 1 anterior projection of aedeagal sheath sternite; 2 basal piece aedeagus; 3 lateral area anterior prolongation of T8; 4 posterior area of aedeagal sheath in region of paraprocts; 5 ventrolateral surface of T8 in spined area; 6 posterolateral area of T8; 7 anterior plates bursa; 8 posterior plates bursa; 9 median oviduct plate.

Pyrophanes Olivier
[Figs 221–227]

Pyrophanes Olivier, 1885:368; in Baer, 1886:132; 1902:72; 1907:56; 1911b:102. McDermott, 1964:46; 1966:116. Ballantyne, 1968:106, 107; 1987b:173–176. Ballantyne in Calder, 1998:180. Ballantyne & Lambkin, 2000:70: 2009: Figs 94, 95, 106, 107, 503, 509.

Type Species: *Pyrophanes similis* Olivier, designated by McDermott, 1966:116.

Diagnosis. *Pyrophanes* belongs to a group of 7 Luciolinae genera with males characterized by: an elongate slender aedeagus with LL concealed behind the ML when viewed from beneath, pronotal width less than width across the elytral humeri, parallel-sided elytra, aedeagal sheath elongate slender, widest across the middle, with posterior half of sternite not emarginate on either side, and tapering evenly towards a narrow entire apex. It is distinguished from all other genera by a combination of MFC and paraprocts on the aedeagal sheath; without deflexed elytral apices; femora 3 are swollen and curved in four of the five species; the posterior margin of V7 is trilobed with incurving lobes and small pointed projections between the PLP and MPP; the underside of T8 has depressions at the sides housing very short spines and hairs. Females are macropterous and the bursa in certain species has wide paired plates. Larvae lack laterally explanate margins in *Pyrophanes similis* (Blair, 1927; Bertrand, 1972). This larva is not however reliably associated and an accurate identification of larval type for this genus is not available. This genus needs more extensive revision than is currently possible here.

List of species

- *appendiculata* Olivier
- *beccarii* Olivier
- *quadrimaculata* Olivier
- *similis* Olivier
- *semilimbata* (Olivier) **comb. nov.**

Key to species of *Pyrophanes* Olivier using males

1. Hind femora not swollen or curved (Figs 223, 224) . . . . *semilimbata* (Olivier) **comb. nov.**
   Hind femora swollen and curved 2
2. Elytra medium to dark brown, often with lateral and sutural margins semitransparent and pale (Figs 223, 224) 3
   Elytra dingy or pale, clear yellow, always with apex dark brown to black; base of elytra may be brown (Fig. 225) 4
3 Elytra medium to dark brown, lateral margin, and often also sutural margin, yellow . . . . *appendiculata* Olivier
   Elytra medium to dark brown, without any paler margins . . . . *beccarii* Olivier
4 Elytra yellow with apical and basal dark markings . . . . *quadrimaculata* Olivier
   Elytra yellow with only apices dark brown . . . . *similis* Olivier

Remarks. Olivier (1885) considered *Luciola indica* Motsch. approached *Pyrophanes*, and (1902) formally incorporated it. This species does not belong in *Pyrophanes* and is being addressed (Boontop, Lambkin and Ballantyne in prep.). Certain diagrams of the terminal abdomen of *Pyrophanes* are inaccurate e.g. Olivier (1885, Plate V, Fig.12) and Olivier (1907 Plate 3 Fig. 10) are inaccurate representations of the terminal ventrite; McDermott's (1964) brief redescription of *Pyrophanes* was probably influenced by the atypical abdomen of *P. macdermotti* McLean which he is known to have examined at this time and he misinterpreted various aspects. Ballantyne in Calder (1998) synonymised *Luciola complicata* Lea from far north Queensland with *Pyrophanes beccarii* Olivier.

Pyrophanes semilimbata (Olivier) comb. nov.
[Figs 223, 224,227]

Luciola semilimbata Olivier, 1883:76; 1913b: 417. Gorham, 1903: 326. Thancharoen *et al.* 2007:61.
Luciola venusta Olivier, 1883:76; 1902: 85 (synonymy). Thancharoen *et al.* 2007:61.
Luciola (Luciola) semilimbata Olivier. McDermott, 1966: 113.

Types. *Luciola semilimbata* Olivier. Female. 'Indes Orientales' labelled 1. Female symbol; 2. Handwritten Luciola semilimbata Chr. Ind or; 3. Typed label Coll Chevrolet; 4. Handwritten *Luciola semilimbata* with Ern Oliv typed in corner; 5. Typed label Specimen typicum originale auctoris Ern Olivier (MNHN). Fig. 227.
Luciola venusta Olivier. Male. Java ouest labelled 1. Typed label Specimen typicum originale auctoris Ern Olivier; 2. Handwritten *Luciola venusta* with Ern Oliv typed in corner (MNHN). Figs 223, 224.

Diagnosis. The only known *Pyrophanes* species with hind femora not swollen and hind tibiae not curved; very similar in dorsal colouration to *Pyro. appendiculata* colouration differing in having only the lateral elytral margins pale (*appendiculata* has both lateral and sutural margins pale, often widely so).

Remarks. Olivier (1883) described *L. semilimbata* from a female with elytral punctation in lines. Immediately below he described a male, from 'Java ouest' as *L. venusta*, with the last 3 abdominal ventrites white, and V7 trilobed. Olivier subsequently (1902) synonymised the two species. Both sexes conformed in the narrowly pale colour of the sutural ridge and lateral elytral margins. Olivier did not describe the elytral punctures in lines in the male. Gorham (1903) was unsure of the identification of specimens he described as *venusta*. Olivier (1913b) probably incorrectly recorded *semilimbata* (but not the sex of his specimens) from New Guinea, at Erima and Stephansort. Thancharoen *et al.* (2007 Fig. 5) distinguished 11 species, including *semilimbata*, where the original description indicated elytral punctures in lines.

Neither male nor female in MNHN has elytral punctation in lines. Males are very similar in dorsal colouration to *Pyrophanes appendiculata* and it is possible that Olivier misidentified some of his New Guinean material.

Trisinuata gen. nov.

[Figs 228–265]

Type species: *Trisinuata caudabifurca* **sp. nov.**

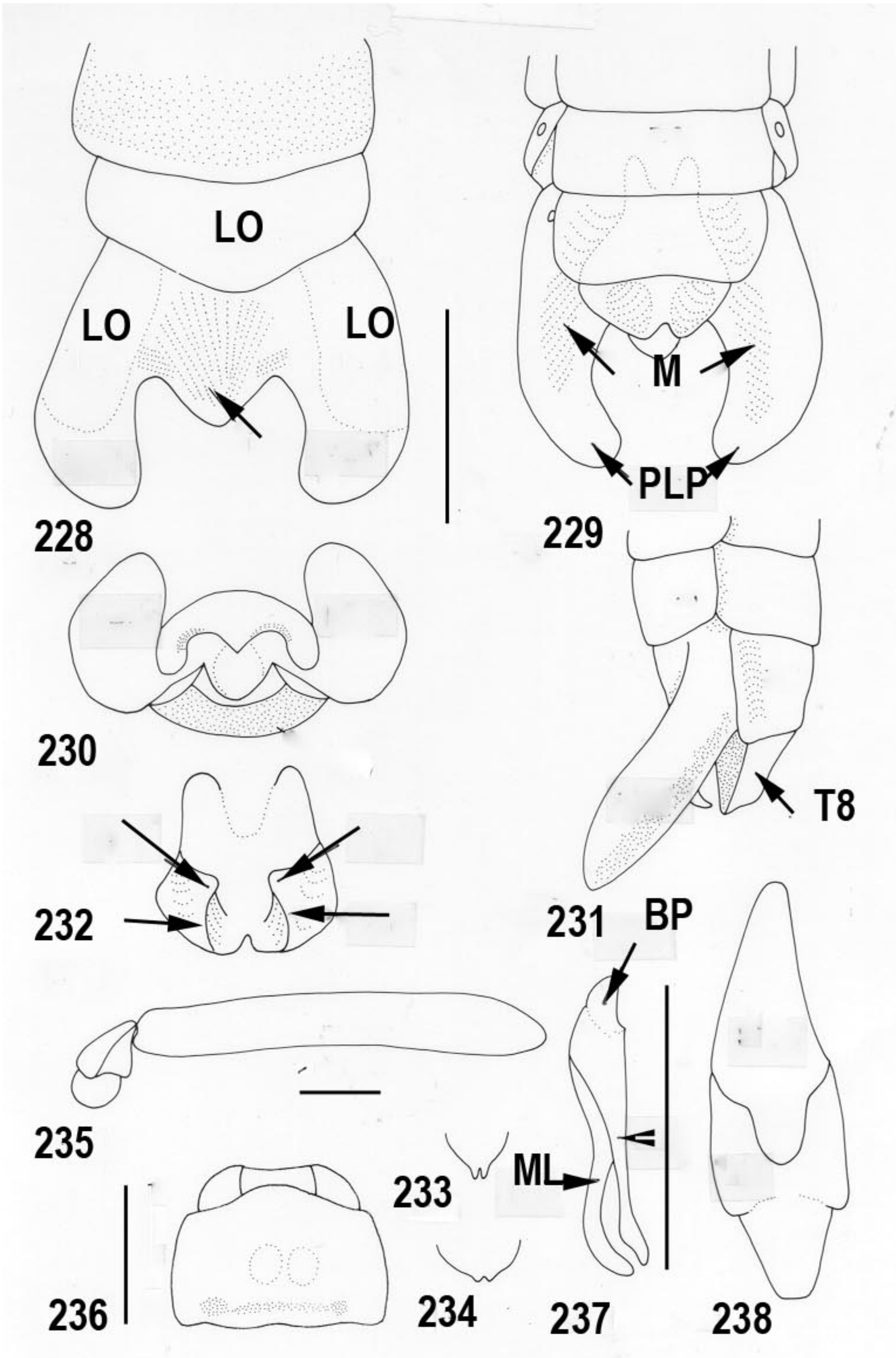
Diagnosis. *Trisinuata* **gen. nov.** is a New Guinean genus that belongs in a group of 7 genera characterized by: an elongate slender aedeagus with LL concealed behind the ML when viewed from beneath, pronotal width less than width across the elytral humeri, parallel-sided elytra, aedeagal sheath elongate slender, widest across the middle, with posterior half of sternite tapering evenly towards a narrow entire apex; bulbous paraprocts absent. Males have bipartite LOs in V7, expanded horizontal PLP, trisinuate posterior margin of V7, and several species have deflexed elytral apices. Males are distinguished from *Colophotia* in lacking a median carina on V7, and oblique PLP; from *Pteroptyx* in lacking bulbous paraprocts and an MFC; from *Pyrophanes* and *Poluninius* **gen. nov.** in lacking incurving lobes along the posterior margin of V7; from *Australoluciola* **gen. nov.** which has entire LOs in V7 by the bipartite LOs; from *Medeopteryx* **gen. nov.** in having bipartite LOs in V7 with expanded PLP. It differs from *Luciola indica* in lacking the bulbous median lobe and paraprocts on the aedeagal sheath. Three species are dorsally brown; the remaining species have orange yellow pronota with dark brown elytra. Females associated by label data are macropterous. Larvae are not associated.

Male. Pronotum: dorsal surface without irregularities in posterolateral areas and longitudinal groove in lateral areas; punctation dense; anterior margin not explanate; subparallel-sided, with margins straight (A=B=C), except in *papuana* and *similispapuae* where C>A and B, with lateral margins diverging posteriorly along their length in *papuana,* and *dimidiata* where B>A, C (Figs 239, 242, 251); width < humeral width; anterolateral corners rounded obtuse; lateral margins without indentation at mid-point, or sinuousity in either horizontal or vertical plane; without indentation in lateral margin near posterolateral corner, and irregularities at corner; posterolateral corners angulate, inclined either at 90° or obliquely to the median line in *papuae*; posterolateral corners either not projecting, or projecting as far as median posterior margin and separated from it by scarce emarginations.

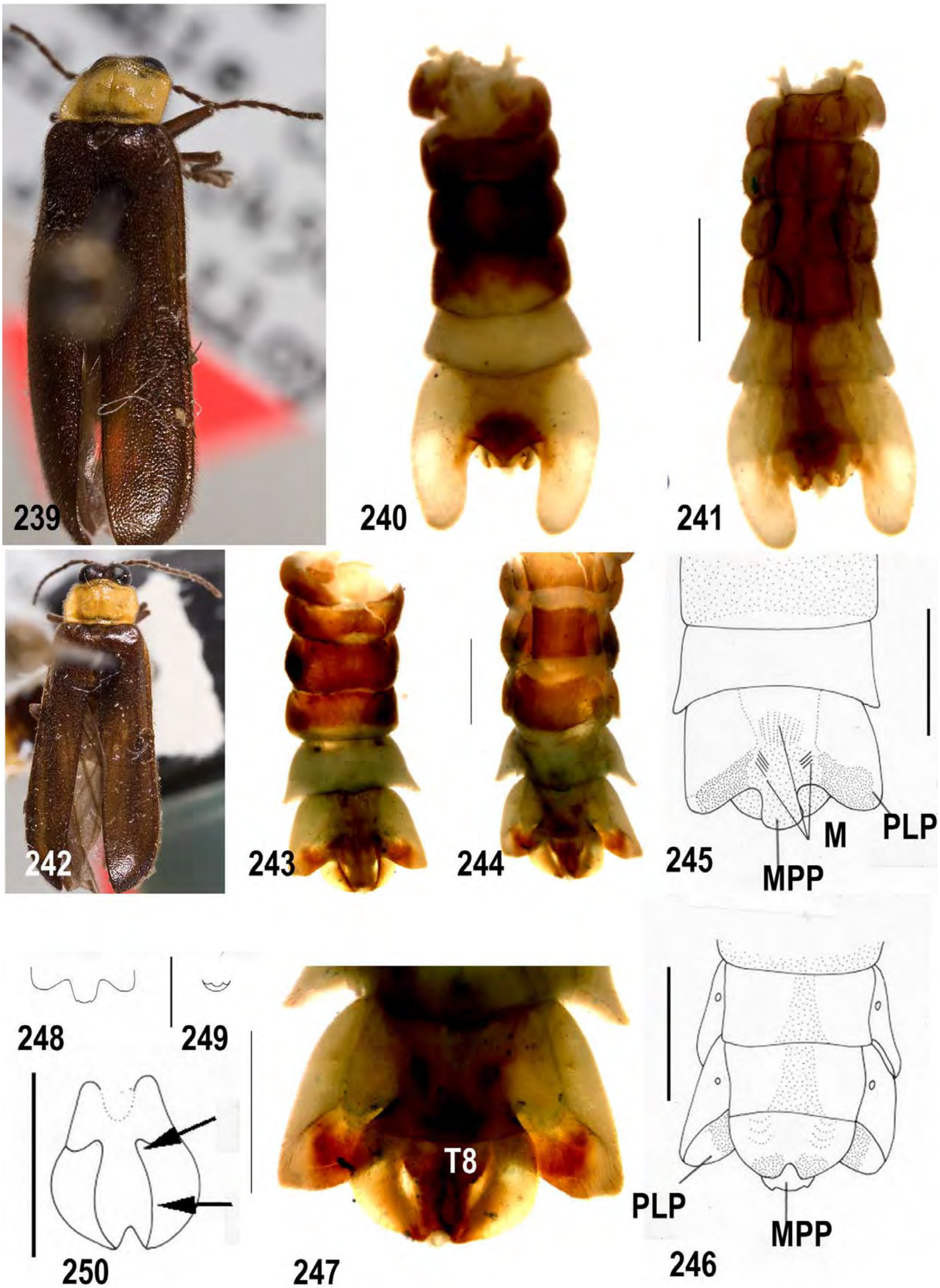
Hypomera: closed; median area of hypomeron not elevated in vertical direction; median area more widely flattened than elsewhere; pronotal width/ GHW 1.2.

Elytron: punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices deflexed in four species, weakly so in *minor*; non deflexed apices rounded; epipleuron and sutural ridge extend beyond mid-point, almost to apex but not as ridge around apex, neither thickened in apical half; no interstitial lines; elytral carina absent; in horizontal specimen viewed from below epipleuron at elytral base wide, covering humerus; viewed from above the anterior margin of the epipleuron arises level with or 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.



FIGURES 228–238. *Trisinuata caudabifurca* **sp. nov.** holotype and paratype males (234, 237) (ANIC). 228–231 abdomen, ventral (228 arrow indicates muscles in area of MPP), dorsal (229), end on ventral surface uppermost (230), left lateral (231); 232 tergite 8 ventral (anterior arrows indicate flanges, posterior arows lateral ridges); 233, 234 apex of MPP; 235 semidiagrammatic left lateral view showing head, pronotum and elytron; 236 head and pronotum dorsal; 237 semidiagrammatic aedeagus left lateral (arrow to right indicates LL); 238 aedeagal sheath dorsal. Figure legends: BP basal piece; LO light organ; M muscles; ML median lobe; PLP posterolateral processes V7; T8 tergite 8. These figures share scale lines: 228–234.



FIGURES 239–250. *Trisinuata* spp. 239–241 *Trisinuata caudabifurca* **sp. nov.** (239 holotype male, 240, 241 paratype male Banz). 242–250 *Trisinuata dimidiata* **sp nov**. (242, 245, 246, 248, 249, 250 holotype male ANIC; 243, 244, 247 paratype male). 239, 242 body dorsal; 240, 243, 245 abdomen ventral; 241, 244, 246, 247 abdomen ddorsal (247 detali terminal two segments only); 248 V7 posterior margin from above; 249 apex of MPP of V7 posterior view dorsal surface uppermost; 250 T8 ventral (upper arrow flange; lower arrow ridge). Figure legends: M muscle; MPP median posteriorprojection of V7; PLP posterolateral projection of V7; T8 tergite 8. These figures share scale lines: 240, 241; 243, 244; 248, 249.

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 close to moderately separated; frons-vertex junction rounded, without median elevation; posterolateral eye excavation not strongly developed, not visible in resting head position; antennal sockets on head between eyes, not contiguous, ASD < or subequal 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 or sometimes beyond. Mouthparts functional; apical labial palpomere strongly flattened, shaped like narrow triangle (narrowest at base and L 2–3 X W) and at least half as long as apical maxillary palpomere except in *Tri. dimidiata* **sp. nov.** where it is a short broad triangle (W/L=5/9), and 0.4 as long as apical maxillary palpomere, with inner edge entire. Antennae 11 segmented; length>GHW to twice GHW; no segments flattened, shortened, or expanded; pedicel not produced; FS1 not shorter than pedicel.

Legs: inner tarsal claw not split; without MFC; no femora or tibiae swollen or curved; no basitarsi expanded or excavated.

Abdomen (Figs 228–234, 240, 241, 243–250, 253, 254, 259–262): without cuticular remnants in association with aedeagal sheath; no ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment except in some *Tri. caudabifurca* **sp. nov.** where V3 is recurved; LO in V7 bipartite, inner margins not contiguous, reaching into PLP; posterior half of V7 not arched or swollen, muscle impressions visible between LO halves; LO present in V6, occupying almost all V6. MPP present, symmetrical, apex rounded or squarely truncate, either entire or shallowly emarginate, not laterally compressed, as long as or longer than width (L=W or L>W), not inclined dorsally nor engulfed by T8 apex, without dorsal ridge, median longitudinal trough; shorter than or subequal in length to PLP, MPP narrower than PLP except in *Tri. dimidiata* **sp. nov.** where they are subequal in width (Fig. 245); emarginations between PLP and MPP obliquely truncate (deeper at inner corners nearest MPP) in *Tri. dimidiata* **sp. nov.** (Fig. 245); V7 without median carina, median longitudinal trough, incurving lobes or pointed projections, median 'dimple', or reflexed lobes; posterior margin of V7 trisinuate with PLP moderately to considerably produced, as wide as or wider than MPP, longer than wide except in *Tri. papuana* where L=W (Figs 253, 254). T7 without prolonged anterolateral corners. T8: sclerotised, symmetrical, W=L, visible posterior area not narrowing abruptly, median posterior margin shallowly and narrowly emarginate; widest across middle with lateral margins tapering evenly in both an anterior and posterior direction; without prolonged posterolateral corners, 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 with well developed median longitudinal trough (except in *Tri. similispapuae* where it is quite short), margined by well defined symmetrical ridges; anterior end of ridges with flanges which are short to long, narrow to wide, and apically rounded or acute (Figs 232, 250, 255); flanges symmetrical except in *Tri. apicula* **sp. nov.,** *papuae* and *similispapuae* (Fig. 261); without lateral depressed troughs, median posterior ridge; concealed anterolateral arms of T8 as long as visible posterior portion of T8, not laterally emarginated before their origins, not expanded dorsoventrally, expanded only in horizontal plane; without bifurcation of inner margin and ventrally directed pieces; lateral margins of T8 not enfolding sides of V7.

Aedeagal sheath (Figs 238, 257): approx. 3–3.5 times as long as wide; without bulbous paraprocts; symmetrical in posterior area where sheath sternite tapers evenly to a narrow rounded apex; anterior half of sternite relatively narrow, apically rounded; tergite without lateral arms extending anteriorly at sides of sheath sternite; tergite without projecting pieces along posterior margin of T9, anterior margin without transverse band.

Aedeagus (Figs 237, 258, 259, 264): L/W 5/1; LL lack lateral appendages; LL apices not visible from beneath at sides of ML, LL/ML narrow; LL of equal length, slightly shorter than ML, contiguous along inner dorsal margins; separated longitudinally by most of 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, may be slightly produced or not; LL without lateral hairy appendages along their outer ventral margins, not produced preapically nor narrowly on inner apical margin, apices of LL not inturned, nor out-turned; without projection on left LL; inner margins without slender leaf-like projection; ML symmetrical, without paired lateral teeth and tooth to left side, not strongly arched, apex not shaped like arrowhead, not bulbous, not inclined ventrally; BP not strongly sclerotised, not hooded, not strongly emarginated along anterior margin.

Female. Macropterous; associated by label data only for two species. Pronotum without irregularities in posterolateral areas; punctation moderate to dense; pronotal width less than humeral width; without 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; no interstitial lines; elytral carina absent. No legs or parts thereof swollen and /or curved. LO in V6 only, without any elevations or depressions or ridges on V7; median posterior margin of V7 widely emarginate, median area not broadly rounded; median posterior margin of V8 entire. Bursa plates consisting of 2 wide pairs in *Tri. papuana* and *Tri. similispapuae* (Fig. 265).

Larva. Unknown.

Etymology. *Trisinuata* (feminine) is a noun latinised from the English trisinuate, describing the shape of the posterior margin of V7 where the expanded and lengthened PLP enhance the appearance of the trilobed posterior margin.

List of species of *Trisinuata* gen. nov.

- *T. apicula* **sp. nov.**
- *T. caudabifurca* **sp. nov.**
- *T. dimidiata* **sp. nov.**
- *T. microthorax* (Olivier) **comb. nov**.
- *T. minor* (Ballantyne) **comb. nov.**
- *T. papuae* (McDermott) **comb. nov.**
- *T. papuana* (Olivier) **comb. nov**.
- *T. similispapuae* (Ballantyne) **comb. nov.**

Key to species of *Trisinuata* gen. nov. using males

1. Elytral apices deflexed. 2
   Elytral apices not deflexed 6
2. Deflexed elytral apex scarcely wider than epipleuron (Ballantyne & McLean 1970 Fig. 16m) . . . . *minor* (Ballantyne) **comb. nov**.
   Deflexed elytral apices well defined 3
3. Pronotum orange, lateral margin may be finely dark marked. 4
   Pronotum brown 5
4. Pronotum orange, without dark marginal markings; PLP apically emarginate (Ballantyne & McLean 1970 Fig. 5 a–d) . . . .*microthorax* (Olivier) **comb. nov**.
   Pronotum orange with fine dark margins; PLP not apically emarginate. . . . . *apicula* **sp. nov.**
5. MPP of V7 elongate, slender, subequal in length and width to PLP or longer than PLP (Figs 259, 260); aedeagus 2.5 times as long as broad; LL of aedeagus closely approximate dorsally; flanges of T8 asymmetrical (Fig. 261; Ballantyne & McLean 1970 Fig. 17) . . . .*similispapuae* (Ballantyne) **comb. nov**.
   MPP of V7 narrower and shorter than PLP; aedeagus 4.5 times as long as broad; LL of aedeagus approximate only at their apices (Ballantyne & McLean 1970 Fig. 10); flanges symmetrical . . . . *papuae* (McDermott) **comb. nov**.
6. Dorsal surface of body brown to dark brown (Figs 251, 252) . . . .*papuana* (Olivier) **comb. nov**.
   Pronotum yellow, elytra dark brown. 7
7. PLP no longer than MPP; (Figs 243, 245) . . . .*dimidiata* **sp. nov.**
   PLP longer than MPP, considerably produced, longer than wide, and may incline ventrally (Figs 228–231, 240, 241) . . . . *caudabifurca* **sp. nov.**

Trisinuata apicula sp. nov.

Holotype. Male. **NEW GUINEA**. North East: 146.40E, 7.22S, Wau, Bulolo River, 850–900m, 24.viii.1965, J. and M. S. (BPBM).

Paratypes (3). Same locality as holotype, male 4.ii.1966, JS (BPBM). Morobe District, 4 miles n Wau elev. C 2800 feet, near Kunai creek Lae road, 15.xi.1969, J. E. Lloyd, male (G263) (ANIC). Morobe District, Mt Missim, 880–1050m, 8–9.ii.1963, J S. male (BPBM).

Diagnosis. Superficially similar to both *Tri. papuae* and *Tri similispapuae*, distinguished by the yellow pronotum, which may be dark margined laterally; elytra dark brown; elytral apex truncate, PLP narrow and T8 with asymmetrical flanges.

Male. 5–5.5 mm long. Colour: pronotum bright shiny pale orange yellow with a very fine dark border (without dark margin in Kunai Creek male); remainder of body dark brown except for narrow pale posteromedian area on V5, largely pale LO in V6, 7 (darker markings of these segments indicated as stippling in Ballantyne 1987a Fig. 13q), apical 3 tergites and reflexed margins of V6, 7 pale brown. Pronotum: 0.8–0.9 mm long; 1.4–1.5 mm wide; punctures broad, shallow, some contiguous, some separated by their width in median area of disc. Head: moderately depressed between eyes; GHW 0.9–1.3 mm; ASD = ASW. Elytron: apices truncate, outer margin (B) slightly curved, inner margin (C) sinuous (Ballantyne 1987a Fig. 13o). LO in V7 extending into PLP (Ballantyne 1987a Fig. 13q) or not (G236); MPP shallowly emarginated, posterolateral corners very short and acute. Flanges of T8 asymmetrical (Ballantyne 1987a Fig. 13r).

Etymology. The name *apicula* (Latin, apicula, ae = bee) is a play on words, referring to the designation of these specimens as Species B (Ballantyne & McLean 1970; Ballantyne 1987a).

Remarks. Ballantyne and McLean (1970) briefly described and illustrated a single male with unusual deflexed elytral apices as "Species B". Ballantyne (1987a:162) described an additional Wau male. Two additional males are associated and the treatment formalised here. The apical labial palpomere is not dentate on its inner margin, and the apparent dentition observed by Ballantyne (1987a) is attributed to a clumping of hairs.

Trisinuata caudabifurca sp. nov.

[Figs 228–241]

Holotype. Male. **NEW GUINEA**: 7.20S, 146.45E, Morobe Pr., 4.5 mi w Wau, Edie Cr. Rd., at Namie Cr. elev. ca 500', November 17, 1969, J.E. Lloyd, (G615.) (ANIC).

Paratypes* (5). **NEW GUINEA:** 144.37E, 5.47S, Western Highlands Pr.: Banz, Fatima school, xi.7.1969, J. Buck, male (Tube B/9, labelled 'flickerer'); 8.15pm., xi.6.1969, J. Buck, male (Tube B/4). Simbu Pr., Chimbu Dist.: Kundiu (*sic*), Catherine Mission, Oct. 25, 1969, J. E. Lloyd, male (JELC); Kondiu Farm site 1, sweep of fly outs Nov. 30, 1969, E. Ball. male; Kondiu 16.x.1969, J. Buck (Tube II/2), male (ANIC).

*All specimens collected by Buck and Ball have label data quoted exactly as it appears in the tubes, to allow association with field records. The following paratypes have no associated flashing data.

NEW GUINEA: 6.13S, 143.39E, Papua, S. Highlands, Mendi, 1660 m, 13.x.1958, light trap, JLG, male (BPBM). Arabuka, 1500–2000 m, 7.i.1968, JS, male (BPBM). Kundiu, 9 Nov., 1969, J.E. Lloyd, male (G544) (ANIC). 7.15S, 146.48E, Mt Missim, 1600 m, 27.v.1966, malaise trap, JLG, male (BPBM). 7.20S, 146.45E, Wau, Morobe District: 1100–1200 m, vi. 1968, NK, male (BPBM); 1150–1600 m, 9.ii.1968, JS, male (BPBM); 1200 m, 30.xii.1964, M. V. light trap, JS, male; 5–6.xii.1961, 2 males; 14.vii.1961 light trap, male; 1250 m 12.iii.1969, male; 12.iv.1965 malaise trap, male; 1200–1300 m, 14.iii.1963, male; 16.vi.1965 male; 1450 m, 6.ii.1963 male (BPBM); same data as Holotype, 2 females (G623, 624) (JELC). Wau, Morobe Distr., Namoi Creek: 1670 m 26.viii.1963, malaise trap, JS, male; 1700–1800 m, xii. 1965, JS, male; 1750 m 17.viii.1965, malaise trap, JS, male (BPBM). Wau, Bulolo River, 850–900 m, 24.viii.1965, JS, male (BPBM). Western Highlands, Goiburung, East of Korn farm, 1560 m, x.15.1958, light trap, JLG, male (BPBM).

Diagnosis. Males with orange pronotum and dark brown elytra, distinguished by the greatly developed PLP of V7.

Code names. *Luciola* "super fork tail", "Swallow tail"; *Luciola* 14, Lloyd (1973a).

Male. 5.7–7.0 mm long. Colour (Fig. 239): pronotum bright yellow, semitransparent; (paler area of irregular retraction of fat body across anterior and posterior margins and median area where fat body not retracted may appear darker); MS, MN, elytra, head between eyes, antennae, and palpi, very dark brown; ventral surface of pronotum yellow, except for brown prosternum and precoxal bridges; entire ventral surface of meso and metathorax, and all of legs very dark brown; basal abdominal ventrites dark brown; posterior margin of V5 narrowly white; V6 white; LO halves in V7 creamy white, remainder of V7 yellowish, with white areas where underlying muscle is visible externally (Fig. 240), and a brown area anterior to the median posterior projection of V7 (Fig. 240); median posterior projection of V7 in Tubes B/4, B/9 is brown; T1–5 light brown; T6–8 semitransparent laterally and pale brown medially (Fig. 241); or T8 light brown (Kondiu, farm site 1). Pronotum (Fig. 236, 239): 1.5–1.7 mm wide; 0.8–1.0 mm long; W/L = 1.5–2.0; punctures shallow, separated by their width; midanterior margin broadly rounded, moderately projecting beyond acute anterolateral corners; median posterior margin indented; most of disc gently and smoothly convex, otherwise excavated as figured. Elytra: punctures dense, some contiguous; apex of left elytron on holotype slightly down-turned, probably damaged. Head: slightly depressed between eyes; GHW 0.9–1.3mm; SIW 0.3mm; ASD = ASW. Abdomen (Figs 228–232, 240, 241): LO extending into PLP which are bluntly rounded at apices and may incline gently ventrally (Fig. 231); muscle blocks may be visible in dorsal surfaces of PLP (Fig. 229); MPP narrowed at apex which may be entire or finely emarginated, and incline dorsally (Figs 228, 230, 231, 233, 234, 240). T8: flanges short rounded (Fig. 232). Aedeagus (Fig. 237): elongate slender (L = 5XW) with apex of ML flattened (viewed from side).

Female. Macropterous, coloured as for male except for LO restricted to V6; associated by label data only.

Etymology. The specific name emphasises the development of V7 (cauda = tail; bifurca = 2 forked).

Remarks. Lloyd's nickname "Swallowtail" (pers comm.) describes the posterolateral processes of V7. Their ventral inclination and the dorsally inclined median posterior projection of V7 might indicate a wedge or clasper for the female abdomen, or more likely a consequence of dehydration. Ballantyne (1987a Fig. 2a, b) described the terminal abdomen of '*Luciola* species 14' and discussed terminal abdomen modifications in the Luciolinae and their possible significance.

Lloyd (1973a) noted males of this species "active in the crown of a 50 ft tree standing in the ravine ..."; males emitted rapid flickers of variable duration.

Lloyd's field records for G615 are "looks like long flicker from Mengendi, but (he) also saw short (flickers) in this area i.e. ¾ (second) flicker each 1.5 seconds", and for G413 "long flicker". The two females are associated by label data only. Their field data reads "glowing on road edge near tree with long flicker sp. (i.e. *caudabifurca)* in it".

Trisinuata dimidiata sp. nov.

[Figs 242–250]

Holotype. Male. **NEW GUINEA**: Western Highlands Pr., Chimbu District, Kondiu, Catherine Mission, October 25, 1969, J.E. Lloyd, (G414) (ANIC).

Paratype (1). **NEW GUINEA**: Western Highlands Pr., Chimbu District, Kondiu recorded male November 9 1969, J.E.Lloyd (G541) (ANIC).

Code name. *Luciola* 13 (Lloyd 1973a)

Male. 7.5–7.8 mm long. Colour (Fig. 242): pronotum shiny yellow, semitransparent; MN pale brown with median brown area; MS and elytra uniformly dark brown; ventral surface of pronotum yellow; remainder of ventral surface of body, including posterior margin of V7, dark brown, except for narrow white posterior margin of V5, white LO in V6, and white LO halves in V7 (Fig. 243); basal abdominal tergites dark brown; T6, 7 and 8 pale cream with brown mottling in holotype, T8 white and T7 white with brown markings along posterior half in paratype (Fig. 247). Pronotum (Fig. 242): 1.2–1.3 mm long; 1.6–1.8 mm wide; W/L 1.3–1.4; punctures small, shallow, contiguous or separated by up to their width; midanterior margin rounded, projecting considerably beyond rounded obtuse anterolateral corners; lateral margins diverging in anterior half, and converging posteriorly in posterior half with slight sinuousity on right side in holotype; posterolateral corners narrowly rounded. Elytra shiny, punctures dense, some contiguous. Abdomen (Figs 243–250): posterolateral corners of V6 narrowed, appearing prolonged if viewed from above in ethanol preserved G541 (Figs 243, 244, 247). LO (Figs 243, 245) not extending into PLP which are slightly truncate along their inner posterior margins; lateral margins of V7 strongly divergent in ethanol preserved G541; MPP moderately broad, apex truncate or very slightly emarginated (Figs 248, 249). T8: flanges narrowly elongate, apex rounded (Fig. 250).

Female, larva unknown.

Etymology. *dimidiata* (dimidius, Latin = half) emphasizes the pattern of light production of the single paratype male. Lloyd's field records for the holotype (G414) are "single at ½ sec".

Trisinuata microthorax (Olivier) comb. nov.

Luciola microthorax Olivier, 1885:364; Olivier, 1896:2.
Pteroptyx microthorax (Olivier). Olivier, 1909a:318; Olivier, 1910b:48; Olivier, 1913b:417. Ballantyne and McLean, 1970:265. Ballantyne, 1987a:156.

Lectotype. Male. **INDONESIA:** Papua: 1.14S, 134.01E Hatam, lectotype male of *Luciola microthorax* designated by Ballantyne (1987a) (MCSN).

Diagnosis. 6.0 mm long; pronotum and MP dingy yellow, MS dark brown; deflexed elytral apex rounded; distinguished by the bilobed PLP (Ballantyne 1987a Fig. 5a, b, c).

Remarks. Olivier (1885) named the species for the small size of its pronotum, and Ballantyne and McLean (1970) adopted an E/P index (ratio of elytral width measured across bases to pronotal width) in an attempt to characterise it. The use of this index has been discontinued; *microthorax* is amply characterised by features of its terminal abdomen. Helgen *et al.* (2008) indicated Hatam is a village in the Arfak Mountains of the Vogelkop peninsula.

Trisinuata minor (Ballantyne) comb. nov.

Pteroptyx minor Ballantyne, in Ballantyne and McLean, 1970:261; Ballantyne, 1987a:157.

Holotype Male. **NEW GUINEA**: 147.24E, 9.25S, Bisianumu, east of Port Moresby, 500 m., ix.25.1955 (BPBM).

Other specimens examined. NEW GUINEA: 146.40E, 7.22S, Edie Creek, near Wau, 1700m, 2.iv.1966, JLG, 2 males. 7.13S, 146.49E, Mt Missim, 1600–2000m, 21–24.ix.1964, M. S., male (BPBM).

Diagnosis. Small (ca 4.5 mm long) with elytral apex barely deflexed; pronotum orange, elytra black.

Remarks. This species is now represented in collections by five males. The elytral apices (Ballantyne, 1987a, Fig. 6 e, f) are swollen and bulbous and thicker than the remainder of the epipleuron, so their interpretation as "deflexed elytral apices" differs slightly from others, where the deflexed apex of the elytron is anteriorly prolonged and no thicker than the rest of the elytron.

Trisinuata papuae (McDermott)

Pteroptyx papuae McDermott, 1959:9; McDermott, 1966:117. Ballantyne & McLean, 1970:252.

Holotype. Male. **NEW GUINEA**: 148.23E, 8.37S, Monda, Buna District, xii.28.1943 (Cornell University).

Other specimens examined. NEW GUINEA: 147.10E, 7.53S, Garaina, 800m, 16.i.1968, J. & M. S., male (BPBM). 147.44E, 8.52S, Kokoda, 400m, iii.22.1956, JLG, 2 males (BPBM). 148.10E, 8.55S, Mt Lamington District, C. T. McNamara, v.1927 2 males, female; vii.1927, male, female; viii.1927, female; i–ii.1929, female (AMSA).

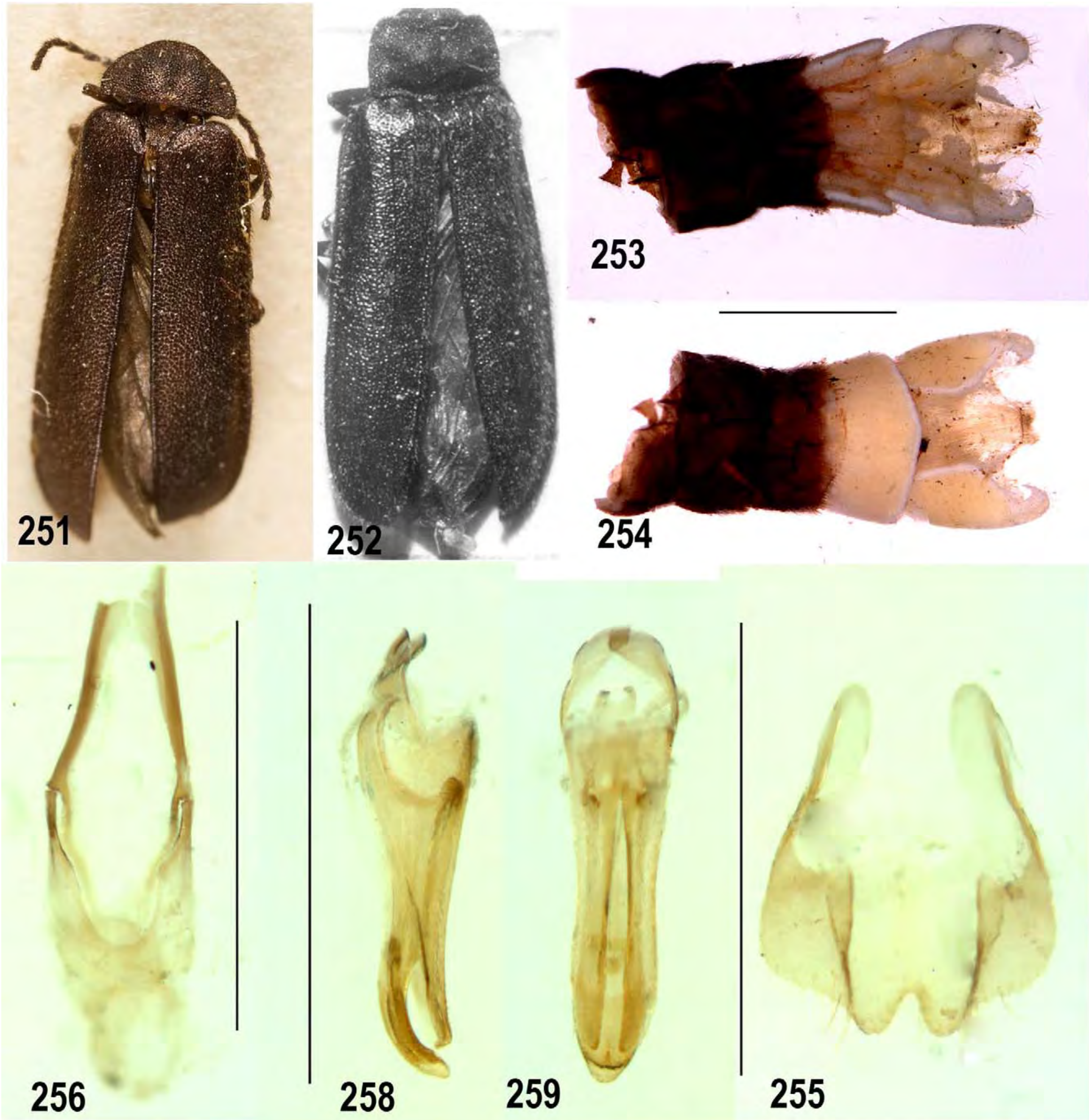
Diagnosis. Small (4.4–4.6 mm long); entirely brown dorsally except for 4 median orange spots on the pronotum; deflexed elytral apex somewhat truncate along margin B with margin C slightly sinuate; distinguished most obviously from *Tri. papuana* by the presence of the deflexed elytral apex.

Remarks. This study extends the number of males known in collections. *Luciola papuana* Olivier was described from a female coloured like *M. papuae*. Males lacking the deflexed elytral apex are associated with *Luciola papuana* and the species assigned to *Trisinuata* **gen. nov.** and redescribed below. Table 9 lists Luciolinae sharing similar pale brown dorsal colouration, of which three species, including this one, are assigned to *Trisinuata* **gen. nov.**

Trisinuata papuana (Olivier)
[Figs 251–258]

Luciola papuana Olivier, 1913b:417.
Luciola (Luciola) papuana Olivier. McDermott, 1966:111.

Holotype. Female. **NEW GUINEA**: North East: Sattelberg, Huon Gulf (Természettudományi Museum, Budapest).



FIGURES 251–258. *Trisinuata papuana* Males (Komba SAMA) and type female (252). 251, 252 dorsal; 253, 254 abdomen, dorsal (253) and ventral; 255 T8 ventral; 256 aedeagal sheath dorsal (anterior margin of sheath sternite missing); 257, 258 aedeagus left lateral (257) and dorsal. These figures share scale lines: 253, 254; 257, 258.

Other specimens examined. NEW GUINEA: 5.38S, 146.28E, Finisterre Range, Saidor, Kiambavi village, vii.22–29.1958, WB, male, female (BPBM). Saidor, Matoko village, WB, ix.6–24.1958 2 males; 28.ix–5–1958, 3 males; 29–ix–5–1958, 2 males (BPBM). Finisterre Mts, Komba, 2 males, 8 females L Wagner (SAMA). 7.00S, 147.00E, Morobe District, Huon Peninsula, Gang Creek Camp, Mt Rawlinson, 4500 feet, H. Van Deusen, vi–21–26–1964, male; vi–8–1964, 2 males (AMNH).

Diagnosis. One of four species from New Guinea with brown dorsal colouration; distinguished from *Aus. fuscamagna* **sp. nov.** and *Aus. fuscaparva* **sp. nov.** by the bipartite LO in V7, and *Tri. papuae* by the absence of a deflexed elytral apex.

Male. 6.7–7.2 mm long. Colour (Fig. 251): entirely dark brown except for white V6, 7 and pale T6–8 (Figs 253, 254). Pronotum: 1.5–1.7 mm wide; 1.0–1.1 mm long; W/L 1.5–1.7; punctures shallow, separated by width of puncture or contiguous; pronotal disc smooth and shiny between punctures; lateral margins diverge along length (C>A, B). Head: GHW 1.3–1.4 mm; ASD < ASW. Abdomen (Figs 253, 254, 255): muscles attaching in median area between LO halves are visible through cuticle, LO extending to sides of V7 and into PLP; MPP wider than long, curving dorsally at its apex which is bifurcate into 2 fine points, shorter and narrower than wide PLP (Fig. 254). T8 (Fig. 255): well defined, wide lateral ridges and short wide apically rounded flanges. Aedeagus (Figs 257, 258): anterior prolongation of ML not long and slender; apices of LL concealed behind ML and not laterally expanded; lateral margins of LL very slightly curved.

Remarks. Olivier (1913b) based this species on a female. The similarity of pronotal colour to the type female is most obvious in these males. Table 9 lists Luciolinae with dark dorsal colouration.

***Trisinuata similispapuae* (Ballantyne) comb. nov.**
[Figs 259–265]

Pteroptyx similispapuae Ballantyne, in Ballantyne & McLean, 1970:261; Ballantyne 1987a:159.

Holotype. Male. **INDONESIA** West Irian: 135.31E, 3.23S, Nabire, South Geelvink Bay, 0–30m, vii.2–9.1962, light trap (BPBM).

Specimens examined. **NEW GUINEA**: Western Highlands 5.32S 144.08E Baiyer River, tube bears label 'MP (mating pair) *2 8.15 male yellow female Gr. 11.xi.69 light male 2nd BR 2; no collector (see Ballantyne 1987a:160) (ANIC).

Diagnosis. This mating pair was characterised (Ballantyne 1987a p. 159). Males small (5–6 mm long); dorsally entirely brown with small median orange spots on the pronotum, or median area of pronotum entirely dingy orange; very similar to *Tri. papuae,* distinguished by the outline of the terminal abdomen (Fig. 259, 260), and the asymmetrical flanges on T8 (Fig. 261); short paired cuticular strips extend anteriorly across the dorsal face of V7 from the sides of the MPP (Fig. 260). Female coloured as for male except for pale LO in V6 only.

Female. 5.6 mm long. Colour: as for male except for yellowish brown ventral surface of metathorax, pale LO in V6 only, not reaching to brown lateral margins, light brown basal abdominal tergites and darker brown T7, 8. V7 posterior margin gently bisinuate, median area narrowly indented, and posterolateral corners rounded (Fig. 263). Bursa: with broad paired plates (Fig. 265).

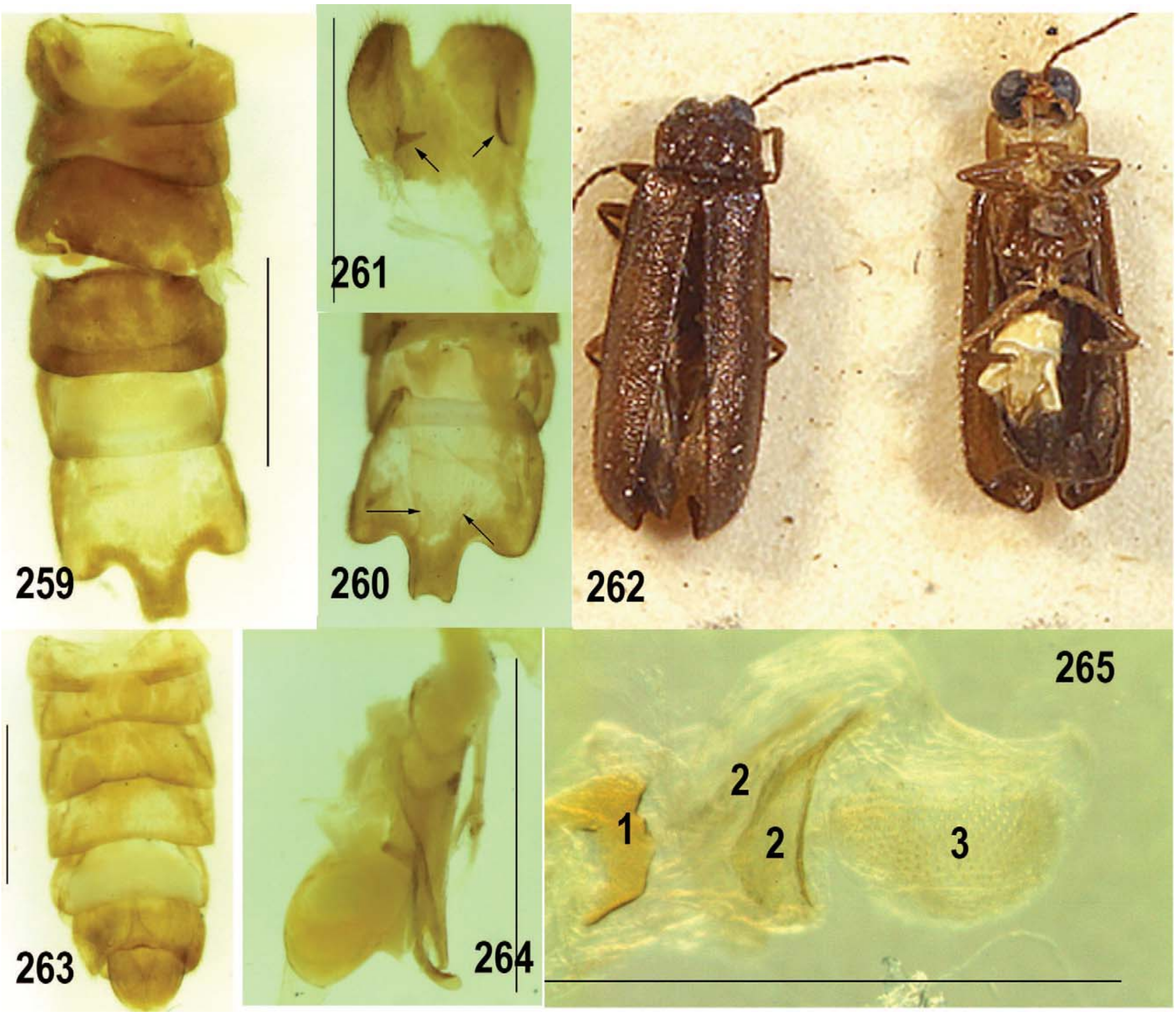
Remarks. This species was described from two specimens which differed from the similarly coloured *Pteroptyx papuae* in the outlines of the terminal abdominal ventrite (Ballantyne & McLean, 1970). Ballantyne (1987a) described two further specimens (a mating pair) and the light colour (male yellow, female green), but had difficulty in determining if the LO in V7 was bipartite. A reexamination here including the presence of cuticular strands (Fig. 260) to which muscles attach in the median area of V7 indicates a bipartite LO in V7. Ballantyne (1987a:160) described the aedeagal sheath split by a mating "plug" (spermatophore) retained as a very hard ball attached to the ejaculatory orifice (Fig. 264).

Species Incertae

Luciolinae

***Luciola* 'species C'**

Ballantyne and McLean (1970:266) described certain groups of specimens which they were unable to assign reliably to a species as Species A–E. Species A is included in *M. antennata* here; Species B is described as a new species *Tri. apicula* **sp. nov.;** Species D could be a male of *Luciola melancholica* and is considered below; and Species E is assigned to *M. tarsalis*. Species C represented by specimens with trisinuate V7, entire LOs in V7, and orange pronota, remains unassigned.



FIGURES 259–265. *Trisinuata similispapuae* males and female (259–261, 263, 265 Baiyer River mating pair; 262 Mt Lamington males). 259, 263 abdomen ventral; 261 T8 ventral (anterior prolongation on left side missing; flanges arowed); 262 whole body, dorsal (262) and ventral; 264 aedeagus left lateral with extruded spermatophore; 265 bursa lateral. Figure legends: 1 median oviduct plate; 2 posterior bursa plates; 3 anterior bursa plates. These figures share scale lines: 259, 260.

Luciola melancholica Olivier

Luciola melancholica Olivier, 1913b:417. McDermott, 1966:109. Ballantyne & McLean, 1970:267.

Holotype. Female. **NEW GUINEA**: Iles Bertrand, holotype female of *Luciola melancholica* (MCSN).

Remarks. The holotype female was described with dark brown elytra and an orange pronotum with dark marginal markings. There are several examples herein where different species have marginal dark markings on the pronotum (e.g. *Aus. anthracina*, *M. fulminea*, *M. pupilla*, *Tri. apicula* **sp. nov**.). No males from the type locality of the Bertrand Islands have been located.

Ballantyne and McLean (1970:267) described as "Species D" two males where the pronotal colour most closely approached that of the holotype of *melancholica*. While they described the LOs as “filling sternites 6 and 7” their diagrams (Fig. 8 n, o) indicate a situation where interpretation of the nature of the LO in V7 as either entire or bipartite is not clear, and no further action on these two specimens is taken here. They also included specimens in *Pteroptyx cribellata* Groups 3 and 4 (page 247) where the male pronota had dark markings along the lateral and anterior margins, and in one case also along the posterior margin. All these specimens in Groups 3 and 4 have entire LOs in V7. Ballantyne (1987a:163) included two females as possible *melancholica*, and indicated that certain *Pteroptyx* (now *Medeopteryx*) *fulminea* have lateral pronotal margins finely dark. Certain specimens from Mt Lamington tentatively assigned to *Aus. anthracina* have either dark margined or completely pale pronota in the males.

Luciola ruficollis (Boisduval)

Lampyris ruficollis Boisduval, 1835:128. Guérin-Méneville, 1838:75. Motschulsky, 1854: 53.
Luciola ruficollis (Guérin-Méneville). Lacordaire, 1857: 338. Olivier, 1902:85; 1907:54; 1910b:45. **Nec** Girard, 1873, plate xxxv, figs 9, 9a, 9b.
Luciola (Luciola) ruficollis (Guérin-Méneville). McDermott, 1966:112. Ballantyne, 1987a:131.

Type. NEW GUINEA. not located.

Remarks. This species has not been reliably identified in collections. Based on its original description as a small species (ca 6 mm long) with orange pronotum, dark brown elytra, and V7 trilobed Ballantyne (1987a:131) considered that *Pteroptyx antennata* Olivier could have been based on similar specimens. No reference to *ruficollis* mentions deflexed elytral apices in the male. The described ventral colouration of yellowish thorax and abdomen is approached by *Australoluciola australis* which lacks a trisinuate V7.

This species has been attributed to Guérin-Méneville (1830). The actual publication date of this work was 1838, and the species is here attributed to Boisduval (1835) as the first description to be associated with the name.

Luciola tenuicornis Olivier

Luciola tenuicornis Olivier, 1885:365, plate v, fig. 9; 1902: 87.
Luciola (Luciola) tenuicornis Olivier. McDermott, 1966: 114.

Type. CELEBES. Not located**.**

Remarks. Olivier described a small (5–6 mm) male with yellow pronotum, light brown elytra with paler lateral margins, and V7 prolonged and abruptly narrowed, from the Celebes. McDermott (1966) incorrectly recorded it from New Guinea.

Incorrect New Guinean records

Luciola timida Olivier

Luciola timida Olivier 1883:76; 1902:87. Bourgeois 1890:87. Olivier 1913b:417. McDermott 1966:114.

Type. Saigon (MNHN).

Remarks. Olivier (1913b) recorded this species from various locations in New Guinea (Friedrich Wilhelms-hafen = Madang) and islands of Kiriwina, Fergusson and Trobriand. Apart from the type we are unable to relocate any of these specimens.

Photinus cinctellus Motschulsky

Photinus cinctellus Motschulsky 1854:36. Lacordaire 1857:322. McDermott 1966:37. Powell 1965:88.

Type not examined.

Remarks. Ballantyne as Powell (1965) recorded 9 specimens (6 males) from Lae. McDermott identified these as *Photinus cinctellus* and considered that mislabelling should be considered. No such specimens have been collected since.

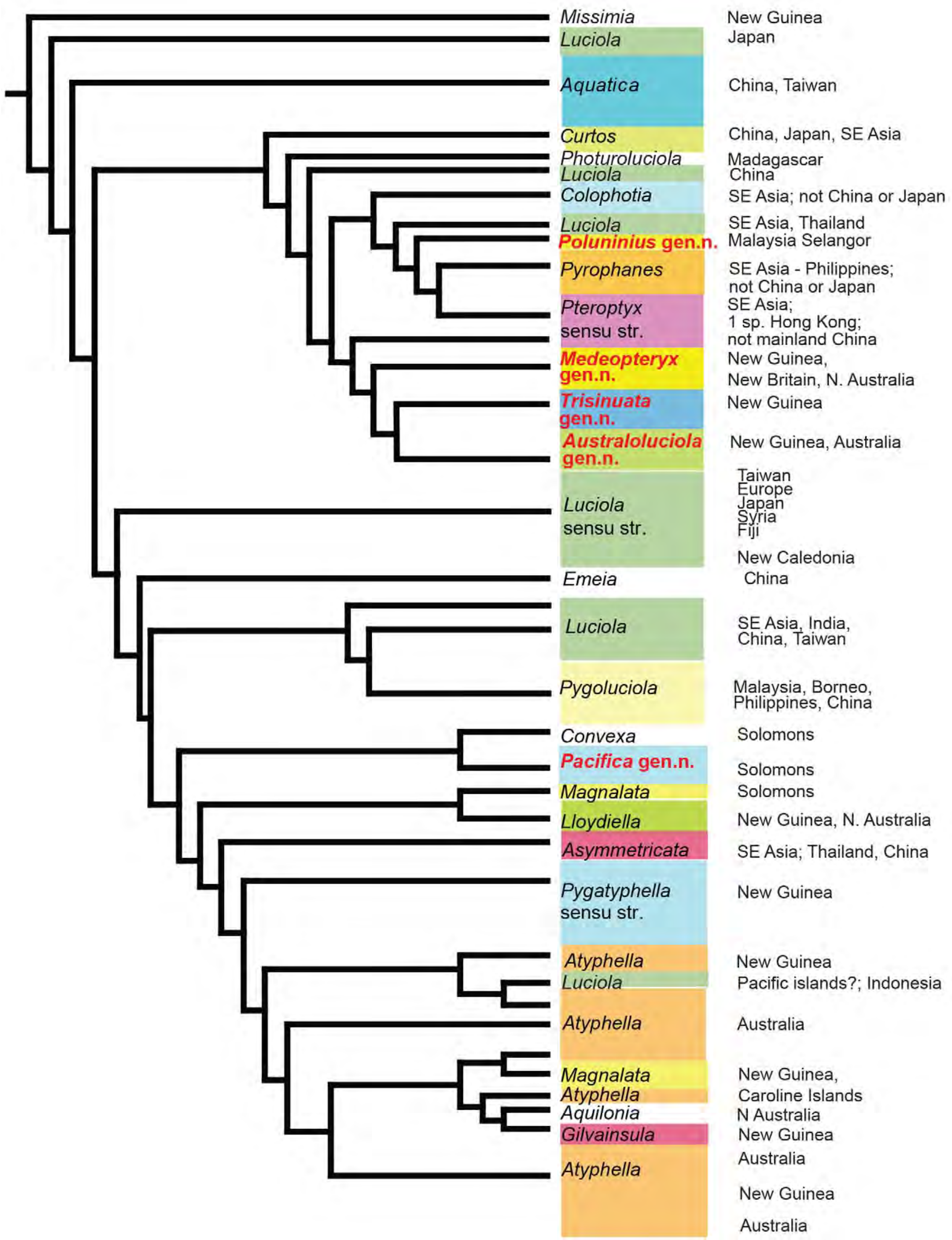


FIGURE 266. Majority rule tree for the complete analysis of the Luciolinae showing genera and distribution.

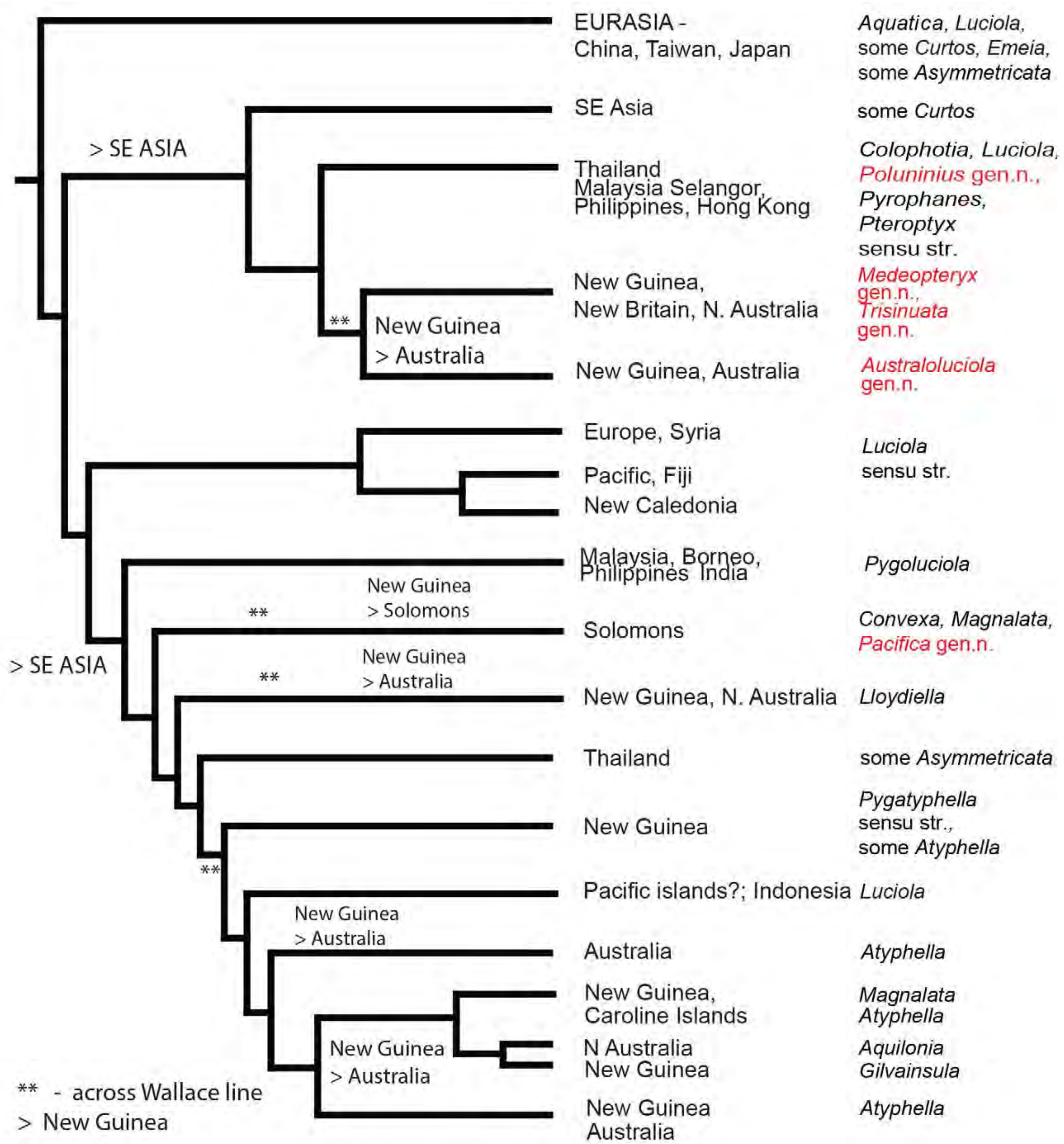


FIGURE 267. Simplified tree of the Luciolinae showing suggested major biogeographic movements, distribution, and genera. ** across Wallace Line into New Guinea.

Discussion

Taxonomic outcomes—overview

The taxonomic issues stemming from the 1969–70 New Guinea voyage of the scientific vessel *Alpha Helix* are now resolved. Eight species tentatively identified as *Pteroptyx* spp. in Lloyd (1973b) were addressed with many described as new in Ballantyne (1987a, b). These species are transferred to *Medeopteryx* **gen. nov.** herein. Of the 14 species tentatively assigned to *Luciola* in Lloyd (1973b) six were addressed in Ballantyne and Lambkin (2009) and assigned to four genera within the *Atyphella* complex. One of these species is reassigned to *Pacifica* **gen. nov.** herein. The remaining seven species are assigned to one of three new genera (*Australoluciola* **gen. nov.**, *Medeopteryx* **gen. nov.**, and *Trisinuata* **gen. nov.**) with several species described as new.

Additionally, this work represents a major step forward in the taxonomic treatment of the Luciolinae, which is now represented by 23 well-supported genera, of which five are described as new (Table 5). The Luciolinae is not now recognised with any further subdivisions (e.g., McDermott 1964). While the taxonomy is still primarily male based, female characters permit differentiation of some genera, but species identification of isolated specimens, especially in museum collections, may still be difficult unless the females possess unusual colour patterns or significantly reduced wings. In addition, an extended treatment of larvae is now possible.

This taxonomy is presently limited to SE Asia and the adjacent Australopacific region. Regretably, the Luciolinae of Africa remain largely unknown and comparisons are impossible. As a consequence of the early natural history explorations of SE Asia by Europeans, most type specimens and identified material are housed in European museums, with local collections largely consisting of unidentified, or misidentified material (Ballantyne 2012).

Previous investigations into the bent-winged firefly group indicated subdivisions within the genus *Pteroptyx* Olivier distinguishing New Guinean and Asian *Pteroptyx* (Ballantyne & McLean 1970; Ballantyne 1987a; 2001; Ballantyne & Lambkin 2009). Here further subdivisions of the New Guinean and Australian fauna, based primarily on the nature of the LO in V7, resulted in two new genera from New Guinea and Australia: *Medeopteryx* **gen. nov.** with entire LO, and *Trisinuata* **gen. nov.** with bipartite LO, both of which contain species with and without the deflexed elytral apex. The now exclusively SE Asian *Pteroptyx* **s. str.** also contains one species (presently undescribed; Table 4) which lacks the deflexed elytral apices in the male.

The extent of *Luciola* **s.str.** is not addressed apart from scoring a population of the type species *Luciola italica* from Pisa, and wider knowledge of its possible variability across Europe is necessary before this particular clade can be completely resolved. Here we submerge *Bourgeoisia* Olivier (from the Pacific) and *Lampyroidea syriaca* in *Luciola*. Of nine species previously assigned to *Luciola,* seven *(*four Australian and three New Guinean) are assigned to *Australoluciola* **gen. nov.**, with two further New Guinean species being assigned to *Medeopteryx* **gen. nov**. and *Trisinuata* **gen. nov**. respectively. Not all clades identified within the genus *Luciola* have a formal treatment as yet (several are in prep.) but all species groups are distinguished in the key to genera.

Use of females in Luciolinae taxonomy—overview

We have investigated the possibility of using internal female anatomy, especially the nature of the bursa plates, as an aid in identification. Forty-two species are scored here from features of females (Tables 6, 7).

Developing a female based taxonomy requires reliably associated females, and the capacity to distinguish sex in fireflies. Establishing reliable associations between males and females is difficult—they may be established by breeding (rarely e.g. Ballantyne & Menayah 2000, 2002; Fu & Ballantyne 2006, 2008) or by taking the mating pair *in copulo*. Ballantyne & Lambkin (2000, 2006) made certain pragmatic recommendations to allow at least tentative association of the sexes, based on similarity of location, and knowledge of the number of different species in any area. While many of the more recent taxonomic treatments used reliably associated females, in Ballantyne's opinion not all of the following characterisations would necessarily result in adequate identification of isolated female specimens (i.e. not taken with the males) (e.g. Ballantyne & McLean 1970; Ballantyne 1987a; Ohba & Sim 1994; Ballantyne & Menayah 2000, 2002; Ballantyne & Lambkin 2000; Jeng *et al*. 2003; Jeng, Yang *et al*. 2003; Kawashima 2003).

On the other hand sex determination is straightforward – females have 7 abdominal ventrites (visible ventrites 2–8, of actual segments 2–8), the LO is restricted to V6, the lateral margins of V7 and 8 taper posteriorly, V7 is almost always medianly emarginate across its posterior margin, and the head and eyes of females are usually smaller than those of the male, especially so in flightless females (Ballantyne, 1987b; Ballantyne & Lambkin, 2000, 2001, 2006, 2009). Males by contrast have 6 abdominal ventrites (of actual segments 2–7), an internal and membranous sternite 8, LO usually in both V6 and 7, usually parallel-sided terminal two visible ventrites, and V7 (the terminal visible ventral segment) and often also T8 with a variety of developments along the posterior margin which are reassessed here (Ballantyne 1987b; Ballantyne and Lambkin 2006, 2009).

Certain genera and some species may be easy to identify. *Curtos* females possess the distinctive elytral carina and elytral punctation characterising the male (Fu *et al.* 2012 Fig. 34; Ballantyne & Lambkin, 2000, 2009). In *Pygoluciola* three species have features on the terminal abdomen, recurved hooks in the bursa, and a distinctive pronotal outline (Ballantyne & Lambkin 2001, 2006; Ballantyne 2008). Australian *Atyphella* have brachelytral females with varying degrees of wing loss (Ballantyne & Lambkin, 2000, 2009). In any particular area there may be only one species present (Ballantyne, 1988; Ballantyne & Buck, 1979). Certain Japanese females are distinguished by flash patterns, as well as some morphological data (Ohba 1983a & b, 1984, 1985, 1986, 2000, 2001, 2003; Ohba *et al*. 1994, 2001). For the rest, determination of species remains difficult especially where many species like *Medeopteryx* **gen. nov.** possess a similar colour pattern.

Patterns of cuticularisation in the bursa have already been used for species determination in beetle families especially within the Elateroidea (Calder, 1986, 1996; Karg 1962; Zacharuk 1985). Such cuticularisation is absent in many other Coleopteran families (Surtees 1961). Preliminary investigations indicated the potential usefulness of bursa plates as a taxonomic aid in fireflies (Fu & Ballantyne 2006, 2008; Ballantyne & Lambkin 2006, 2009; Ballantyne 2008) and this approach is extended.

Treatment of dried pinned specimens proved less satisfactory than hoped and it may not be possible to determine presence or absence of plates from their dissection. An exception is Pygoluciola satoi where the only parts of the bursa still visible on dissection of a dried specimen were the two bursa hooks (Ballantyne 2008). Prolonged soaking of dried pinned abdomens in cold KOH may reveal the arrangement of plates if they are large and wide. The presence of bursa plates can be reliably established only on alcohol preserved specimens, and the internal reproductive anatomy investigated in detail only on freshly eclosed specimens.

Morphology and functional interpretations

Ballantyne (1987b) overviewed Luciolinae morphology and suggested possible functions for many of the modifications described. It is timely to review those suggestions.

Males

1. <u>Head and pronotum</u>. It is now inappropriate to consider that in the Luciolinae the head is 'covered' by the pronotum, or that it concentrates the vision of the male downwards during flight. Ballantyne (2008) indicated Olliff (1890) had incorrectly assigned *Atyphella lychnus* to the Lampyrinae where head concealment arises because the anterior pronotal margin is explanate. In the Luciolinae any head concealment can only result from retraction within the prothoracic cavity (*lychnus* being one of the few *Atyphella* species where the male head is small enough to be so retracted). Males of *Atyphella* Olliff have their eyes occupying a large area of the ventral head.

In the four New Caledonian and Fijian species of *Luciola* (Fig 4 node 39) and *Pygoluciola cowleyi* (Fig. 4 node 48) the head cannot be retracted into a prothoracic cavity nor covered from above, while the eyes are huge and subcontiguous ventrally thus enhancing downwards vision when the insect is flying. Four of these species have dorsolateral eye emarginations which may accommodate the increased eye area. Nothing is known of male female interactions or the nature of the female except in *L. hypocrita* from Fiji where females are flightless and luminous (Deheyn & Ballantyne 2009). It is possible in all these species that the females are flightless. However in *Atyphella* spp., where most of the known females are flightless, eye emarginations in males are not strongly developed (Tables 6, 7). The non-lucioline non-luminous males of *Rhagophthalmus* spp. have strong eye emarginations and huge eyes which are almost contiguous ventrally, and females are larviform and luminous (Ho *et al*. 2012). An explanation for the development of eye emarginations is not presently obvious.

Male eyes are not emarginated in *Australoluciola* **gen. nov**., *Colophotia*, *Medeopteryx* **gen. nov**., *Pteroptyx*, *Pyrophanes*, *Trisinuata* **gen. nov**., where the more rectangular outline of the pronotum and wider head might allow increased head flexibility and and greater visual acuity (Fig. 3 Node 18; Ballantyne 1987b).

Dentition of apical labial palpomeres is variable, (sometimes varying in number of teeth from right to left palp in the one individual), but where both males and females of the one species are known they have similar dentition or lack of it (Fu *et al.* 2012a).

2. <u>Legs.</u> Many modifications that occur in males but not females are thought to be of sexual significance but no observations confirm this (Ballantyne 1987b; Ballantyne *et al.* 2011; Tables 12, 13). No function for the MFC has been observed. The following species which have curved femora and/or tibiae all lack the MFC: *Pygoluciola wittmeri* Ballantyne, *Australoluciola baderi* **sp. nov.** *Aus. japenensis* **sp. nov**.

TABLE 12. Characteristics of species with trisinuate V7 in males 1.

Species	LO in V7 entire	LO in V7 bipartite	Elytral spices deflexed	Presence T8 flanges	Length T8 flanges [1]	Symmetry T8 flanges [2]	Nature of apex T8 flanges [3]	Inclination of T8 flanges [4]
Australoluciola anthracina (Olivier)	Yes	No	No	-				
Aus. aspera (Olivier)	Yes	No	No	+	1	1	1	2
Aus. baduria **sp. nov.**	Yes	No	No	-				
Aus. foveicollis (Olivier)	Yes	No	No	-				
Aus. fuscamagna **sp. nov.**	Yes	No	No	-				
Aus. fuscaparva **sp. nov.**	Yes	No	No	-				
Aus. japenensis **sp. nov.**	Yes	No	No	-				
Aus. maxima **sp. nov.**	Yes	No	No	-				
Aus. pharusaurea **sp. nov.**	Yes	No	No	+	1	S	1	2
Colophotia concolor Olivier	No	Yes	No	+	2	1	1	1
C. plagiata Erichson	No	Yes	No	+	2	1	1	1
C. praeusta Eschsch.	No	Yes	No	+	2	1	1	1
Medeopteryx amilae (Satô)	Yes	No	Yes	+	2	1	1	2
Med. antennata (Olivier)	Yes	No	Yes	+	2	1	2	2
Med. corusca (Ballantyne)	Yes	No	Yes	+	2	1	2	2
Med. cribellata (Olivier)	Yes	No	Yes	+	2	1	2	2
Med. effulgens (Ballantyne)	Yes	No	Yes	+	2	1	1	2
Med. elucens (Ballantyne)	Yes	No	Yes	+	1	1	1	2
Med. flagrans (Ballantyne)	Yes	No	Yes	+	1	1	1	2
Med. fulminea (Ballantyne)	Yes	No	Yes	+	2	1	1	2
Med. hanedai (Ballantyne and McLean)	Yes	No	Yes	?	-	-	-	-
Med. platygaster (Lea)	Yes	No	Yes	+	2	1	2	2
Med. similisantennata (Ballantyne)	Yes	No	Yes	+	2	1	2	2
Med. pupilla (Olivier)	Yes	No	No	+	2	1	1	2
Med. similispupillae **sp. nov.**	Yes	No	No	+	2	1	1	2
Med. sublustris (Ballantyne)	Yes	No	Yes	+	1	1	2	2
Med. tarsalis (Olivier)	Yes	No	Yes	+	2	1	1	2
Med. torricelliensis (Ballantyne)	Yes	No	Yes	?	-	-	-	-
Poluninius selangoriensis **sp. nov.**	No	Yes	No	-				
Pteroptyx asymmetria Ballantyne 2001	No	Yes	Yes	-				
P. bearni Olivier	No	Yes	Yes	-				
P. decolor Olivier	No	Yes	Yes	-				

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TABLE 12. (Continued)

Species	LO in V7 entire	LO in V7 bipartite	Elytral spices deflexed	Presence T8 flanges	Length T8 flanges [1]	Symmetry T8 flanges [2]	Nature of apex T8 flanges [3]	Inclination of T8 flanges [4]
P. gelasina Ballantyne	No	Yes	Yes	-				
P. macdermotti McLean	No	Yes	Yes	-				
P. maipo Ballantyne	No	Yes	Yes	+	1	1	2	2
P. malaccae (Gorham)	No	Yes	Yes	-				
P. masatakai Kawashima	No	Yes	Yes	-				
P. sulawesiensis Kawashima	No	Yes	Yes	-				
P. tener Olivier	No	Yes	Yes	-				
P. truncata Ballantyne	No	Yes	Yes	-				
P. valida Olivier	No	Yes	Yes	+	1	1	2	2
Pyrophanes appendiculata Olivier	No	Yes	No	+	2	1	2	2
Pyro. beccarii Olivier	No	Yes	No	+	2	1	2	2
Pyro. quadrimaculata Olivier	No	Yes	No	+	2	1	2	2
Pyro. similis Olivier	No	Yes	No	+	2	1	2	2
Trisinuata apicula **sp. nov.**	No	Yes	Yes	+	2	2	1,2	2
T. caudabifurca **sp. nov.**	No	Yes	No	+	1	1	1	2
T. dimidiata **sp. nov.**	No	Yes	No	+	2	1	1	2
T. papuana (Olivier)	No	Yes	No	+	1	1	1	2
T. microthorax (Olivier)	No	Yes	Yes	+	2	1	2	2
T. minor (Ballantyne and McLean)	No	Yes	Yes	+	2	1	2	2
T. papuae (McDermott)	No	Yes	Yes	+	2	2	1	2
T. similispapuae (Ballantyne)	No	Yes	Yes	+	2	2	1, 2	2

Footnotes: 1. Length of apex 1 = short, 2 = long. 2. Symmetry of apex 1 = symmetrical, 2 = asymmetrical. 3. Nature of apex 1 = rounded, 2 = acute. 4. Inclination of apex 1 = Left and Right flanges incline in opposite directions, 2 = Left and Right flanges incline in same direction.

TABLE 13. Characteristics of species with trisinuate V7 in males 2.

Species	Incurving lobes on V7	Median carina on V7	Expanded PLP V7	MFC	Emarginated basitarsus 1	Curved tibiae 3	Swollen femora 3
Australoluciola anthracina (Olivier)	No	No	No	No	No	No	No
Aus. aspera (Olivier)	No	No	No	No	No	No	No
Aus. baduria ***sp. nov.***	No	No	No	No	No	Yes	Yes
Aus. foveicollis (Olivier)	No	No	No	No	No	No	No
Aus. fuscamagna **sp. nov.**	No	No	No	No	No	No	No
Aus. fuscaparva **sp. nov.**	No	No	No	No	No	No	No
Aus. japenensis **sp. nov.**	No	No	No	No	No	Yes	Yes
Aus. maxima **sp. nov.**	No	No	No	No	No	No	No
Aus. pharusaurea **sp. nov.**	No	No	No	No	No	No	No

.... *continued on the next page*

TABLE 13. (Continued)

Species	Incurving lobes on V7	Median carina on V7	Expanded PLP V7	MFC	Emarginated basitarsus 1	Curved tibiae 3	Swollen femora 3
Colophotia concolor Olivier	No	Yes	Yes	No	No	No	No
C. plagiata Erichson	No	Yes	Yes	No	No	No	No
C. praeusta Eschsch.	No	Yes	Yes	No	No	No	No
Medeopteryx amilae (Satô)	No	No	No	No	No	No	No
Med. antennata (Olivier)	No	No	No	No	No	No	No
Med. corusca (Ballantyne)	No	No	No	No	No	No	No
Med. cribellata (Olivier)	No	No	No	No	No	No	No
Med. effulgens (Ballantyne)	No	No	No	No	No	No	No
Med. elucens (Ballantyne)	No	No	No	No	No	No	No
Med. flagrans (Ballantyne)	No	No	No	No	No	No	No
Med. fulminea (Ballantyne)	No	No	No	No	No	No	No
Med. hanedai (Ballantyne and McLean)	No	No	No	No	No	No	No
Med. platygaster (Lea)	No	No	No	No	No	No	No
Med. similisantennata (Ballantyne)	No	No	No	No	No	No	No
Med. pupilla (Olivier)	No	No	No	No	No	No	No
Med. similispupillae **sp. nov.**	No	No	No	No	No	No	No
Med. sublustris (Ballantyne)	No	No	No	No	No	No	No
Med. tarsalis (Olivier)	No	No	No	No	No	No	No
Med. torricelliensis (Ballantyne)	No	No	No	No	No	No	No
Poluninius selangoriensis **sp. nov.**	Yes	No	No	No	No	No	No
Pteroptyx asymmetria Ballantyne 2001	No	No	No	Yes	Yes	No	No
P. bearni Olivier	No	No	No	Yes	Yes	No	No
P. decolor Olivier	No	No	No	Yes	Yes	No	No
P. gelasina Ballantyne	No	No	No	Yes	No	No	No
P. macdermotti McLean	Yes	No	Yes	Yes	?	No	No
P. maipo Ballantyne	No	No	No	Yes	No	No	No
P. malaccae (Gorham)	No	No	No	Yes	?	No	No
P. masatakai Kawashima	No	No	No	Yes	?	No	No
P. sulawesiensis Kawashima	No	No	No	Yes	?	No	No
P. tener Olivier	No	No	No	Yes	Yes	No	No
P. truncata Ballantyne	No	No	No	Yes	Yes	No	No
P. valida Olivier	No	No	No	Yes	No	No	No
Pyrophanes appendiculata Olivier	Yes	No		Yes	No	Yes	Yes
Pyro. beccarii Olivier	Yes	No		Yes	No	Yes	Yes

.... *continued on the next page*

TABLE 13. (Continued)

Species	Incurving lobes on V7	Median carina on V7	Expanded PLP V7	MFC	Emarginated basitarsus 1	Curved tibiae 3	Swollen femora 3
Pyro. quadrimaculata Olivier	Yes	No		Yes	No	Yes	Yes
Pyro. similis Olivier	Yes	No		Yes	No	Yes	Yes
Trisinuata apicula **sp. nov.**	No	No	Yes	No	No	No	No
T. caudabifurca **sp. nov.**	No	No	Yes	No	No	No	No
T. dimidiata **sp. nov.**	No	No	Yes	No	No	No	No
T. papuana (Olivier)	No	No	Yes	No	No	No	No
T. microthorax (Olivier)	No	No	Yes	No	No	No	No
T. minor (Ballantyne and McLean)	No	No	Yes	No	No	No	No
T. papuae (McDermott)	No	No	Yes	No	No	No	No
T. similispapuae (Ballantyne)	No	No	Yes	No	No	No	No

3. Wings. Ballantyne *et al.* (2011:33) suggested a possible origin for the deflexed elytral apices in *Pteroptyx maipo* where the elytra become deflexed shortly after eclosion

In *Pteroptyx maipo* and *P. valida* the deflexed elytral apices function in a copulation clamp, where the female abdomen is held with the male deflexed elytral apices pressing downwards on the female abdomen, anterior to the female bursa, and the male MPP pressing upwards. Ballantyne *et al.* (2011) challenged the idea suggested by Wing *et al*. (1983) that bursa plates of the female could prevent damage to the female abdomen in a clamp situation, since in their observations the deflexed elytral apices pressed on the softer female abdomen anterior to the bursa.

Whether other species with deflexed elytral apices use them in a copulation clamp is not known. Some may be predisposed to do so. Many *Medeopteryx* species (with deflexed elytral apices) as well as *M. pupilla* and *M. similispupillae* **sp. nov**. (without deflexed elytral apices) have cuticular strips reaching from the MPP and across the dorsal face of the entire LOs in V7, where they attach to ventral longitudinal abdominal muscles (Ballantyne 1993). Pulling on these strips in an anterior direction will cause the MPP to arch dorsally (Ballantyne 1987b). However the significance of this modification in species without the deflexed elytral apices is not immediately apparent unless it simply allows the abdomen to flex (see below for further explanations of abdominal morphology). Ballantyne observed that in some pinned specimens of *Pyrophanes* (which lack deflexed elytral apices) the posterior margin of V7 (not including the PLP) arches upwards, making a right angle with the rest of the abdomen, and presumably caused by rigour in the longitudinal muscles. The incurving lobes of V7 brush against hairs and possibly spines on the ventral surface of T8. Similar arching of the MPP (excluding the PLP) was observed in *Pteroptyx malaccae* by Ballantyne (2001 Fig. 19) and other examples are figured (Figs 198, 199). Ballantyne and Lambkin (2001) suggested the abdominal modifications seen in *Luciola* (*Pygoluciola*) *kinabalua* might contribute to a copulation clamp. The elytral apices are not deflexed and there is no evidence to support this surmise, and the probable function of these modifications is adequately explained below.

Branham (2010) incorrectly stated that morphological structures adapted to form copulation clamps are restricted to a few species of *Luciola* and *Pteroptyx*, that a copulation clamp using deflexed elytral apices is restricted to males of *Pteroptyx* from New Guinea, and that males of non New Guinean *Pteroptyx* do not possess deflexed elytral apices. A copulation clamp using deflexed elytral apices has only been demonstrated in two species of SE Asian *Pteroptyx* (but no *Luciola*). *Pteroptyx* s. str. are not from New Guinea and, with the exception of two undescribed species scored here, have deflexed elytral apices. We have found no further evidence to support the suggestion of Ballantyne and Lambkin (2001) of a copulation clamp involving only terminal abdomen structures in species of *Pygoluciola*.

4. Terminal abdomen modifications.

4.1 Numbering of abdominal plates.

The taxonomic treatment of the Luciolinae has been expanded over a considerable duration in terms of numbers of species and characters used. The most significant changes in interpretation over this period relate to naming and numbering of the ventral plates of the abdomen. These are now termed ventrites, and are numbered to reflect their actual, not visible, number (e.g. the LOs are in V6 and 7, but since there is a loss of one segment at the base of the abdomen, they are in visible segments 5 and 6).

4.2 Effect of loss of ventrite 8.

Ballantyne (1987b:178) concluded that many of the male abdomen modifications were not of copulatory significance in themselves but rather mechanical modifications resulting from the loss of V8 and the need for increased surface area for muscle attachment as well as reinforcing. "Mechanical modifications (i.e. not obviously directly related to actual muscle insertions) may follow as a consequence of muscle development in other areas". Virtually all of the developments along the posterior margin of V7 can be explained in this light (see Tables 12, 13). Nothing observed in this study suggests these observations could be incorrect apart from an expanded discussion concerning the reduction in LO area (see below).

4.3 Effect of modifications of V7 on mating.

Ballantyne *et al.* (2011) observed that the female abdomen in a mating pair of *P. maipo* is drawn into a "pocket" formed between the widely splayed T8 and V7 of the male. No developments of the posterior margin of the male V7 (like the elongate MPP of some *Pygoluciola*, or the extended paired MPP hooks of *Colophotia* species) would have any effect in deterring another male from attempting to mate, when the T8 and V7 are so far apart. However these modifications of the male abdomen would, in *P. maipo*, press upwards on the female abdomen just before the LO in V6 near the junction between the median oviduct and the vagina, and any possible correlations remain to be investigated.

4.4 Functions of ventral surface of T8.

It is possible the lateral ridges and anterior flanges of the ventral surface of T8 could act as some sort of positioning guide for the apex of the female abdomen (Ballantyne, 1987b:178).

4.5 Difficulties in interpretation.

Interpretation of the posterior margin of V7 as trisinuate or not proved difficult with two ethanol preserved specimens viz. single males of *Aus. pharusaurea* **sp. nov**. and *Aus. fuscaparva* **sp. nov**. The relationships between the trisinuate V7 and certain other morphological features are indicated in Tables 12 and 13. These two species are the only ones in *Australoluciola* **gen. nov.** which might not have PLP produced and V7 thus not trisinuate, and the problem of method of preservation affecting interpretation should be strongly considered.

5. LO reduction in V7.

5.1 Bipartite LO.

Ballantyne (1987b) considered the bipartite LO in V7 had arisen because of insertion of median longitudinal muscles between LO halves. While this could be the correct explanation in certain *Pteroptyx* and *Trisinuata* **gen. nov.,** the situation in other genera appears more complicated. Species of *Medeopteryx* **gen. nov.** with entire LOs in V7 may have cuticular strips passing over the dorsal surface of the LOs and connecting anteriorly with longitudinal abdominal muscles. In *Med. clipeata* **sp. nov.** the anterior area of the LO is missing and occupied by muscle attachments, and this situation might represent an intermediate stage between the entire and bipartite LOs in V7 at least in *Medeopteryx* **gen. nov.** species. However in *Poluninius* **gen. nov.** the LO halves are virtually contiguous in the median line with no obvious muscle attachments causing their separation. In *Colophoti*a spp. a median carina is developed on the ventral face of V7 between LO halves. *Pteroptyx maipo* has bipartite LOs in V7, the inner margins of which approach closely in the posterior half of V7, while being well separated in the anterior half.

5.2 LO with anterior emargination.

Asymmetricata circumdata has the LO entire in V7 with a small triangular emargination along the middle of the anterior margin. This coincides with a longitudinal groove (developed in some but not all specimens) which runs along the anterior half of the ventral face of V7, but there is no explanation for its function. Ballantyne and Lambkin (2009) surmised that *As. circumdata* (with entire LO in V7) and *As. ovalis* (with bipartite LO in V7) could be the same species with a series of intermediate steps in LO reduction. No such specimens have been discovered.

Luciola substriata and other related species (Fig. 5 Node 62) have a set of three sclerites surrounding the aedeagal sheath. Muscles from the largest (ventral) sclerite attach at least in part on the dorsal face of V7 and account for the emargination of the LO in this area

5.3 LO with posterior emargination.

In *Pygatyphella* spp. the posterior margin of the entire LO in V7 is often emarginated, sometimes deeply, and the emargination allows for muscle attachment (Ballantyne & Lambkin 2009).

6. Loss of LO. There are circumstances where the LO is actually being lost rather than being reduced for functional purposes of muscle attachemnt as in 5 above. Here it would be assumed the species come to rely on other, possibly olfactory, clues. The New Guinean *Atyphella scabra* Olivier has very reduced LOs occurring as lateral plaques in both V6 and 7 (Ballantyne & Lambkin 2009), but the female is unknown. *Luciola hypocrita* has no LO in V7 and anterolateral LO plaques in V6 only (Deheyn & Ballantyne 2008); the female is flightless. *L. oculofissa* **sp. nov**. is the only Luciolinae species known thus far where there is no LO. Both *hypocrita* and *oculofissa* have eye emarginations, huge in the latter species. The non-lucioline *Rhagophthalmus* spp. males lack a LO but have huge emarginated eyes, and short antennae, and their females are brightly luminous and larviform (Ho *et al*. 2012)

7. Origin of LOs in V7. Ballantyne *et al.* (2011) indicated that the larval and adult LOs may not be homologous, since studies on light production by late instar larvae and pupae indicate the LOs are broken down and reassembled (larvae have a LO in abdominal segment 8, while in adult males the LO is in segments 6 and 7, and in females only in segment 6). Yiu's (2011) study on the light configurations of several Luciolinae larvae and adults illustrate larval LO remnants in V8 in the female which disappear as the adult LOs in V6 are developed.

Females

Ballantyne's (1987b) brief treatment of female modifications offered little in the way of possible functional explanations. This study and Ballantyne *et al.* (2011) has extended knowledge of lucioline females considerably, especially with respect to the functioning of the female reproductive system and the occurrence in various genera of bursa plates.

Adult female modifications and functional interpretations (Table 6)

Twenty of the twenty-three genera recognised here are characterised using some aspects of female morphology (Table 6). Bursa plates have been observed in eight genera. Four genera are reliably determined to lack bursa plates.

1. Head and pronotum. Female heads are almost always smaller and narrower than those of the males. The eyes are retracted from both anterior and posterior margins such that the head appears prolonged in front of the anterior eye margins with mouthparts and antennal insertions on the prolonged area. In winged females this prolongation is very short; in flightless females depending on the extent of eye reduction it can be quite long with lateral margins tapering from eye to mouthparts, and characterised here as a wingless female head type. The head is almost always capable of partial and sometimes complete retraction into the prothoracic cavity. Antennae are simple, with the scape often clavate but no flagellomeres produced or expanded. Only *Missimia flavida* females lack a clypeolabral suture (Ballantyne & Lambkin 2009). Mouthpart development indicates flighted females are probably all capable of feeding. Dentition patterns for apical maxillary and labial palpomeres follows that of the male.

The pronotum has a similar outline to that of the male in winged females, the exception being the often more rounded anterolateral corners and expanded hypomeron which permit retraction of the smaller head into the prothoracic cavity.

2. Legs. Females lack leg modifications with the exception of *P. guigliae* where all tibiae are strongly curved (Ballantyne 1968). Function of this curvature is not determined.

3. Wings. The extent of wing development and the potential for flight are outlined in Tables 6 and7. Ballantyne and Lambkin (2009) discussed female flightlessness in detail, and suggested a method of being able to interpret flight capability in females which had only a slight shortening of fore and/or hind wings using head structure. (Table 7).

We do not agree with interpretations about *Luciola parvula*, recorded in South *et al.* (2010) as being capable of flight. The *L. parvula* specimens scored here had no hind wings and are consistent with previous observations (Ballantyne 1968, Hayashi & Suzuki 2003; Kawashima *et al.* 2003). However, South *et al.* (2010:1101) indicated that prior work supported an association between spermatophore production and female flight. They scored *L. parvula* on their neoteny scale as 1 (a score of 0 signifying no neotenic states present while 4 was highly neotenic), thus implying that the specimens they examined were winged and probably capable of flight.

With one exception, known females of *Atyphella* Olliff are flightless but would be more difficult to classify according to the scale used by South *et al*. (2010). Although these females are about the same length as the males, they exhibit a variety of fore and hind wing modifications (Tables 6 and 7). There is presently no information on production of spermatophores in this genus. However, it is possible there may be other explanations for female aptery here not related to male nuptial gifting. Along the eastern Australian coast, many *Atyphella* species are isolated in refugial rain forest patches, where they are often in protected environments like National Parks. They may be the only species known in such isolated localities (Ballantyne & Lambkin 2009; Tables 6 and 7). Even if habitat isolation due to successive glaciations led to the loss of female flight there is no information that indicates just how long a period of isolation would be necessary to lose flight, although the thoracic flight apparatus is known to be very costly (Syrgley & Chai 1990). Habitat isolation has been increased due to forest conversion, which has occurred very recently within the last 200 years .

4. Abdomen. While the obviously brachelytral females have large pale soft expanded abdomens (Tables 6, 7) they do not exceed the male size except sometimes in girth; there are no known examples of the gigantism seen in certain non-lucioline SE Asian firefly females (Hayashi & Suzuki 2003).

V8 has a narrow anterior apodeme reaching to the posterior section of the bursa above the LO (V6). Muscles along the female valvifers attach on to the anterior end as well as to the sides of the vagina. Contraction of these muscles can widen or contract the oviduct when eggs are laid (Zacharuk 1985). Torsion in these muscles especially in dried pinned specimens may produce external artefacts, such as those seen in certain *Pygoluciola* females (Ballantyne & Lambkin 2006; Ballantyne 2008).

5. Internal reproductive anatomy

5.1 Bursa plates-structure.

Cuticular plates in the bursa of the female reproductive system yield patterns that can be used for identification of females to genera and sometimes to species, while absence of such plates characterises other species. Species identification has been less successful and may relate to the method of preservation of the specimens dissected. Seven genera possess bursa plates which consist of either a single pair or two pairs on each side of the often somewhat flattened bursa; single plates can be fine strips as in *Aquatica* Fu *et* Ballantyne, slightly thicker strips with median hooks in *Pygoluciola* Wittmer, or much wider plates with their inner surfaces rugulose in some *Pteroptyx* Olivier. Wide paired bursa plates (one or two pairs) occur in related genera; *Australoluciola* **gen. nov.**, *Colophotia*, *Pteroptyx, Pyrophanes*, *Medeopteryx* **gen. nov**. and *Trisinuata* **gen. nov**. (see Tables 12, 13 for male characteristics.). Certain species e.g. *Luciola cruciata*, *L. italica*, and some *Atyphella* Olliff lack bursa plates.

5.2 Bursa plates function.

The anterior area of the plates in *Pteroptyx maipo* Ballantyne appear to hold the spermathophore tightly in place, with its anterior half projecting into the spermatophore digesting gland. Posterior plates may act as a guide for the spermatophore. However the function of bursa plates in other genera where they are thin strips is not explained. Whether bursa plates always occur in species producing spermatophores, and not in species without spermatophores, remains to be investigated.

5.3 Median oviduct plate.

A plate occurring at the base of the median oviduct adjacent to its junction with the vagina was not investigated in all species. Fu and Ballantyne (2006) conjectured its possible function in *Aq. leii* to direct the spermatophore into the bursa and not the median oviduct.

6. Spermatophore production.

Hayashi and Suzuki (2003) examined prespermatophores in the males to infer spermatophore production and indicated that spermatophores were not often seen in the bursa. In their study females of species not producing spermatophores had wing degeneration and increased body size, indicating a possible larger reserve of nutrients and less reliance on nutrients provided by a spermatophore. They also found that the temporal pattern of egg production was related to spermatophore production; if oocytes mature at adult eclosion the female output depends on larval feeding period and there may be no spermatophore. Of species examined here only *Pteroptyx maipo*, which has a winged female, is known to produce spermatophores (Ballantyne *et al.* 2011).

Larval morphology

This study and Fu *et al.* (2012b) expand our understanding of larval morphology considerably. Ballantyne (1987b) briefly recognised two larval types but did not address species with aquatic larvae. Ballantyne and Lambkin (2009) scored 28 species from 31 larval characters but did not expand on larval morphology. Aquatic and terrestrial larvae can now be distinguished by the presence/absence of lateral abdominal gills or terminal spiracles (Fu *et al*. 2012b). Additionally, antennal segment 3 surmounted by hairs appears to be characteristic of terrestrial larvae, although the wider occurrence of this feature needs investigation. Ballantyne (1987b) suggested a correlation between the shape of the larval protergum and the adult pronotal outline in the Australian fauna. This correlation could be more widespread. These genera have larvae with laterally explanate (and dorsoventrally compressed) tergal margins: *Asymmetricata*, *Atyphella*, *Gilvainsula*, *Lloydiella*, *Magnalata* and three species of *Luciola* s. str. (Fu *et al.* 2012b). All have lateral margins of protergum diverging and explanate and the protergum wider than long with the exception of the *Luciola* spp. where the protergum is about as wide as long. *Emeia* Fu *et al.* larvae have tergal margins of different shapes in thorax and abdomen, and in the adult male the pronotum parallel sided with margins closely adpressed along their length (Fu *et al.* 2012a, b).

Fu *et al.* (2012b) suggested that larval morphology could support the monophyly of certain taxa proposed by Ballantyne and Lambkin (2009). Here, further evidence for larval morphology supporting certain taxa is provided (Fig. 8). Aquatic gilled larvae are characteristic of two species of Japanese *Luciola* and all species in *Aquatica*. Back swimming larvae characterise species with elytral punctation in lines, and sclerites surrounding the male aedeagal sheath. Known larvae of two species of *Pygoluciola* closely resemble those of a related clade including *Luciola praeusta* in having strongly sclerotised tergal plates. Larvae of *Australoluciola*, *Colophotia* and *Pteroptyx* are slim, agile and lack laterally explanate tergal margins. Males of these genera together with *Trisinuata* **gen. nov.** share many featgures (Tables 12, 13).

Biogeography (Figs 266, 267)

Constraints

This discussion is constrained by several factors. Little is known of the firefly fauna of many areas such as the Philippines, Indonesia especially Papua, much of mainland China, as well as Africa, where the subfamily is well represented but poorly known. The European Luciolinae is also little known. We are unable to borrow material from Indian museums due to governmental regulations requiring payment of a substantial fee. Lampyridae are not known from New Zealand. Luciolinae appear to be strictly old world in distribution and are unknown in the Americas. Unfortunately our phylogenetic analyses thus include few representatives from Africa or Europe, and as a consequence, have focussed on the Indo-Pacific fauna (Figs 3–5, 266, 267). Our discussion is therefore limited to inferences that can be derived from the distribution of the taxa represented in our analyses included in Figures 3 to 5.

Additionally with respect to the biota of New Guinea, Heads (2002:286) cautioned that care must be taken in any interpretations of fairly sketchy distribution data, especially that of Irian Jaya, having been so “hopelessly undercollected that valid generalisations about distribution there are impossible”. However, Heads (2001a:73) also acknowledged that “problems of detail…..cannot prevent effective, albeit preliminary, biogeographic analysis and biodiversity assessment”. There is little question that the major part of what we see in firefly distribution, especially in the more eastern areas of the island, is a reflection of major collecting efforts of the Archbold expeditions, D’Albertis, Loria, the Bishop Museum, and more recently, the Alpha Helix expedition. A large part of what is examined here comes from the latter two sources.

Origins of the Cantharoidea

Cantharoids are absent from Canadian amber (Upper Cretaceous) (Bocàkovà *et al.* 2007). The oldest fossils are of Cantharidae and Lycidae found in Baltic amber (Eocene), while there are unconfirmed reports of compression fossils of Lampyridae from Germany (Miocene) and Florissant, Colorado at the Eocene-Oligocene boundary (Grimaldi & Engel, 2005). Heyden (1862) described a fossil *Luciola* from Rott brown coals (Lower Oligocene) in Germany. Krebs (1910) had described as *Luciola* sp. a fossil from Baltic amber. Kazantev (2012) reported a new genus of Luciolinae from Baltic amber based on a single winged female lacking light organs. Many Lampyridae, including rare larvae, have been found in recent (20 Ma) Dominican amber (Grimaldi & Engel, 2005). Thus most lineages of Cantharoidea are considered younger than the Eocene (Bocáková *et al.*, 2007; Grimaldi & Engel, 2005).

Interpreting contrasting hypotheses about the nature of the ancestral cantharoid female, such as flight or flightlessness, are central to our further deliberations. Either flightless females are ancestral for cantharoids, with a secondary origin of fully developed winged females, or females with fully developed wings are ancestral (Crowson, 1972). However, Crowson did not consider the two explanations mutually exclusive, but clearly favoured the idea that flightless females were ancestral, apparently because he saw the restricted earlier geographical distribution of cantharoids as evidence that they were younger than other Coleopteran superfamilies. This suggested to him that the capacity of females to disperse was of recent origin. He further reasoned that the early Cantharoidea developed too late to have spread over the connections between the S Gondwanaland continents with the consequence that their spread in the northern hemisphere was hampered by the epicontinental seas. Larviform females are widely represented in the oriental region in Lampyridae and Lycidae. Further support for a Eurasian origin of the Lampyridae is the lack of endemic cantharoid taxa above the generic level in either Australia or Madagascar.

However, parsimony analyses strongly argue for the independent origin of larviform traits (loss of wings), in particular as the various cantharoid lineages are only distantly related to each other (Bocàkovà *et al.* 2007).

Additionally, in Lampyridae larviform females are seen in particular species, rather than larger clades, supporting the hypothesis of multiple convergent origins of larviform females (McDermott, 1964; South *et al.* 2010). Ballantyne and Lambkin (2009) interpreted flightlessness of a variety of different morphological forms as a secondary development and it is scored thus here.

Overview of geology and plate tectonics.

From a plate tectonic model of SE Asia and the SW Pacific during the Cenozoic (65 Ma to present (Hall & Holloway, 1998)) based on palaeomagnetic data, spreading histories of marginal basins deduced from ocean floor magnetic anomalies, and interpretation of geological data, Hall (1998) concluded there were three important periods in regional development: at about 45 Ma, 25 Ma and 5 Ma when plate boundaries and motions changed. In the Eocene (57–35 Ma (Hall & Holloway, 1998)), mountain building, resulting from the collision of India with Asia, led to major changes in habitats, climate, and drainage systems, and promoted dispersal to and from Gondwana via India into SE Asia as well as creating barriers between SE Asia and the rest of Asia (Hall, 1998).

From a biogeographic and tectonic viewpoint, the major Cenozoic tectonic event in SE Asia occurred about 25 million years ago partly due to collision between the north Australian margin and arcs to the north providing possible pathways for migration of faunas and floras between SE Asia and Australia via East Sulawesi, the Moluccas and lesser Sunda islands across areas which were mainly shallow marine and locally included land (Hall, 1998). Around the same time collision of the Melanesian arcs and the Ontong Java plateau resulted in a very long discontinuous island arc link between Asia and Melanesia, changing the tectonics of the oceanic-arc region east of Asia (Philippines, Celebes Sea, Sulu Sea, Philippine Sea, Caroline Sea, north New Guinea, New Britain, Solomons, Tonga). As the distance between Australia and Sulawesi closed, the deep Banda Sea opened and movement of plants and animals between Australia and Sundaland would have remained difficult. Possibly these barriers, close to a region of deep and former deep ocean barriers separating Borneo and Australia, are the origin of Wallace's line as the narrow Makassar Strait could not alone have been a major barrier to dispersal (Hall, 1998).

Hall's reconstructions (1998, 2001) for the region at 30 Ma show the east Philippines, northern Moluccas and north New Guinea terranes (including New Britain) forming a fairly continuous arc, parallel with, but anything from 1 to 2000 km north of New Guinea. Heads (2002) considers such a reconstruction, which ultimately involved this arc moving south west and 'docking'with New Guinea, could explain the close connections seen in certain animal groups between these regions and also the differences between New Britain and the New Guinea mainland. The mid Oligocene (Hall 1998 Fig. 11) was a time of major falls in sea levels with probably more emergent areas than at any subsequent time till the end of the Cenozoic. The Sulawesi-Philippines-Halmahera arc could have provided a pathway into the Pacific via volcanic island 'stepping stones'as long as the organism could cross sea water. At about 25 Ma (Hall 1998 Fig. 12) the north Australian margin contacted Sulawesi and the Halmahera arc and another discontinuous land connection was formed. Holloway and Hall (1998) also suggested a possibility for dispersal between the proto north Moluccas (including Waigeo) and the Solomons prior to the formation of the S Caroline arc.

Plate motions and boundaries changed again at about 5 Ma, possibly as a consequence of arc-continent collision in Taiwan, and a number of new dispersal pathways developed across the region, linking Taiwan and New Guinea through the Philippines and North Moluccas, and connecting New Guinea to Thailand via the Banda and Sunda arcs. During the last million years there have been periods of low sea-level associated with glacial intervals when far greater areas of land were emergent than at present, and the present areas are significantly greater than those during the Neogene (23–1.6 Ma (Hall & Holloway, 1998)). Much of the Sunda shelf would have been emergent although in eastern Indonesia there are many narrow deep water areas (such as the Makassar Strait) which would have remained physical barriers (Hall, 1998). Hollaway and Hall (1998) considered that modern biotas of most areas east of Sundaland and north of Australia will have owed much to the random processes of dispersal through time as submarine features became emergent and thus available for colonisation. However for a number of reasons Hall (1998) considers the eastern edge of SE Asia difficult to reconstruct.

The Southwest Pacific region includes the Melanesian archipelagos formed after the Oligocene (23–35 Ma) collision of the Pacific and Australian plates (Fiji, Samoa, Tonga, and Vanuatu), and Hawaii but not New Zealand and New Caledonia, which have always been considered part of the Gondwanan continent (Sanmartín & Ronquist, 2004).

The abrupt division between Asian and Australian floras and faunas in Indonesia, first recognised by Wallace in the nineteenth century, has its origin in the rapid plate movements and reorganisation of land-masses in SE Asia over the Cenozoic (Hall, 1998). If our hypothesis of a Eurasian centre of origin is correct, it would appear that dispersal across the Wallace line has occurred several times (clades 19, 55, 62).

<u>Origins of the Luciolinae</u>. Flightless females lacking the ability to disperse appear to have convergently evolved several times in the Lampyridae. We hypothesise that the Luciolinae have dispersed and have secondarily lost the ability to fly (Ballantyne & Lambkin 2009). We have examined the extant distribution of the Luciolinae as shown on our cladogram in Figures 3–5. Like Crowson (1972), we consider that the Oriental region (Eurasia) may be the centre of origin of the Luciolinae and from which they have dispersed to Europe, SE Asia, the Pacific Islands, New Guinea, and Australia in four or five successive waves.

Long distance dispersal is not necessarily invoked as the explanation for widespread distributions of flora and fauna in the southern hemisphere. Neither does a sequence of vicariance events account for all the patterns seen in the southern continents. It is possible that dispersal may have played a much greater role in the assembly of the southern biota than has previously been thought (Sanmartin & Ronquist 2004). Here we explore both dispersal and vicariance events as possible mechanisms responsible for the distribution of the present day firefly fauna in our study area (Figs 266, 267).

The basal lineages in our cladograms are Asian (Fig. 3, (clades 1 and 3)) , with *Aquatica* and two species of *Luciola s. latu* restricted to China, Taiwan, and Japan. These species share gilled, aquatic larvae and winged females, and may be constrained in their capacity to disperse by the need to find appropriate bodies of fresh water for their larval stages.

While the centre of origin of the Luciolinae may be Oriental our cladogram suggests that dispersion of the group has occurred repeatedly from Eurasia and in several different directions (clades 5, 35, 43, 53, 56, and 60) . Dispersal from a centre of origin in Central Asia (clades 5, 35, 42, 43, 59) appears to have occurred in several distinct waves to SE Asia (clades 5, 43, 60) across the Wallace line into New Guinea (clades 19, 55, 62) and into the Solomons (clades 53, 56), or into Australia (clades 20, 28, 57, 67) (Figs 3–5). Clade 35 comprising *Luciola* sensu str. would appear to infer that the group also dispersed from Central Asia to the west into Europe and also into the Pacific (Fiji) and then to New Caledonia where speciation has occurred. However those inferences are compromised by the lack of a comprehensive taxon sampling of the European fauna. For the same reason, the presence of *Photuroluciola* in Madagascar cannot be explained with any confidence as we have none of the African fauna in the analyses.

The distribution of many fireflies in the SE Asian and the Australopacific area aligns either side of Wallace's line with these genera only represented to the west: *Asymmetricata*, *Colophotia*, *Curtos*, many *Luciola* (e.g. *indica*, *praeusta*, *cerata*), *Pteroptyx* s. str., *Poluninius* **gen. nov**., and *Pygoluciola*. To the east are *Aquilonia*, *Atyphella*, *Australoluciola* **gen. nov.**, *Convexa*, *Gilvainsula*, *Lloydiella*, *Magnalata*, *Medeopteryx* **gen. nov.** (except for *amilae* in the Philippines), *Missimia*, *Pacifica* **gen. nov**., and *Trisinuata* **gen. nov.** Only *Pyrophanes* is currently distributed on both sides of Wallace's line with the largest number of species occurring in the Philippines while only one species is found in New Guinea and far north Queensland (Calder 1998). On the basis of its poor representation in collections it is presently considered a relatively uncommon genus. However its possible association with mangroves in the Philippines could be the reason for its wider distribution.

The area west of Wallace's line, including the Malaysian Peninsula, Philippines, Sumatra, Borneo, and the Inner Banda Arc, consists mainly of fragments which broke off from Australia and drifted northwards, colliding with the Eurasian plate around 400 Ma) (Metcalfe, 1996; Sanmartín & Ronquist, 2004; Turner *et al*. 2001). The region thus has a composite and complex biogeographic history (Burret *et al*., 1991; Sanmartín & Ronquist, 2004). Turner *et al.* (2001) believe that plants and animals present in West Malesia are mainly of SE Asian origin, since the region was already in place before many of the recent plant and animal taxa evolved

Clade 5, the stem lineage of the *Curtos* clade (6), is found throughout China, Japan, and SE Asia, where the soft bodied larvae may restrict the genus to mesic habitats. The adults of many *Curtos* species have a yellowish brown dorsum with black elytral apices, a color pattern which occurs commonly in other unrelated SE Asian

Luciolinae. This similarity is indicative of convergent adaptive evolution, possibly as a selective response to similar ecological pressures, such as predation.

Other species restricted to SE Asia include a group with aquatic metapneustic larvae (Fig. 5 clade 44), which possibly has restricted its wider distribution. This group is now distributed throughout mainland and offshore China, as well as through SE Asia, from India to Indonesia (Java). The closely related *Luciola praeusta* group (Fig. 4, clade 46), is widespread in SE Asiaand their terrestrial larvae share the hardened dorsal plates of the otherwise aquatic larvae. Almost all adults of both these clades share the typical Asian colour pattern of brownish yellow dorsum and black tipped elytra and females are winged.

Within *Pygoluciola* there appear to have been several sweeps out of Asia (Fig. 4, clade 48). *Pygoluciola qingyu* occurs only on mainland China, but *P. cowleyi*, the only Australian species of *Pygoluciola*, shares with *qingyu* the undevelopment of the male terminal abdomen, which caused Wittmer to name the genus accordingly. Movements of members of this genus out of Asia and the subsequent restriction of their ranges in Borneo or the Philippines may have led to parapatricly isolated populations that likely increased their diversification (Fig. 4, clade 51).

A second, wider movement of species out of Eurasia and into the more southern parts of what is now SE Asia, with some apparent isolation from their parent populations, led to the evolution of the closely related genera *Colophotia, Pyrophanes, Poluninius* **gen. nov**. and *Pteroptyx* s. str. (Fig. 3, clade 10). The relatedness of these genera is supported by traits outlined in Tables 12, 13.

Almost all *Pteroptyx* and *Colophotia* species have pale dorsum with black tipped elytra. *Pteroptyx* appears to be associated with mangroves (Ballantyne *et al.* 2011 Table 1), but does not occur in China apart from one species in mangroves in coastal Hong Kong. Speciation in *Pteroptyx* may have been triggered by the isolation of populations in suitable mangrove habitats that provided suitable conditions for its specialized larval ecology. Historically, these vulnerable habitats are exposed to frequent and catastrophic isolating events, such as cyclones and tsunamis, as well as having more regular, but over longer time periods, massive variations in sea level. All of these perturbations have likely acted to fragment the highly specialized, local populations. Little is known of distribution in *Colophotia*, but at least one species appears to occur in mangove areas in peninsular Malaysia (Ballantyne obs.), and anecdotal evidence indicates that large numbers of *Pyrophanes* spp. occur on the Donsol River in the Philippines; most *Pyrophanes* have been recorded from the Philippines (McDermott 1966; Wong. pers com).

Ancestral members of this group dispersed across the Wallace line into and through New Guinea and northern Australia, where they diversified into three genera described here as new: *Medeopteryx* **gen nov.,** *Australoluciola* **gen nov**. and *Trisinuata* **gen. nov.** (Fig. 3, clade 19; Tables 12, 13). The dorsal colour pattern of orange pronotum and black elytra is particularly widespread among *Medeopteryx* **gen. nov.** species in New Guinea and several *Australoluciola* **gen. nov**. in Australia. Within New Guinea representatives of these three genera are clustered along or above the northern margin of the Australian craton with the exception of a cluster of species of two of the genera around the Fly River (a craton is that part of the continental plate that has been relatively undisturbed since the Precambrian era www.thefreedictionary.com; see Heads 2001a Fig. 1 Page 68 for a simplified representation). They are not represented in the Solomon Islands. Both *Medeopteryx* **gen. nov**. and *Australoluciola* **gen. nov**. have representatives in New Britain, New Ireland and in Australia. Two species of the former occur in far north Queensland, while two species of the latter are widely distributed in wet sclerophyll forest along the east coast as far south as Brisbane where one species is known in relict rain forest. *Trisinuata* **gen. nov.** is not known from either Australia or the New Britain New Ireland area.

New Guinea. The biotic region of New Guinea has been considered to include the Solomon and New Hebrides Islands as they show close faunal affinities (Muona, 1991; Raven & Axelrod, 1972; Sanmartín & Ronquist, 2004). New Guinea is a tropical island largely covered with rain forest and with mountains up to 5000 m high (Heads 2002). It is composed of the northern part of the Australian craton plus about 32 terranes of various origins that have accreted to it (see Figure 1 page 68 in Heads 2001 for a simplified representation), as well as volcanic island arcs to the north which are of Palaeogene and Quaternary origin. The southern part of New Guinea has thus always been closely associated with Australia (Turner *et al.* 2001). The craton margin runs through the middle of New Guinea and major differences occur between the respective biotas of the component terranes (Heads 2006), not unsurprisingly as Heads indicates the terranes originated far apart from each other, had quite different histories, and may have moved thousands of kilometres before ‘docking’ with New Guinea. Pigram and Davies (1987) consider the New Guinean terranes could have moved in from the Pacific, rather than resulting from simple continent/island arc collision. Our capacity to comment on this variability in relation to the Luciolinae is constrained by the fact that much of the variability we see is a result of a specific collecting expedition.

Heads (2006) considers that differences in communities of various New Guinean biota could be due to tectonic activity rather than altitudinal factors. In particular uplift rates in New Guinea can raise a community from sea level to 3000 metres in just 1 Myr (Heads 2006). Within New Guinea Turner *et al.* (2001) believe a sequence of vicariance events occurred between peninsular New Guinea and the more western parts, and then across mountain ranges involving the Markham and Fly River valleys, and across Torres strait, with the west Pacific Island arcs invaded from New Guinea. Many *Pygatyphella* occur at altitude, and the events outlined above with respect to the Markham and Fly River valleys could explain the distribution around the Fly River of several *Medeopteryx* **gen. nov**. species.

Politically New Guinea is now divided into a western half, the Indonesian Irian Jaya (or west Papua), and in the east the state of Papua New Guinea including New Britain, New Ireland and Bougainville.

The largest movement of species and the most extreme radiation occurs in the *Atyphella* "complex" into Palau, Micronesia, the Solomon Islands, New Guinea and Australia (Fig. 5, clade 53). Of this *Atyphella* "complex", species of *Asymmetricata* have remained in SE Asia where they are widely distributed. Larvae are terrestrial and adult females winged, with adults having laterally pale margined elytra in common with much of the Solomon Island fauna.

Lloydiella (Fig. 5 clade 56) is found in New Guinea, where it is known from three species, and a further species from Cape York Peninsula in northern Australia (see discussion about Australian fauna below) and differs in having dark brown non margined elytra. Associated females are winged. *Pygatyphella* is widely distributed throughout New Guinea, where it is found along or north of the Australian craton margin, but is not found in Australia. Most species are characterised by a dorsal colour pattern Ballantyne and Lambkin (2009) and Ballantyne (1968) described as resembling bird droppings, and which is scored here as a cryptic pattern. Females are winged.

The more typical Asian colour pattern (yellowish brown dorsum with black tipped elytra) is rarer in the east and is seen in two species of *Gilvainsula* from islands to the eastern end of New Guinea, *Aquilonia costata* from the coastal west side of Cape York peninsula, *M. tarsalis* from both New Ireland and the Fly River in mainland New Guinea, and *Aus. japenensis* from Indonesia (Papua). Females are winged. Likewise *Atyphella* s. str. spread widely through New Guinea, islands to the north, and into Australia where it has radiated considerably. Species of *Atyphella* in Australia have flightless females (Ballantyne & Lambkin 2000, 2009).

<u>The Republic of Palau and the Federated States of Micronesia</u>. Both these areas are a series of islands spread over almost 2700 kms longitudinally just north of the Equator, and northeast of New Guinea (here we restrict the term Micronesia to the island nation). Representatives of two genera occur in the Palau archipelago which consists of more than 700 islands of which only 12 are inhabited, and show a great diversity of landforms and substrates. *Aty. palauensis* found on Pelelieu has flightless females, while *Magna. carolinae* from several islands in the Caroline Island complex occurs in three colour patterns (entirely dark grey dorsally to grey elytra with orange pronotum). Females are unknown.

<u>Solomon Archipelago</u>. A rich and endemic firefly fauna occurs in the Solomons. The Solomon archipelago is a double chain of islands aligned northwest – southeast across 1300 kms of the W Pacific and comprising the nation of the Solomon Islands and the adjoining islands of Bougainville and Buka (politically part of Papua New Guinea). There are seven major islands in the Solomon Island nation, with a further 340 smaller ones that are populated. It is a highly volcanic area formed at the SW boundary of the Pacific plate in contact with the Australian plate. *Convexa, Pacifica* **gen. nov**. and *Magnalata limbata* occur only in this myriad of islands, and most have orange pronota, and dark brown elytra with paler margins. Ballantyne and Lambkin (2009 Table 7) indicate the distribution of four species in three genera, all with pale margined elytra. *Convexa wolfi* is a large species with pale margined elytra, occurring from Bougainville to Guadalcanal, but not on Malaita or Makira. *Magnalata limbata* does not occur towards the east on Bougainville, Choiseul or Vella Lavella. *Pac. limbatifusca* occurs only on Makira, while the distribution of *Pac. limbatipennis* (which has pale margined elytra) essentially parallels that of *Pac. salomonis* (which has black non margined elytra) except for Makira (San Cristobal). Both species exhibit a variety of morphological modifications, none of which appear to be island specific (Ballantyne & Lambkin 2009:100, Table 9). Two species occurring on Makira, *A. kirakira* and *Pac. limbatifusca* occur on no other island. The former has dark non margined elytra and a bipartite light organ in V7; the latter is close to *Pac. limbatipennis*

differing most obviously in the pronotal colouration (Ballantyne & Lambkin 2009). Makira has more inland swamps than any other island in the group, and a wide variety of unique plants and animals, probably resulting from extended periods of isolation during times of high sea levels (Wikipedia).

Australia. Ballantyne and Lambkin (2000) overviewed the origins of the Australian fauna and it appears that most of the east coast fauna probably arose from migration from the north through New Guinea across at least two land bridges. The Australian wet tropics is a remnant of rain forest that once covered much of Australia. Lowland rain forests were largely wiped out during the last glacial maximum, and species survived in refugial areas of a chain of upland isolates (Van der Wal *et al*. 2009). While isolation to appropriate habitats in the northern wet tropical rain forests could be the explanation for the development of flightless females in some *Atyphella* species, it does not explain the widespread distribution of *A. similis* in SE Queensland and northern NSW, which also has flightless females.

There is one SE Asian element in the Australian fauna—*Pygo. cowleyi* in northern Australia near Darwin, where it appears relatively common. This species may have come across a separate land bridge but not through Cape York peninsula. The huge eye development with lateral emarginations is similar to that of certain Pacific Island species. In these cases females are unknown and it is possible that females are flightless. This could indicate a long period of separation from the original population.

Matthews (2000) classified the Australian fauna into 4 elements; of these he referred *Pteroptyx* to an Indomalayan element "composed of a relatively recent influx of northern species across an archipelago of Gondwanan fragments". His remarks refer to an older (taxonomic) concept of *Pteroptyx* where all bent-winged fireflies were assigned to the one genus. Here bent wings are assigned to three genera (two of them new); *Pteroptyx* s. str. lies to the west, and the other two genera (with the exception of *M. amilae* in the Philippines) to the East.

Fiji. Theories on the origin of Fiji and consequently its biota are contradictory (Evenhuis & Bickel 2005). Either Fiji emerged about 50 Ma as part of a volcanic arc (Vanuatu-Fiji-Lau-Tonga ridge) that migrated eastward, or it originated 48–40 Ma on the Pacific plate with Fiji only emergent in the last 10 My. Any hypothesis of recent emergence is at odds with the presence of poorly dispersive elements in the biota. The single Fijian firefly species *L. hypocrita* has lost the LO in V7, has diminished LO area in V6, and flightless but partly winged females. Our analyses suggest a taxonomic relationship with the New Caledonian fauna.

New Caledonia. Any attempted explanations for the origins of the New Caledonian firefly fauna in particular must be viewed with certain provisos in mind. Our analysis suggests species on Fiji and New Caledonia belong to *Luciola* s str. which is otherwise represented in Europe, Japan, and Taiwan. Our characterisation of the type species *Luciola italica* is based on large numbers of a population of males and females from Pisa Italy, identified by Floriano Papi. The species is not well characterised in Europe, nor its exact range determined, with no recent information on larval type. On that basis and given the wide disjunct between the Pacific Islands and SE Asia (no *Luciola* s str. occur in Australia, New Guinea or the intervening area of Indonesia and the Philippines), we suggest a Eurasian origin for this Pacific Island fauna, across Asia, into Japan and across the islands into the Pacific. However while the New Caledonian firefly fauna has certain distinctive features the relationship our analyses suggest with *L. hypocrita* on Fiji and *Luciola italica* may relate to other shared and possibly convergent features like colour patterns (these are volcanic islands), and be confused by the present poor taxon sampling in Europe.

There are two current schools of thought about the origins of the New Caledonian flora and fauna, both contentious (Edgecombe & Giribet 2009; van Doesburg, Cassis & Monteith 2010). One suggests it is a continental island with an ancient biota, predating Gondwanaland, the other that it is a recently emerged land mass housing long-distance dispersers. Grandcolas *et al.* (2011) considers the New Caledonian diversity to have resulted from "relatively ancient adaptive diversifications with abundant recent small-scale speciation involving niche conservatism". Heads (2010) overviewed the distributions of many New Caledonian taxa and found 24 tracks of endemism involving New Caledonia, and different areas of Gondwana, Tethys and the central Pacific (but not Eurasia or central Europe). Heads believes that most of the New Caledonian terranes formed as oceanic island arcs with flora and fauna surviving for tens of millions of years on ephemeral islands, with the biotas later juxtaposed and fused during terrane accretion. Sharma and Giribet (2009:280) suggest "An unambiguous counterargument to this generalisation" (the dispersalist model) "would best be provided by a taxon endemic to New Caledonia with demonstrably poor dispersalist ability, whose origin and diversification were both comparatively ancient".

All of the New Caledonian species have large eyes and similar dark greyish dorsal colouration; females are unknown and larvae are terrestrial (Tables 10, 11). Heads (2008) overviewed four main Grande Terre terranes and in his Figure 4 illustrated their distribution, as well as that of the main west Caledonian fault. *L. aquilaclara* **sp. nov.** occurs from north to south both above and below 300m on all these terranes, and with two exceptions (Mt Taom summit and Foret de Thi) to the north of the fault line. Apart from one possibly anomalous record of a larval *L. oculofissa* **sp. nov.** at Tuoho TV Tower in the north this species only occurs at the southern end of the island on the ultramafic terrane both above and below 300m and west of the fault line. The restricted distribution suggests a flightless female is more likely in this species.

Summary

1. Taxonomic outcomes. The Luciolinae is now recognised from 23 genera all of which have been described/redescribed and keyed either here or in Ballantyne and Lambkin (2009) and Fu *et al.* (2012). Twenty-two of those genera occur in the study area as we define it here. Morphological characters of males, and especially females and larvae have been expanded. The taxonomic issues relating to the 1969-70 voyage to New Guinea of the scientific vessel Alpha Helix are now resolved.
2. Functional morphology of males is reassessed with an extension and in some cases reevaluation for functional interpretations. Female and larval morphology is considerably extended and structure and function of internal female anatomy expanded.
3. An oriental centre of origin for the Luciolinae is proposed. The geologic history of the study area is explored from the perspective of plate tectonics, and an exodus from a centre of origin involving multiple waves across SE Asia and across Wallace's line into New Guinea and Australia is proposed.

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Appendix 1. List of characters and states

Characters and states are numbered to reflect their number in Ballantyne & Lambkin (2009) e.g. 5(30) = character 5 here was character 30 there. To accommodate the much greater range of variability encountered here, new characters are necessary and modifications are made to many others (93 extra characters occur here). All descriptors in the male characters are extended to indicate the section they refer to e.g. character 1 "Pronotum" added to existing descriptor; character 35 "Elytron" added and so on. The listing below indicates the extent of these changes e.g. Pronotum (30, 33) indicates that in this category Ballantyne and Lambkin (2009) had 30 characters and this is expanded to 33 here. New and modified characters are as follows:

Male characters: Pronotum (31, 34) new 30, 31; modified 8–11, 14, 15, 23; Elytron (20, 24) new 41–43, 47; modified 44, 45; Head (33, 37) new 62, 80; modified 89; Legs 10, 10) no new or modified; Abdomen (56, 115) new 119, 122, 123–126, 130, 136, 139, 140, 142, 143, 146, 147, 149–51, 156, 180, 181, 183, 189, 190, 194, 199, 200, 223; modified 118, 121, 133, 164, 176, 179, 182, 193, 197, 198, 201, 202, 207, 214; Aedeagal sheath (25, 40) new 220, 221–223, 225, 226, 228, 230, 233, 234, 235, 237, 245, 246, 256, 258, 259; modified 224, 231, 232, 243, 244, 247, 248, 252; Aedeagus (50, 67) new 265, 268, 271, 282, 286, 287, 289, 293, 296, 297, 298; modified 267, 283, 291, 302, 303, 304; Female (29, 33) new 347, 353, 358; modified 328, 335, 355, 357; Larva (31, 48) new 361, 364, 365, 366, 367, 370, 375, 378, 380, 381, 388, 393, 396, 397, 402, 405–407; modified 360, 372, 373, 392, 395; Colouration (18, 26) new 408, 409, 413, 414, 421, 424, 425, 431; modified 410, 420, 427, 432.

<u>MALE CHARACTERS 1–326.</u>

<u>PRONOTUM 1–33.</u>

1. Pronotum. Irregularities in posterolateral areas (Ballantyne & Lambkin 2009, Figs 488, 491): absent **(0)**; present **(1)**.

2. Pronotum. Lateral margins with longitudinal groove delimiting edges (Ballantyne & Lambkin 2009 Fig. 40): absent **(0)**; present **(1)**.

3. Pronotum. Lateral areas of disc density of punctation (Ballantyne & Lambkin 2009 Fig. 490): moderate to dense closely spaced **(0)**; sparse **(1)**.

4 (5). Pronotum. Dimensions. Width across posterior portion of pronotum relative to width across elytral humeri (elytra closed, specimen horizontal) (Ballantyne & Lambkin 2009 Figs 73, 75, 76): Less than **(0)**; Subequal to **(1)**; Greater than **(2)**.

5 (30). Pronotum. Dimensions. PN width/GHW index from below: 1.6 or greater **(0)**; 1.4–1.5 **(1)**; 1.3 **(2)**; 1.2 or less **(3)**.

6. Pronotum. Anterior margin explanation (Ballantyne & Lambkin 2009 Figs 494, 495): Narrowly **(0)**; Not explanate **(1)**.

7. Pronotum. Anterolateral corners shape: Obliterated **(0)** (Ballantyne & Lambkin 2009 Fig. 494); Rounded **(1)** (Ballantyne & Lambkin 2009 Figs 489, 490, 492); Angulate **(2)** (Ballantyne & Lambkin 2009 Figs 488, 491, 497).

8 (8, 9). Pronotum. Lateral margins subparallel sided: No **(0)**; Yes **(1)**. Definition of subparallel–sided pronota amended to exclude those where the pronotum is widest across the middle (i.e. where B >A, C); state 0 here. Incorporates old character 8 states 1, 2 and all of character 9.

9 (4). Pronotum. Lateral margins dimensions of subparallel sided pronota: B=C **(0)**; A=B=C **(1)**. Incorporates old character 4 states 0, 3; some 0 become 1 and 3 becomes 0.

10 (4). Pronotum. Lateral margins dimensions of non subparallel sided pronota: B > A or C **(0)**; C > A or B **(1)**; C<A or B **(2)**. Incorporates old character 4 states 1, 2 and 4; 1 becomes 0, 2 becomes 1 and 4 becomes 2.

11 (8). Pronotum. Lateral margins, inclination lateral pronotal margins (anterior half) when margins are not subparallel sided: Diverge posteriorly **(0)**; Converge posteriorly **(1)** (Ballantyne & Lambkin 2009 Fig. 492). Wording of descriptor changed to exclude subparallel–sided pronotal margins; 2 becomes 1 and state 2 is omitted and incorporated into character 8 above.

12 (9). Pronotum. Lateral margins, nature of posterior half of margins that diverge in anterior half (Ballantyne & Lambkin 2009 Figs 488–490): Convergent **(0)**; Subparallelsided **(1)**; further divergent with posterior convergence **(2)**; divergent along length **(3)**.

13 (10). Pronotum. Lateral margins, nature of divergence in posterior half (Ballantyne & Lambkin 2009 Figs 40, 488, 491): in line with anterior **(0)**; divergent beyond line **(1)**.

14 (11). Pronotum. Lateral margins where C > A or B, nature of posterior convergence of lateral margins that diverge in anterior half or more (Ballantyne & Lambkin 2009 Figs 63, 64, 490): rounded convergence **(0)**; angulate convergence **(1)**. Descriptor modified to include "where C > A, B".

15 (12). Pronotum. Lateral margins, nature of lateral margins that diverge along their length (Ballantyne & Lambkin 2006 Fig. 1): no indentation at mid point **(0)**; slight indentation at mid point **(1)**. Wording of descriptors slightly modified, no change to scoring or states.

16 (13). Pronotum. Lateral margins, sinuousity of lateral margins (vertical plane) (Ballantyne & Lambkin 2009 Fig. 40): Not **(0)**; Yes **(1)**.

17 (15). Pronotum. Lateral margins, indentation near posterolateral corner (Ballantyne & Lambkin 2009 Fig. 64): Absent **(0)**; Present **(1)**.

18 (16). Pronotum. Posterolateral corners, irregularities (Ballantyne & Lambkin 2009 Fig. 341): Absent **(0)**; Present **(1)**.

19 (17). Pronotum. Posterolateral corners, shape (Ballantyne & Lambkin 2009 Figs 64, 488, 491, 542): Rounded **(0)**; Angulate **(1)**.

20 (18). Pronotum. Posterolateral corners, angle of rounded posterolateral corners: obtuse or subequal to 90 **(0)**; less than 90° **(1)**.

21 (19). Pronotum. Posterolateral corners, inclination of angulate corners relative to median line of pronotum (Ballantyne & Lambkin 2009 Fig. 64): 90° approx. **(0)**; Oblique to median line **(1)**.

22 (20). Pronotum. Posterolateral corners, angle of angulate corners: 90° **(0)**; Less than 90 **(1)**; Very acute **(2)**.

23 (21). Pronotum. Posterolateral corners, projection of posterolateral pronotal corners laterally beyond width of pronotum at B or C (Ballantyne & Lambkin 2009 Fig. 40): No **(0)**; Yes **(1)**. Descriptor modified; beyond the line of the lateral margin changed to "beyond width of pronotum at B or C". No change to scoring.

24 (22). Pronotum. Posterolateral corners, extension relative to median posterior margin (Ballantyne & Lambkin 2009 Figs 40, 64): Not **(0)**; As far as **(1)**; Beyond **(2)**.

25(23). Pronotum. Posterior margin, extent of emargination between posterolateral corners and median posterior margin of pronotum (Ballantyne & Lambkin 2009 Fig. 64): Scarce **(0)**; Developed **(1)**.

26 (24). Pronotum. Hypomera, nature of hypomera: Open **(0)**; Closed **(1)**.

27 (25). Pronotum. Hypomera, elevation of median hypomeron (Ballantyne & Lambkin 2009 Fig. 40): Not **(0)**; Elevated **(1)**.

28 (26). Pronotum. Hypomera, nature of anterior hypomeron (Ballantyne & Lambkin 2009 Figs 13, 24, 84): Flat to neck **(0)**; Not **(1)**.

29 (27). Pronotum. Hypomera, nature of posterior hypomeron (Ballantyne & Lambkin 2009 Fig.84): Narrowly to widely flat **(0)**; Not **(1)**.

30. Pronotum. Hypomera, nature of more widely flattened posterior area of hypomeron: as wide as median area or wider **(0)**; narrower than median area **(1)**.

31. Pronotum. Hypomera, flattening of median area: hypomeron not flattened more widely just in median area **(0)**; hypomeron flattened more widely in median area **(1)**.

32 (28). Pronotum. Hypomera, nature of entire area (Figs 1, 2): Not all flat **(0)**; All flat **(1)**.

33 (29). Pronotum. Hypomera, nature of dorsal and ventral surfaces of widened flattened posterior part of hypomeron: Surfaces not strongly adpressed **(0)**; strongly adpressed **(1)**.

<u>ELYTRON 34–57.</u>

34 (31). Elytron punctuation, size (Ballantyne & Lambkin 2009 Figs 57, 58): not as large as pronotal punctation **(0)**; as large as pronotal punctation and regular in size and distribution **(1)**.

35 (32). Elytron punctuation, density (Ballantyne & Lambkin 2009 Fig. 118): Not sparse **(0)**; Sparse **(1)**.

36 (33). Elytron punctuation, linearity (Thancharoen *et al.* 2007 Fig. 1): No **(0)**; Yes **(1)**.

37 (34). Elytron apex, dorsal surface dimpled (Ballantyne *et al.* 2011 Figs 20, 21): No **(0)**; Yes **(1)**.

38 (35). Elytron apex, deflexed (Ballantyne *et al.* 2011 Figs 2, 21–23, 32): No **(0)**; Weakly **(1)**; Strongly **(2).**

39 (36). Elytron apex, outline: Rounded **(0)** (Ballantyne & Lambkin 2000 Fig. 20); Truncate **(1)** (Ballantyne & McLean 1970 Fig. 12d); Pointed **(2)** (Ballantyne 1987a Fig. 8).

40 (37). Elytron apex, length of truncate apex: Long **(0)**; Short **(1)**.

41. Nature of inner margin (C) of truncate elytral apex: Convex **(0)**; Concave **(1)**.

42. Nature of inner junction between truncate elytral apex margins B and C: Rounded **(0)**; Angulate **(1)**.

43. Elytron apex. Posterior end of non deflexed elytral apex appearing emarginate with small hook along outer edge at end of epipleuron: No **(0)**; Yes **(1)** (Jeng *et al.* 2003 Fig. 2).

44 (38). Elytron. Ventral aspects, extent of epipleuron: Extends no further than half length of elytron (or less) **(0)** (Lloyd & Ballantyne 2003 Fig. 23); Extends to apex or almost so **(1)** (Ballantyne & Lambkin 2009 Figs 6, 10, 13). Descriptor modified to include "ventral aspects"as extent of epipleuron cannot be seen from above; no change to scoring.

45 (39). Elytron. Ventral aspects, extent of sutural ridge: evanescent well before apex **(0)**; to apex or almost so **(1)**. Descriptor modified to include "ventral aspects" as extent of epipleuron cannot be seen from above; no change to scoring.

46. Elytron. Ventral aspects, visibility of humerus from below at base of elytron (Ballantyne & Lambkin 2009 Fig. 33): Widely **(0)**; very narrowly or not visible **(1)**.

47. Elytron. Ventral aspects, epipleuron at elytral base narrow, not widely expanded: Yes **(0)**; No **(1)**.

48 (47). Elytron visibility of anterior lateral margin of epipleuron relative to posterior edge of MS (specimen horizontal) (Ballantyne & Lambkin 2009 Fig. 9): Well behind MS **(0)**; Level with **(1)**; Anterior to **(2)**.

49 (48). Elytron Ventral aspects. Lateral margin of epipleuron developed as a ridge: No **(0)** (Lloyd & Ballantyne 2003 Fig. 23); Yes **(1)**.

50 (40). Elytron Ventral aspects, where elytral apex is not deflexed epipleuron and sutural ridge continue around elytral apex (view from above): No **(0)**; Yes **(1)**. Descriptor modified to include "where elytral apex is not deflexed".

51 (41). Elytron apex, nature of epipleural ridge at apex (view from beneath) (Ballantyne & Lambkin 2009 Figs 9, 11, 118, 119): Not further expanded **(0)**; Considerably expanded **(1)**.

52 (42). Elytron apex, nature of epipleural ridge at apex (view from beneath) (Ballantyne & Lambkin 2009 Fig. 10): epipleural ridge does not continue to apex **(0)**; continues to and around apex **(1)**. Wording of states modified, no alteration to meaning or scoring.

53 (43). Elytron apex, thickening epipleuron and suture in apical half (Ballantyne & Lambkin 2009 Figs 118, 119): Not **(0)**; Yes **(1)**.

54 (44). Elytron interstitial line, development: Four **(0)**; Three **(1)**; Two **(2)**; Humeral carina only **(3)**; None **(4)**.

55 (45). At least some elytral interstitial lines exceed suture (Ballantyne & Lambkin 2009 Fig. 177): No **(0)**; Yes **(1)**.

56 (49). Elytron Margins, approximation of sutural margins in closed elytra: contiguous for > half length **(0)**; not contiguous apical half **(1)** (Ballantyne & Lambkin 2009 Fig. 118).

57 (50). Elytron margins, shape: Parallel–sided **(0)**; Convex–sided **(1)** (Ballantyne & Lambkin 2009 Fig. 186).

HEAD 58–94.

58 (51). Head, depression of vertex: Minimal **(0)**; Moderate to deep **(1)** (Ballantyne & Lambkin 2009 Fig. 85).

59 (52). Head, exposure as retracted into prothoracic cavity: Greatly exposed **(0)**; Moderately exposed **(1)**; Concealed **(2)**.

60 (53). Head, approximation of eyes ventrally: Wide **(0)**; Close to moderate **(1)**; Contiguous **(2)**.

61 (54). Head, eye excavation (visible when head is retracted) (Ballantyne & Lambkin 2009 Fig. 59): Absent **(0)**; Present **(1)**.

62. Head, extent of emargination: Weak **(0)**; Moderate **(1)**; Strong **(2)**.

63 (56). Head, proximity antennal sockets: Contiguous **(0)**; Not contiguous **(1)**.

64 (57). Head, proximity of antennal sockets that are not contiguous relative to ASW: < 1 X ASW **(0)**; = ASW **(1)**; >ASW but not 2 X ASW **(2)**; >2 but not 3 X ASW **(3)**; 3 X ASW or greater **(4)**.

65 (58). Head, frons vertex junction (Ballantyne & Lambkin 2000 Fig. 2): Not acute **(0)**; Acute **(1)**.

66 (59). Head, median area frons vertex junction (Ballantyne & Lambkin 2000 Fig. 2): not elevated or indented **(0)**; elevated, may be indented **(1)**.

67 (60). Head, position of antennal sockets (Ballantyne & Lambkin 2009 Figs 27, 29 30, 32, 84): on head between eyes **(0)**; back margin level with anterior eye margin **(1)**; back margin in front of anterior eye margin **(2)**.

68 (61). Head, presence of clypeolabral suture visible as a distinct external suture (Ballantyne & Lambkin 2009 Figs 27, 28, 30, 31, 84): Present **(0)**; Absent **(1)**.

69 (62). Head, position of clypeolabral suture (Ballantyne & Lambkin 2009 Figs 507, 508). Head held with labrum horizontal: in line with or behind anterior eye margin **(0)**; a little in front of **(1)**; well in front of **(2)**.

70 (63). Head, nature of clypeolabral suture (Ballantyne & Lambkin 2009 Figs 28, 31, 84, 507, 508): Flexible (freely articulated) **(0)**; Inflexible (not freely articulated) **(1)**.

71 (64). Head, nature of sclerotisation of labrum (Ballantyne & Lambkin 2009 Figs 507, 508): not well sclerotised (labrum is flexible) **(0)**; well sclerotised (labrum is inflexible) **(1)**.

72 (65). Head, nature of anterior margin of inflexible labrum (Ballantyne & Lambkin 2009 Figs 507, 508): no projections **(0)**; with small rounded projections ('teeth') **(1)**.

73 (66). Head, length/width labrum: reaches beyond inner edge mandibles **(0)**; reaches inner edges of mandibles **(1)**.

74 (76). Head, proximity of eyes above labrum SIW/GHW: Close (1/6–1/15) **(0)** (Ballantyne & Lambkin 2009 Fig. 84); Moderate (>1/6) **(1)**; Wide (1/3–1/2) **(2)**.

75 (67). Mouthparts, functionality: Functional **(0)**; Non–functional **(1)**.

76 (68). Mouthparts, apical segment labial palp lunate: yes **(0)**; no **(1)**.

77 (69). Mouthparts, nature of non lunate labial palp apical segment –lateral flattening: Not flattened **(0)**; flattened **(1)**.

78 (70). Mouthparts, shape of strongly flattened apical segment labial palp: narrow triangle (L > W) **(0)**; broad triangle (isosceles; W = L) **(1)**.

79 (75). Mouthparts, length of narrow triangular labial palp apical segment: L = W **(0)**; L up to 2–3 x W **(1)**; L > 4 x W **(2)**.

80. Mouthparts, length of triangular labial palp apical segment/length of maxillary palp apical segment: as long as apical segment of maxillary palp or at least half its length or more **(0)**; less than half its length **(1)**.

81 (71). Mouthparts, nature of inner margin of strongly flattened labial palp apical segment: Entire **(0)**; Irregular/dentate **(1)**.

82 (72). Mouthparts, nature of inner margins of labial palpi that are irregular or dentate: irregular, not dentate **(0)**; dentate teeth 2 or less **(1)**; dentate teeth 3 or more **(2)**.

83 (73). Mouthparts, nature of apical segment of labial palp that is not strongly flattened: Ovoid/fusiform **(0)**; Subtriangular **(1)**.

84 (74). Mouthparts. Length/width of ovoid/fusiform palp: L=W **(0)**; L>W **(1)**.

85 (55). Antennae, length: > 2 X GHW **(0)**; > GHW–2 X GHW **(1)**; subequal GHW **(2)**.

86 (77). Antennae, length FS 1 (Ballantyne & Lambkin 2009 Fig. 509): shorter than pedicel **(0)**; as long as or longer **(1)**.

87 (78). Antennae, expansion FS1 (Ballantyne & Lambkin 2009 Fig. 509): not expanded outer apex **(0)**; expanded **(1)**.

88 (79). Antennae, median area FS1 (Ballantyne & McLean 1970 Fig.18): not produced **(0)**; produced **(1)**.

89 (82). Antennae, expansion FS4 towards apex (at anterior apical angle): Not **(0)**; Yes **(1)**. Descriptor "at anterior apical angle" added; no change to states or scoring.

90 (83). Antennae, FS 2–8 (Ballantyne & Lambkin 2009 Figs 21, 22, 34): not expanded **(0)**; expanded at anterior apical angle **(1)**.

91 (80). Antennae, FS 7–9 (Ballantyne & Lambkin 2009 Fig. 105): not conspicuously shorter than rest **(0)**; conspicuously shorter **(1)**.

92 (81). Antennae, number of segments: 11 **(0)**; < 11 **(1)**.

93 (84). Antennae, antennal segments: Not flattened **(0)**; Flattened **(1)**.

94 (85). Antennae, shape of pedicel: Not produced at outer apex **(0)**; Produced at outer apex **(1)**.

<u>LEGS 95–104.</u>

95 (86). Legs, inner tarsal claw: Not split **(0)**; Split **(1)**.

96 (87). Legs, MFC (Ballantyne *et al.* 2011 Figs 49, 50): Absent **(0)**; Present **(1)**.

97 (88). Legs, femora 2 swollen: No **(0)**; Yes **(1)**.

98 (89). Legs, femora 3 swollen: No **(0)**; Yes **(1)**.

99 (90). Legs, femora 3 curved: No **(0)**; Yes **(1)**.

100 (91). Legs, inner margin of basitarsus 2 excavated (Ballantyne *et al.* 2011 Fig. 11): No **(0)**; Yes **(1)**.

101 (93). Legs, swelling tibiae 3 (Ballantyne *et al.* 2011 Fig. 26): Not swollen **(0)**; Swollen/expanded at least at their apices **(1)**.

102 (96). Legs, curvature tibiae 1: No **(0)**; Yes **(1)**.

103 (95). Legs, curvature tibiae 2: No **(0)**; Yes **(1)**.

104 (94). Legs, curvature of tibiae 3: No **(0)**; Yes **(1)**.

<u>ABDOMEN 105–219.</u>

105 (97). Abdomen. VENTRITES V8, presence: Yes **(0)**; No **(1)**.

106 (100). V3, shape posterior margin: Not recurved **(0)**; Recurved **(1)**.

107 (101). V 4, shape posterior margin: Not recurved **(0)**; Recurved **(1)**.

108 (102). V3, V4, protrusion of anterior margin V4 into V3: Not protruding **(0)**; protruding **(1)**.

109 (106, 144). V7, nature of posterior half: Not arched **(0)**; Arched not swollen **(1)**; Arched and swollen **(2)** (Ballantyne & Lambkin 2009 Figs 24, 61, 62).

110 (107). V7, nature of corners in arched or swollen posterior half: Present **(0)**; Obliterated **(1)**.

111 (108). V7, shape of corners in arched or swollen posterior half: Rounded **(0)**; Angulate **(1)**.

112 (109). V7, intrusion arched or swollen posterior half of V7 into light organ: Not reaching into light organ **(0)**; Reaching into light organ **(1)**.

113 (110). V7, depth of intrusion of swollen posterior part of V7 into light organ: Shallow **(0)**; Deep **(1)** (Ballantyne & Lambkin 2009 Figs 24, 61).

114 (137). V7, presence median carina (Ballantyne & Lambkin 2009 Figs 98, 99, 100, 510): Absent **(0)**; Present **(1)**.

115 (138). V7, width median carina (Ballantyne & Lambkin 2009 Figs 98, 99, 100, 510): Broad **(0)**; Narrow **(1)**.

116 (139). V7, height median carina (Ballantyne & Lambkin 2009 Figs 98, 99, 100, 510): Low **(0)**; High **(1)**.

117 (140). V7, presence of median longitudinal trough on ventral face (Ballantyne & Lambkin 2009 Figs 106, 107): Absent **(0)**; Present **(1)**.

118 (143). V7, nature of surface: not very flat (in horizontal plane) **(0)**; very flat in horizontal plane **(1)**. Descriptors modified to read “flat (in horizontal plane)”; no change to scoring.

119. V7. Posterior margin trisinuate i.e. both MPP and PLP developed (e.g. Ballantyne & Lambkin 2009 Fig. 96): No **(0)**; Yes **(1)** (Fu *et al*. 2012a Figs 10, 11).

120. V7, emarginations of trisinuate posterior margin with further developments: No **(0)**; Yes **(1)**.

121 (149). V7, presence incurving lobes along V7 posterior margin in emarginations of trisinuate posterior margin of V7: Absent **(0)**; Present **(1)**. Descriptor modified to include “in emarginations of trisinuate posterior margin”. No change to states or scoring.

122. V7, Nature of apex of incurving lobes: Acute **(0)**; Rounded **(1)**.

123. V7, shape of incurving lobes: Broad flat **(0)**; Elongate rounded **(1)** (Fig. 13).

124. V7, incurving lobes club like (apex wider than base): No **(0)**; Yes **(1)** (Fig. 13).

125. V7, nature of anterior margin of incurving lobes (Ballantyne & Lambkin 2009 Figs 106, 107): not bearing profusion of hairs along anterior margin **(0)**; bearing profusion of hairs along anterior margin **(1)**.

126. V7, nature of posterior margin of incurving lobes: not bearing profusion of hairs **(0)**; bearing profusion of hairs **(1)** (Fig. 13).

127 (150). V7, presence pointed projections along V7 posterior margin in emarginations of trisinuate V7 (Ballantyne & Lambkin 2009 Figs 106, 107): Absent **(0)**; Present **(1)**.

128 (151). V7, presence dimple: Absent **(0)**; Present **(1)**.

129 (152). V7, anterior margin of facing cuticle on dorsal face of V7 reflexed into paired lobes which are visible from the side (Ballantyne 1968 Figs 44, 45): Absent **(0)**; Present **(1)**.

130. V7, lateral margins dorsal surface reflexed and enclosing sides of T8: No **(0)**; Yes **(1)**.

131 (98). Presence of cuticular remnants in intersegmental membrane dorsal to aedeagal sheath (Jeng et al. 2003 Fig. 14): Absent **(0)**; Present **(1)**.

132 (99). Presence of cuticular remnants in intersegmental membrane ventral to aedeagal sheath (Jeng et al. 2003 Fig. 14): Absent **(0)**; Present **(1)**.

133 (126). V7, apex symmetrical T8 engulfing posterior margin of V7 (Ballantyne & Lambkin 2009 Figs 60, 452–454): Not engulfed **(0)**; Engulfed **(1)**. Descriptors modified enveloped changed to engulfed; no change to scoring.

134 (127). V7, lateral margins of symmetrical T8 enfold V7 at sides: No **(0)**; Yes **(1)**.

135 (103). LO. Presence of light organ: Present **(0)**; Absent **(1)**.

136. LO V7, entire or bipartite: Entire **(0)**; Bipartite **(1)**.

137 (104). LO V7, nature posterior margin entire LO: Entire **(0)**; Emarginate **(1)** (e.g. Ballantyne & Lambkin 2009 Figs 24, 61). 104 states 0, 1 only addressed here; 104 state 2 not accommodated here see 141 below.

138 (110). LO V7, depth of posterior emargination of entire light organ (Ballantyne & Lambkin 2009 Figs 24, 61): Shallow **(0)**; Deep **(1)**. 110 addressed emargination where V7 was swollen posterior to light organ; wording changed here to omit swollen posterior half of V7; no change to scoring or states.

139. LO V7, shape of entire LO: Not triangular **(0)**; Triangular **(1)**.

140. LO V7, shape of entire LO (Thancharoen *et al.* 2007 Fig. 1): Not heart shaped **(0)**; Heart shaped **(1)**.

141 (104. 111). LO, bipartite light organ in 7 reaches sides of V7: Yes **(0)**; No **(1)**. 111 did not specify type of light organ; here only bipartite light organ is addressed; 104 state 2 is scored here; 111 states 1, 2 are scored as state 0 here.

142. LO, bipartite light organ in V7 reaches into PLP: No **(0)**; Yes **(1)**.

143. LO, inner margins of bipartite light organ contiguous (Fig. 13): No **(0)**; Yes **(1)**.

144 (104, 111). LO, entire light organ in V7 reaches sides: Yes **(0)**; No **(1)**. 111 did not specify type of light organ; here only entire light organs in V7 are scored; 104 states 0, 1 are scored here; 111 0, 1 are scored as 0 here.

145 (104, 111). LO, entire light organ in V7 reaches posterior margin (may be narrow clear area): Yes **(0)**; No **(1)**. 111 did not specify type of light organ; here only entire light organs in V7 are scored; 104 states 0, 1 are scored here; 111 0 is scored as 0 here.

146. LO, entire light organ in V7 reaches into MPP (e.g. (Ballantyne & Lambkin 2009 Figs 45, 46): No **(0)**; Yes **(1)**.

147. LO, entire light organ in V7 reaches into PLP: No **(0)**; Yes **(1)**.

148 (105). LO V7, nature of medial emargination of entire light organ V7 (Thancharoen *et al.* 2007 Fig. 1): Lacking **(0)**; present **(1)**.

149. LO V7, emarginate anterior margin due to muscle attachment on sclerites surrounding aedeagal sheath (muscles are visible through cuticle): No **(0)**; Yes **(1)**.

150. LO V7, depth of emargination: Shallow **(0)**; moderately deep (posterior area of LO wide **(1)**; very deep (posterior area of LO narrow) **(2)**.

151. LO, width of emargination: Narrow **(0)**; moderately wide (about half width of anterior margin) **(1)**; very wide (covers most of anterior margin of LO) **(2)**.

152 (112). LO, presence in V6: Present **(0)**; Absent **(1)**.

153 (113). LO, size light organs V6: Occupying most if not all the area **(0)**; Restricted to anterolateral plaques **(1)** (Ballantyne *et al.* 2011 Figs 9, 22).

154 (114). LO, size bipartite light organs V7: Half or more **(0)**; Less than half **(1)**; Less than 10% **(2)** (Ballantyne *et al.* 2011 Figs 9, 22).

155 (115). LO, size entire light organs V7: Most **(0)**; Half or less **(1)**.

156 (141). LO, median longitudinal depression on anterior face of entire light organ in V7: absent **(0)**; present **(1)**.

157. (116). MPP, presence: Absent **(0)**; Present **(1)**.

158 (117). MPP, symmetry of apex: Symmetrical **(0)**; Asymmetrical **(1)**.

159 (118). MPP, medial emargination apex (visible from below in horizontal specimen): Absent **(0)**; Present **(1)** (Ballantyne & Lambkin 2009 Figs 98–100).

160 (119). MPP, depth emargination (Ballantyne & Lambkin 2009 Figs 24, 98–100): Shallow **(0)**; Deep **(1)**.

161 (120). MPP, shape non medianly emarginate apex (Ballantyne & Lambkin 2009 Figs 10, 13, 16, 18, 20, 343, 351, 387, 388): Rounded **(0)**; Pointed **(1)**; Squarely truncate **(2)**; Obliquely truncate **(3)**.

162 (121). MPP strongly laterally compressed (Ballantyne & Lambkin 2009 Figs 45, 46): No **(0)**; Yes **(1)**.

163 (122). MPP posterior margin bisinuate (Ballantyne & Lambkin 2009 Figs 309, 310): No **(0)**; Yes **(1)**.

164 (123). MPP, length/width: Short or W>L **(0)**; L=W **(1)**; L>W **(2)**. State 1 modified to read short or W>L; no change to scoring.

165 (124). MPP, length MPP in relation to PLP: Shorter **(0)**; Subequal **(1)**; Longer than **(2)**.

166 (125). MPP, width MPP in relation to PLP: Narrower than **(0)**; As wide as **(1)**; Wider than **(2)**.

167 (128). MPP, dorsal inclination of the apical area of a narrowed MPP (L > W): Not **(0)**; Reflexed dorsally **(1)** (Ballantyne & Lambkin 2009 Fig. 60).

168 (132). MPP, bifurcate into two elongate hooks (Ballantyne & Lambkin 2009 Figs 98–100, 510, 511): No **(0)**; Yes **(1)**.

169 (130) MPP, relation of MPP or posterior margin of V7 to apex of symmetrical T8: MPP not engulfed **(0)**; MPP engulfed **(1)** (Ballantyne & Lambkin 2009 Figs 60, 452–454).

170 (131). MPP, emarginations present at base (Ballantyne & Lambkin 2009 Figs 470, 471): Absent **(0)**; Present **(1)**.

171 (132). MPP, prolonged into two elongate hooks (Ballantyne & Lambkin 2009 Figs 98–100, 510, 511): Not prolonged **(0)**; Prolonged into 2 long symmetrical hooks **(1)**; Prolonged into 2 long asymmetrical hooks **(2)**.

172 (133). MPP, presence of median dorsal ridge (Ballantyne & Lambkin 2009 Figs 342–359): Absent **(0)**; Present **(1)**.

173 (134). MPP, nature of dorsal ridge: Median **(0)**; To left of median **(1)**.

174 (135). MPP, width dorsal ridge (Ballantyne & Lambkin 2009 Figs 304, 306): Narrow **(0)**; Wide **(1)**.

175 (136). MPP. Dorsal ridge with 2 elevated median projections: Absent **(0)**; Present **(1)** (Ballantyne 2008 Figs 5, 6).

176 (140, 142). MPP, median longitudinal trough V surface (Ballantyne & Lambkin 2009 Figs 106, 107): Absent **(0)**; Present not margined **(1)**; Present unevenly margined **(2)** (Ballantyne & Lambkin 2009 Fig. 100); Present evenly margined **(3)**. Characters 140, 142 combined; 140 state 0 is 0 here; 140 state 1 is either 1, 2 or 3.

177 (145). PLP, development (Ballantyne & Lambkin 2009 Figs 96, 98–100, 106, 107; Ballantyne *et al.* 2011 Figs 2, 7–10, 12, 13, 18, 19, 22, 24, 25, 27, 29, 31, 33): absent **(0)**; present **(1)**.

178 (146). PLP, length (Ballantyne & Lambkin 2000 Fig. 26a; Ballantyne 1987b Fig. 2 a, b): Slightly produced **(0)**; Moderately produced may extend beyond tip of MPP **(1)**; Considerably produced **(2)**.

179 (147). PLP, width (measured from below) (Ballantyne & Lambkin 2000 Fig. 26a; Ballantyne & Mclean 1970 Fig. 9a, b): Narrower than MPP **(0)**; As wide as MPP **(1)**; Wider than MPP **(2)**. Character 147 expanded, state 1 split into two, state 1 becomes either 1 or 2 here.

180. PLP. Length/width (width measured from below): L=W or W>L **(0)**; L>W **(1)**.

181. PLP, width of PLP that are considerably produced: Narrow **(0)**; Wide **(1)**.

182 (148). PLP, inclination (Ballantyne & Lambkin 2009 Figs 98–100): Horizontal **(0)**; Gently oblique–vertical **(1)**; Strongly vertical **(2)**. Character 148 expanded, state 1 there (oblique–vertical) expanded to two states here so 1 there becomes either 1 or 2 here.

183. PLP, width of obliquely inclined PLP (view from side if necessary): Narrow **(0)**; Wide **(1)**.

184 (153). ABDOMEN TERGITES. T8, symmetry: Symmetrical **(0)**; Asymmetrical **(1)** (Ballantyne & Lambkin 2009 Figs 108–111).

185 (154). T8, ventral inclination of symmetrical apex (Ballantyne & Lambkin 2009 Figs 452–454): not inclined **(0)**; Weakly inclined **(1)**; Strongly inclined **(2)**.

186 (155). T8, width of ventral inclination of symmetrical apex that is strongly inclined ventrally: posterior half not strongly narrowed **(0)**; posterior half strongly narrowed **(1)** (Ballantyne & Lambkin 2009 Fig. 60).

187 (156). T8, width of ventral inclination of symmetrical apex that is not strongly narrowed in posterior area (Ballantyne & Lambkin 2009 Figs 452–455): Very narrow shelf **(0)**; Wide shelf **(1)**.

188 (157). T8, thickness of ventral inclination of symmetrical apex that is not strongly narrowed in posterior ½ (Ballantyne & Lambkin 2009 Figs 452–455): Thin shelf **(0)**; Thick shelf **(1)**.

189. T8. Lateral margins enfold lateral margins of apex of V7: No **(0)**; Yes **(1)**.

190. T7. Posterolateral corners of T7 slightly prolonged and overlap V7 at their edges: No **(0)**; Yes **(1)**.

191 (158). T8, prolongation posterolateral corners (Ballantyne & Lambkin 2009 Figs 511, 512): Not **(0)**; Prolonged **(1)**.

192 (160). T8, angle of prolongation of posterolateral corners (Ballantyne & Lambkin 2009 Figs 511, 512): Horizontal **(0)**; Inclined ventrally **(1)**.

193 (159, 161). T8, extent of prolongations of posterolateral corners (Ballantyne & Lambkin 2009 Figs 511, 512): Weakly prolonged (very short) **(0)**; Strongly prolonged (long) **(1)**. Descriptors for 159 modified with addition of "very short" to state 1 and "long" to state 2; no change to scoring; 161 states 0 and 1 are 0 and 1 here.

194. T8, presence of median trough: Absent **(0)**; Present **(1)**.

195 (168). T8, length median trough: Very short **(0)**; Long **(1)**.

196 (169). T8, symmetry of margins ventral trough: Symmetrical **(0)**; Asymmetrical **(1)**.

197 (167). T8, nature of margins of median groove ventral surface: finely margined **(0)**; slightly thickened margins **(1)**; low ridges present in posterior half only **(2)**; well developed lateral ridges **(3)**. Character 167 modified; state 0 becomes state 0 in character 194; states 1, 2, 3, 4, become 0, 1, 2, 3 here).

198 (162). T8. Nature of anterior end of well defined ridged margins of median groove on T8: Not produced **(0)**; Produced (flanges) **(1)** (e.g. Ballantyne & Lambkin 2009 Fig. 93). Wording of 162 modified to define area where flanges originate; no change to scoring.

199. T8, symmetry of flanges: Symmetrical **(0)**; Asymmetrical **(1)** (e.g. Ballantyne 1987a Fig. 13r).

200. T8, nature of anterior end of ridged margins that is not produced: Smooth even or rounded **(0)**; Angulate **(1)**.

201 (165). T8. Length of anterior end of ridged margins if produced (=flanges): Short **(0)**; Long **(1)**. Character 165 expanded to reflect the two states scored here – length and width; 165 0 is 0 here; 165 1 is 1 here.

202 (165). T8, width of flanges: Narrow **(0)**; Wide **(1)**. Character 165 expanded to reflect the two states scored here – length and width; 165 0 is 0 here; 165 1 is 1 here.

203 (165). T8, length/width flanges: Short and wide **(0)**; at least as long as wide or longer **(1)**.

204 (163). T8, nature of tip of flanges: Apically rounded **(0)** (e.g. Ballantyne 1987a Fig. 13g, f); Apically acute **(1)** (Ballantyne 1987a Fig. 12e).

205 (164). T8, orientation flanges: both incline in same direction **(0)**; incline in different directions **(1)** (Ballantyne & Lambkin 2009 Fig. 104).

206 (166). T8, presence lateral depressed spiny and hairy troughs (Ballantyne & Lambkin 2000 Fig. 26 c, d): Absent **(0)**; Present **(1)**.

207 (170–174). T8, ventral face with asymmetrical projections (Ballantyne & Lambkin 2009 Fig. 472): Absent **(0)**; Present **(1)**. Ballantyne & Lambkin 2009 scored 2 apparent varieties of *Pygatyphella uberia* as Uberia 1 and 2. These are combined here as *Pygatyphella uberia* and characters 170–174 which refer only to these two varieties are combined; 170–174 state 1 is state 1 here.

208 (175). T8, presence of median posterior ventral ridge (Ballantyne & Lambkin 2009 Figs 360, 361, 404, 423, 436–7, 439–40): Absent **(0)**; Present **(1)**.

209 (176). T8, curvature of median posterior ventral ridge: Not curved **(0)**; Curved **(1)**.

210 (177). T8, width (Posterior visible portion): Very short **(0)**; width = or width>length **(1)**; length > width but not projecting considerably beyond MPP **(2)**; length > width but not projecting considerably beyond MPP **(3)**.

211. T8. Posterior entire (visible) portion of T8 subparallel–sided along its length: No **(0)**; Yes **(1)**; Along anterior half only **(2)**.

212 (178). T8, nature of margins of visible posterior area symmetrical T8: if margins converge not an abrupt narrowing **(0)**; abruptly narrowed **(1)** (Ballantyne & Lambkin 2006 Figs 19, 20).

213 (181). T8, length of anterior concealed prolongations: None **(0)**; Very short **(1)**; not as long as visible posterior portion **(2)**; > 2 x as long as posterior portion **(3)**.

214 (180). T8, narrowing (appears laterally emarginate) before origin of elongate anterolateral projections: No **(0)**; Yes **(1)**. Descriptor modified to read "narrowing (appears laterally emarginate)".

215 (182). T8, width anterior prolongations in horizontal plane: Absent or very short **(0)**; Narrow **(1)**; Wide **(2)** (Ballantyne & Lambkin 2009 Fig. 47).

216 (183). T8, width anterior prolongations in vertical plane (Ballantyne & Lambkin 2009 Figs 47, 273, 274, 311–314, 410, 421): Not expanded D–V **(0)**; Expanded D–V **(1)**.

217 (184). T8, inner area of anterior area of prolongations with bifurcation (Ballantyne & Lambkin 2009 Figs 249, 250, 254): No **(0)**; Yes **(1)**.

218 (186). T8, emargination of median posterior margin (Ballantyne *et al.* 2011 Figs 7, 10, 13, 17, 19, 20, 24, 28): Absent **(0)**; Present **(1)**.

219 (179). T8, paired lobes at side of median emargination (Ballantyne *et al.* 2011 Figs 7, 13): Absent **(0)**; Present **(1)**.

<u>AEDEAGAL SHEATH 220–259.</u>

220. Sheath sternite with elongate darkened area in posterior median area (Fu *et al.* 2010 Figs 5, 13, 22, 23, 24): No **(0)**; Yes **(1)**.

221. Sheath sternite, inclination of dorsal ridge/ darkened area of character 220: Median **(0)**; Oblique **(1)**.

222. Sheath sternite, length of dorsal ridge/darkened area of character 220: begins level with lateral tergite articulations **(0)**; about half length of sternite posterior to tergite articulations **(1)**; much less than half **(2)**.

223. Symmetrical sheath sternite, posterior to tergite articulations tapering evenly on both sides to narrow apex (Ballantyne & Lambkin 2009 Figs 86–93): Yes **(0)**; No **(1)**.

224 (187, 188). Aedeagal sheath symmetry (posterior to tergite articulations) (due to emarginations of sternite): No sternite is symmetrical **(0)** (Ballantyne & Lambkin 2009 Figs 86–93); Yes sternite is asymmetrical **(1)**. Descriptor modified to read "due to emarginations of sternite". 187 and 188 combined to indicate reason for asymmetry of sheath; 187 0 is 0 here; 187 1 is 1 here; 188 0 is 0 here; 188 1 is 1 here.

225. Sheath sternite, posterior to tergite articulations with lateral emargination/s: Yes **(0)** (e.g. Ballantyne & Lambkin 2009 Fig. 37); No **(1)**.

226. Sheath sternite, extent of lateral emarginations: on one side of sternite only **(0)** (e.g. Ballantyne & Lambkin 2009 Fig. 37); on both sides **(1)** (e.g. Ballantyne & Lambkin 2009 Fig. 38).

227 (204). Sheath sternite, level of emargination on right side: begins level with tergite articulations **(0)** (e.g. Ballantyne & Lambkin 2009 Fig. 37); begins at basal 1/3 **(1)** (e.g. Ballantyne & Lambkin 2009 Figs 360, 362); begins at basal 2/3 **(2)**; preapical **(3)**. 204 state 1 is state 3 here.

228. Sheath sternite, nature of lateral emargination on L side: smooth even **(0)** (e.g. Ballantyne & Lambkin 2009 Fig. 37); irregular (margin has at least one short projection) **(1)** (Fu *et al.* 2010 Fig. 5).

229 (203). Sheath sternite, emargination of both sides of lateral margins posterior 1/3 (Ballantyne & Lambkin 2009 Figs 41–44): No **(0)**; Yes **(1)**.

230. Sheath sternite, nature of lateral emarginations on R side beginning at tergite articulations: smooth even **(0)**; irregular (margin has at least one short projection) **(1)** (Fu *et al.* 2010 Fig. 5).

231 (192). Sheath sternite. Nature posterior to tergite articulations: not subparallelsided **(0)**; subparallelsided in at least basal 1/3 **(1)**. Character 192 split into two; 192 states 1–3 are state 1 here.

232 (192). Sheath sternite, extent of subparallel sided sheath sternite: yes in basal 1/3 **(0)**; yes in basal 2/3 **(1)**; along length **(2)**. Character 192 split into two; 192 states 1–3 become 0, 1 ,2 respectively.

233. Sheath sternite, terminates in separate hairy lobe/s: No **(0)**; Single median lobe **(1)**; Paired lobes **(2)** (e.g. Jeng *et al.* 2003 Figs 22 a, b).

234 (197, 201). Sheath sternite, posterior margin emarginate: No **(0)**; Yes **(1)** (Ballantyne & Lambkin Figs 115–117). Incorporates character 201 states 0, 1 as 0, 1 here.

235. Sheath sternite, emargination occurs between separate apical lobes (e.g. Jeng *et al.* 2003 Figs 22 a, b): No **(0)**; Yes **(1)**.

236 (199). Sheath sternite, position of posterior emargination: centre (may be slightly off centre) **(0)**; on one side only **(1)**. Width of medial emargination not specified here; specified in 238 below.

237. Sheath sternite, shape of emargination of posterior margin: Rounded **(0)**; Pointed **(1)**.

238 (198). Sheath sternite, width of emargination of posterior margin: Narrow **(0)**; Wide **(1)** (Ballantyne & Lambkin 2009 Figs 115–117).

239. Sheath sternite, depth of emargination of posterior margin: Shallow **(0)**; Deep **(1)**.

240 (199). Sheath sternite, position of narrow emargination of posterior margin: Centre **(0)**; Offcentre **(1)**.

241 (200). Sheath sternite, presence of pointed projections to either side of median emargination of posterior margin (Jeng *et al.* 2003 Fig. 14): Absent **(0)**; Present **(1)**.

242 (202). Sheath sternite, nature of posterior margin that is not medially emarginate: No rounded projection **(0)**; With rounded projection **(1)** (Ballantyne & Lambkin 2009 Figs 181, 183).

243 (191). Sheath sternite, anterior portion (anterior to lateral tergite articulations) bent to right: No **(0)**; Yes **(1)** (Fu & Ballantyne 2006 Fig. 4). Character 191 modified to reflect anterior parts of the sheath sternite; no change to scoring. Descriptor amplified with "anterior to lateral tergite articulations".

244 (189, 190, 191). Sheath sternite, posterior portion (posterior to lateral tergite articulations) bent to right (Fu & Ballantyne 2006 Fig. 4): No **(0)**; Yes **(1)**. Characters 189, 190 combined to reflect only the posterior parts of the sheath sternite. Descriptor amplified with "posterior to lateral tergite articulations". No change to scoring.

245. Sheath sternite, maximum width occurs at tergite articulations: Yes **(0)** (e.g. Ballantyne & Lambkin 2009 Figs86–93); Occurs posterior to tergite articulations **(1)**.

246. Sheath sternite, nature of maximum width at tergite articulations: sternite expands gradually to this point **(0)** (Ballantyne & Lambkin 2009 Figs86–93); sternite is subparallelsided along most of its anterior length **(1)**.

247 (194, 195). Sheath sternite, nature of sternite that reaches its maximum width posterior to tergite articulations: gradual expansion along length **(0)**; expanding in posterior 1/2–2/3 **(1)**. Character 194 partly incorporated here;194 state 0 is state 1 here; 194 state 1 is 0 here.

248 (196). Sheath sternite, nature of expansion in posterior area: Gentle expansion in posterior 1/3–2/3 **(0)**; Wide often abrupt expansion in posterior 1/3–2/3 **(1)**. State 1 modified with addition of range 1/3–2/3. No change to scoring.

249 (193). Sheath sternite, nature of anterior half (anterior to lateral attachment of tergal arms): gradually narrowing anteriorly to a very narrow anterior end **(0)**; if narrowing then anterior end not extremely narrow **(1)**.

250 (207). Tergite 9, presence of bulbous paraprocts (Ballantyne *et al.* 2011 Figs 15, 16): Absent **(0)**; Present **(1)**.

251 (206). Sheath dimensions, length/width: never > 4 X as long as wide **(0)**; very long and narrow (up to 7 X as long as wide) **(1)**.

252 (208). Tergite 9, elongate anterolateral arms of tergite 9 visible at sides of symmetrical sternite: No **(0)**; Yes **(1)**. Descriptor includes "symmetrical sternite". No change to scoring.

253 (208). Tergite 9, extent of visibility of arms: Narrowly visible **(0)**; Widely visible **(1)**. Character 208 state 1 is state 1 here.

254 (209). Tergite 9 split into two pieces: No **(0)**; Yes **(1)**.

255 (210). Tergite 9, posterior margin with downwardly projecting pieces: No **(0)**; Yes **(1)** (Ballantyne & Lambkin 2009 Figs 41–44).

256. Tergite 9, posterolateral areas narrowly project beyond the posterior margin Ballantyne & Lambkin 2009 Figs 115, 116): No **(0)**; Yes **(1)**.

257 (211). Tergite 9, presence of transverse band anterior to sheath tergite (Ballantyne 2008 Fig. 9): No **(0)**; Yes **(1)**.

258. Tergite 9, shape of median area anterior margin: Not produced **(0)**; Produced **(1)**.

259. Tergite 9, shape of produced median area anterior margin: Pointed **(0)**; Bluntly rounded **(1)**; Bluntly and widely rounded **(2)**.

<u>AEDEAGUS 260–326.</u>

260 (212). Aedeagus dimensions, length/width: 3/1 or greater **(0)**; Less than 3/1 **(1)**.

261 (213). Aedeagus dimensions, maximum width across LL/maximum width of ML: Wide **(0)**; Moderate **(1)**; Narrow **(2)**. Ballantyne & Lambkin 2009 character 213 specifies parameters for these states.

262 (240). Aedeagus, apices of LL visible at sides of ML from above or below: Yes **(0)** (e.g. Ballantyne & Lambkin 2009 Fig. 35); No **(1)** (e.g. Ballantyne & Lambkin 2009 Fig. 36). Descriptor includes visibility from both above and below; no change to scoring.

263 (226). Aedeagus dimensions, length LL where apices can be seen from beneath relative to ML measured from beneath: much shorter than ML **(0)**; subequal to ML or slightly longer or shorter **(1)**; LL much longer than ML **(2)**.

264 (227). Aedeagus dimensions, equality of length LL: Equal **(0)**; Unequal **(1)**.

265. Aedeagus dimensions, length LL where apices cannot be seen from below: Slightly shorter than ML **(0)**; Much shorter than ML **(1)**.

266 (214). Aedeagus, symmetry: Symmetrical **(0)**; Asymmetrical **(1)**.

267 (214, 215). Aedeagus, asymmetry due to curvature of ML in horizontal plane: No **(0)**; Yes **(1)** (Ballantyne & Lambkin 2009 Figs 286–289). No change to states or scoring. Wording of 215 changed to reflect aedeagal symmetry not just ML symmetry; no change to scoring.

268. Aedeagus, asymmetry due in part to curvature of LL: No **(0)**; Yes **(1)**.

269 (216). ML, asymmetry due to asymmetrical projections of ML: No **(0)**; Yes **(1)**.

270. (217) ML, nature of ventral face of asymmetrical ML: lacking median longitudinal groove **(0)**; with median longitudinal groove **(1)** (e.g. Ballantyne & Lambkin 2009 Figs 50, 51).

271. ML, swollen along more than half its length: No **(0)**; Yes **(1)** (Fu *et al*. 2012a Fig. 12).

272 (218). ML, presence of lateral teeth (Ballantyne & Lambkin 2009 Figs 364–376, 428–435): Absent **(0)**; Present **(1)**.

273 (219). ML, width of lateral teeth (Ballantyne & Lambkin 2009 Figs 364–376, 428–435): Narrow **(0)**; Wide **(1)**.

274 (220). ML, shape of apices of lateral teeth (Ballantyne & Lambkin 2009 Figs 364–376, 428–435): Pointed **(0)**; Rounded **(1)**.

275 (221). ML, inclination apex: Not curved ventrally **(0)**; Curved ventrally **(1)**.

276 (222). ML, strongly arched: No **(0)**; Yes **(1)** (Ballantyne & Lambkin 2009 Fig. 514).

277 (223). ML, extent preapical ventral area (Ballantyne & Lambkin 2009 Fig. 514; Ballantyne 1968 Figs 164, 168): Not produced **(0)**; Produced rounded **(1)**; Produced pointed **(2)**.

278 (255). ML. Asymmetrical flap–like projection to left side (Ballantyne & Lambkin 2009 Figs 48–54): No **(0)**; Yes **(1)**.

279 (224). ML, width of symmetrical ML at apex relative to width at base: as wide as or wider than base **(0)**; much narrower than at base **(1)**.

280 (225). ML, apex with arrowhead shape (Ballantyne & Lambkin 2009 Figs 48–50): No **(0)**; Yes **(1)**.

281 (257). ML, bulbous tip (Ballantyne & Lambkin 2009 Figs 188, 189): No **(0)**; Yes **(1)**.

282. ML, base bulbous, at least twice as wide as remainder: No **(0)**; Yes **(1)**.

283 (229, 231). LL, separation of LL visible from beneath: separated by > 1/2 their length **(0)**; separated by < ½ **(1)**; not separated **(2)**. Characters 229, 231 combined and additional state 2 added. No change to scoring.

284. LL, separation of LL along their inner dorsal length: separated along at least part of their dorsal length **(0)**; not separated (LL are fused) **(1)** (Fu & Ballantyne 2008 Fig. 20).

285 (229, 240). LL, extent of separation of LL that cannot be seen from below as a proportion of their dorsal length (measured from base of LL) (view from above): > 0.5 **(0)**; 0.5 **(1)**; <0.5 **(2)**. States expanded to reflect more accurately differences in length of LL; only character 240 state 2 is scored here; character 229 state 0 is state 0 here and state 1 is state 2 here.

286. LL, extent of separation of LL which are separated by < ½ (viewed from above): 1/3 their dorsal length **(0)**; much less 1/7 **(1)**.

287. LL, visibility from beneath of LL at sides of symmetrical ML: visible **(0)**; not visible **(1)**.

288 (241). LL, visibility from beneath of LL at sides of asymmetrical ML: Visible **(0)**; if visible not both in same plane **(1)**; not visible **(2)**.

289. Aedeagus dimensions, length of LL that cannot be seen from below as a proportion of the median lobe length (measured along dorsal side from base of LL): >0.5 **(0)**; <0.5 **(1)**.

290. LL, length of LL as proportion of ML length (Measured from above from base of LL): >0.5 **(0)**; 0.5 or less **(1)**.

291 (228). LL, extent of divergence along inner dorsal margins LL: not divergent along most of their length (basally) **(0)**; not divergent in basal half (diverge in apical half) **(1)**; diverging along length **(2)**. New states 1, 2 accommodate old state 1.

292 (232). LL, LL at apices relative to ML apex (Ballantyne & Lambkin 2009 Figs 184, 185): much wider than widest point of ML **(0)**; subequal to ML **(1)**; narrower than ML **(2)**.

293. LL, separation at their apices of LL which are not visible from beneath: Contiguous **(0)**; Separated **(1)**.

294 (233). LL. Apices visible from beneath broadly and evenly expanded in horizontal plane: No **(0)**; Yes **(1)**.

295 (234). LL, which are visible at sides of ML with broad basal portion and narrowed apical portion (Ballantyne & Lambkin 2000 Fig. 21k): No **(0)**; Yes **(1)**.

296. LL, width of apical pieces: Narrow **(0)**; Wide **(1)**.

297. LL, length of apical pieces: Long **(0)**; Short **(1)**.

298. LL, extent of separation of basal portion of character 284: Not separated **(0)**; Separated (short) **(1)**.

299 (235). LL, ventrobasal area of LL produced into lobes that may overlap base of ML (Lloyd & Ballantyne 2003 Fig. 18): No **(0)**; Yes **(1)**.

300. LL, anterior margin of dorsal base of LL produced: No **(0)**; Yes **(1)**.

301 (236). LL, anterior margin of dorsal base of LL asymmetrically produced: No **(0)**; Yes **(1)**.

302 (237) LL, excavation of anterior margin of base: No **(0)**; Yes **(1)**.

303 (238). LL, nature of anterior projection of base of LL: broadly rounded **(0)**; broadly truncate **(1)**; apically acute medially entire **(2)**; apically acute medially emarginate **(3)**. Symmetrical removed from descriptor.

304 (239). LL, elongate sausage shaped lobes on ventral surface (Fu & Ballantyne 2008 Fig. 20): Absent **(0)**; Present **(1)**. Nature of lobes on ventral surface of LL expanded here; 239 state 1 becomes 0 for *L. italica*, *L. parvula* and *L. syriaca*.

305 (239). LL, anterior end inner ventral surface extending into flattened and apically acute projection (Jeng *et al.* 2003 Figs 21 a–c)): No **(0)**; Yes **(1)**. Nature of lobes on ventral surface of LL expanded here; 239 state 1 is 1 for *L. italica*, *L. parvula* and *L. syriaca*.

306 (242). LL, lateral appendages of LL (Lloyd & Ballantyne 2003 Figs 17, 18, 21): Absent **(0)**; Present **(1)**.

307 (245). LL, preapical lateral margin LL produced (Ballantyne & Lambkin 2009 Figs 286–303): Not **(0)**; Slightly **(1)**; Strongly **(2)**.

308 (246). LL, shape of expanded preapical lateral margin (Ballantyne & Lambkin 2009 Figs 293, 294, 302, 303): Rounded **(0)**; Angulate **(1)**.

309 (247). LL, production of inner apical margin (Ballantyne & Lambkin 2009 Figs 286–303): No **(0)**; Yes **(1)**.

310 (248). LL, length inner apical margin (Ballantyne & Lambkin 2009 Figs 302, 303): Short **(0)**; Medium **(1)**; Long **(2)**.

311 (249). LL, width of inner apical production (Ballantyne & Lambkin 2009 Figs 270, 271, 302, 303): Wide **(0)**; Narrow **(1)**.

312 (250) LL, preapical inner margin obliquely truncate (Ballantyne & Lambkin 2009 Figs 212–216): No **(0)**; Yes **(1)**.

313 (251). LL, inner preapical margin of LL that are obliquely truncate on their inner margins with tooth (Ballantyne & Lambkin 2009 Figs 242, 243): No **(0)**; Yes with small tooth **(1)**; Yes with large well defined tooth **(2)**. Size of tooth reflected in scoring, new state 2; state 1 of 251 becomes either 1 or 2 here depending on size.

314 (252). LL, whole of apices of LL out-turned (Not narrowed inner portion): No **(0)**; Yes **(1)**.

315 (253). LL, shape of outer margin of out-turned apices of LL: Rounded **(0)**; Angulate **(1)**.

316 (254). LL, apices of LL inturned (meet or nearly so in midline) (Ballantyne & Lambkin 2009 Figs 513, 515, 516): No **(0)**; yes strongly bent so meet or nearly so in mid line **(1)**. State 0, 1 of character 254 merged into state 0 here; state 2 is state 1 here.

317. LL, apices incline inwards and hooked: No **(0)**; Yes **(1)**.

318. LL, nature of inturned hooked apices: Broad **(0)**; Very narrow **(1)**.

319 (256). LL, projection on left LL (Ballantyne & Lambkin 2009 Figs 48–54): Absent **(0)**; Present **(1)**.

320 (260). LL. Inner margins of LL approach closely at half their length from base (Ballantyne & Lambkin 2009 Figs 523, 515, 516): No **(0)**; Yes **(1)**.

321 (261). LL, longitudinal emarginate hair bearing area on outer margin LL (Ballantyne & Lambkin 2009 Figs 246, 247): No **(0)**; Yes **(1)**.

322. LL, inner dorsal margins of separated LL toothed (Fu *et al.* 2010 Fig. 10): No **(0)**; Yes **(1)**.

323 (243). BP, strongly sclerotised: No **(0)**; Yes **(1)**.

324 (244). BP, shape (Ballantyne & Lambkin 2009 Figs 212–216): Not hooded **(0)**; Hooded **(1)**.

325 (258). BP, with emarginated median anterior apex (Ballantyne & Lambkin 2009 Fig. 518): No **(0)**; Yes **(1)**.

326 (259). BP, width when viewed from beneath (Ballantyne & Lambkin 2009 Figs 513, 515): Not narrow **(0)**; Very narrow **(1)**.

<u>FEMALE 327–359.</u>

327 (262). Pronotum, pronotal irregularities: Absent **(0)**; Present **(1)**.

328 (263, 269). Pronotum, punctation in lateral area of disc: Moderate to dense **(0)**; Sparse **(1)**. Two characters addressing same character combined; 269 0 is 0 here; 269 1 is 1 here.

329 (264). Pronotum, dimensions, A=width across anterior 1/3; B=width across middle; C=width across posterior: A=C **(0)**; B>A or C **(1)**; C >A, B **(2)**; B = C **(3)**; C < A or B **(4)**.

330 (265). Pronotum, width across posterior PN margin/ width across elytral humeri: Less than **(0)**; Subequal to **(1)**; Greater than **(2)**.

331 (266). Pronotum. Indentation of lateral margin of pronotum near posterolateral corner: No indentation **(0)**; Slight indentation **(1)**.

332 (267). Pronotum, irregularities at apex of posterolateral corner: Absent **(0)**; Present **(1)**.

333 (268). Elytra, punctation: not as large as pronotal **(0)**; conspicuous and as large as pronotal **(1)**.

334. Elytra, density of punctation: Not sparse **(0)**; Sparse **(1)**.

335 (270). Elytra, development of fore wings (Ballantyne & Lambkin 2009 Figs 25, 130, 132, 133, 136): Fully developed (or covering all but two terminal segments) **(0)**; elytra longer than pronotum but shortened such that they cover 1/2–2/3 of abdomen **(1)**; elytra subequal to or shorter than PN length and medianly contiguous **(2)**; elytra shorter than 1/2 PN length and often medianly contiguous **(3)**; elytra shorter than 1/2 PN length and widely separated **(4)**. Descriptor of state 2 expanded with “or shorter than”.

336 (271). Wings, development of hind wings: fully developed **(0)**; always shortened, usually at least half as long as macropterous state, lacks apical fold **(1)**; vestigial or absent **(2)**.

337 (272). Elytra. Interstitial line development: Four well defined lines **(0)**; Three well defined lines (lines 1, 2 and 3 or 4) **(1)**; Two well defined lines (lines 1, 2 closest to the suture) **(2)**; One **(3)**; No lines **(4)**. State 0 includes lines 1–4; the humeral carina is scored as state 3. No change to scoring.

338 273). Elytral carina: Absent **(0)**; present **(1)**.

339 (274). Head, size of eyes: not greatly reduced **(0)**; considerably reduced **(1)**.

340 (275). Head, position of antennal sockets on head relative to eyes (labrum is horizontal): on head between eyes **(0)**; on short prolongation **(1)**; on long anterior prolongation **(2)**.

341 (276). Head, nature of anterior prolongation of head: not developed **(0)**; parallel sided **(1)**; sides converge anteriorly **(2)**.

342 (277). Head, clypeolabral suture: present junction flexible **(0)**; present junction inflexible **(1)**; absent **(2)**.

343 (278). Legs, tibiae 3 curved: No **(0)**; Yes **(1)**.

344 (279). Legs, tibiae 2 curved: No **(0)**; Yes **(1)**.

345 (280). Legs, tibiae 1 curved: No **(0)**; Yes **(1)**.

346 (281). Light organ, extent: V6 and V7 **(0)**; V6 only **(1)**.

347 Light organ, extent of LO that is confined to V6: entire occupies most of area **(0)**; bipartite (split into two widely separated areas) **(1)**.

348 (282). Anteromedian elevations on T7 (Ballantyne & Lambkin 2001 Figs 18, 19): Absent **(0)**; Present **(1)**.

349 (283). Median transverse ridge ventral face of V7 (Ballantyne & Lambkin 2001 Fig. 16): Absent **(0)**; Present **(1)**.

350 (284). Lateral elevated areas ventral face of V7 (Ballantyne & Lambkin 2001 Fig. 30): Absent **(0)**; Present **(1)**.

351 (285). Lateral depressed areas V7 (corresponding to dorsoventral muscles): Absent **(0)**; Present **(1)**.

352 (286). Bursa plates, presence: No **(0)**; Yes **(1)**.

353. Bursa plates, number of pairs of plates: One **(0)**; Two **(1)**.

354 (287). Single pair of bursa plates appear as paired strips (Fu & Ballantyne 2006 Fig. 8): No **(0)**; Yes **(1)**. Descriptor modified to read “single pair of bursa plates”. No change to scoring.

355 (288). Single pair of bursa plates appear as hooks (Ballantyne & Lambkin 2006 Fig. 37): No **(0)**; Yes **(1)**. Descriptor modified to read “single pair of bursa plates”. No change to scoring.

356 (289). Bursa plates appear as wide (paired) plates (Ballantyne *et al.* 2011 Figs 59, 60): No **(0)**; Yes **(1)**.

357 (290). Presence of plate at base of median oviduct (Ballantyne *et al.* 2011 Figs 53, 54, 56): No **(0)**; Yes small **(1)**; Yes large **(2)**. States modified to include state 2; 1 becomes either 1 or 2 here.

358. Nature of spermatophore digesting gland: Membranous thin walled **(0)**; Muscular **(1)**.

359. Female genitalia, size of apical segment of styli to preapical segment: Subequal in width **(0)**; Much narrower **(1)**.

LARVA 360–407.

360 (291). Production of lateral tergal margins: Not explanate **(0)**; Explanate **(1)**. States reduced to two, presence or absence; 1 and 2 become 1.

361. Nature of non–explanate tergal margins: not produced **(0)**; produced laterally and thickened **(1)** (e.g. Fu & Ballantyne 2008 Figs 2, 4).

362. Lateral tergal margins covering laterotergites from above: No **(0)**; Yes **(1)** (e.g. Fu & Ballantyne 2008 Figs 2, 4). Tergal margins may not be laterally explanate yet can project sideways sufficiently to cover the laterotergites; this character accommodates such situations.

363 (292). Laterotergites visible from above (Ballantyne & Lambkin 2000 Fig. 36B): No **(0)**; Yes **(1)**.

364. Lateral margins of thoracic and abdominal terga of differing shapes: No **(0)**; Yes **(1)** (Figs 5, 6, 30).

365. Posterolateral corners of abdominal terga prolonged: No **(0)**; Yes **(1)** (e.g. Figs 5, 6, 30).

366. Prolonged posterolateral corners of abdominal terga single or bifurcate: Single **(0)** (e.g. Figs 5, 6, 30); Bifurcate **(1)** (Fig. 50).

367. Angle of single prolonged corners: Straight **(0)** (Fig. 52); Curved **(1)** (e.g. Figs 5, 6, 30).

368 (293). Length/width protergum: L>W **(0)**; L=W **(1)**; W>L **(2)**.

369 (294). Nature of tergal margins: Not ridged **(0)**; Ridged and/or thickened **(1)** (e.g. Fu & Ballantyne 2008 Figs 2, 4).

370. Antennal segment 3 surmounted by hairs (Fu *et al*. 2012a Figs 26-28); (Fu & Ballantyne 2008 Fig. 29): Yes **(0)**; No **(1)**.

371 (296). Width of sense cone (Fu & Ballantyne 2008 Fig. 29): Wide **(0)**; Slender **(1)**.

372 (295, 297). Length of sense cone (Fu & Ballantyne 2008 Fig. 29): Short **(0)**; Long **(1)**. Two characters combined here; where sense cone is long antennal segment 3 is also long. No change to scoring.

373 (298). Single pair of tubercles (present as dorsal and ventral tubercles) along anterior margin protergum (Ballantyne & Lambkin 2000 Fig. 15a, c): Absent **(0)**; Present **(1)**. Descriptor changed, no change to scoring.

374. Protergum with tubercle like projections along posterior margin only: No **(0)**; Yes **(1)**.

375. Dorsal surface of protergum with tubercles along anterior, lateral and posterior margins (Fig. 53): No **(0)**; Yes **(1)**.

376 (299). Shape of posterolateral corners protergum: Not narrowly produced **(0)** (Ballantyne & Lambkin 2000 Fig. 36B); Narrowly produced **(1)** (Figs 51, 53).

377 (300). Shape of posterolateral pronotal corners that are not produced (Ballantyne & Lambkin 2000 Figs 12c, 15 a–c, 36b): Round **(0)**; Acute **(1)**.

378 (301). Shape posterolateral corners protergum that are narrowly produced: Entire **(0)**; Bifurcate **(1)**.

379 (302). Shape of posterolateral corners pronotum that are narrowly produced: Rounded **(0)**; Pointed **(1)**.

380 (303).Shape posterolateral corners meso and metaterga: Not narrowly produced **(0)**; Narrowly produced **(1)** (Figs 51, 53).

381 (304). Inclination of narrowly produced posterolateral corners of meso and metaterga: oblique to median line **(0)**; parallel to median line **(1)**.

382 (305). Median line with lateral margins: No **(0)**; Yes **(1)**.

383 (306). Ridges along margins of median line on terga 1–10: Absent **(0)**; Present **(1)**.

384 (307). Median line extending to anterior and posterior margins of most terga: Yes **(0)**; No **(1)**.

385 (308). Size punctures in anterior half terga 2–10: No larger than rest **(0)**; Larger than rest **(1)** (Fig. 51).

386 (309). Extent posterolateral corners tergum 12: Not produced **(0)**; Produced **(1)**.

387 (310). Posterior margins of abdominal terga 1–7 or 8 with projections to either side of median line (Figs 50–53): Absent **(0)**; Present **(1)**.

388. width of projections: Wide **(0)**; Narrow **(1)**.

389 (311). Nature of projections along posterior margins of terga 1–7 or 8 (Figs 50–53): Rounded **(0)**; Acute **(1)**.

390 (312). Presence of dense brush of white hairs arising from the apex of the tibia and enveloping apical (tarsungulus) claw (Fig. 55): Absent **(0)**; Present **(1)**.

391 (313). Presence thickened lateral margin protergum: Absent **(0)**; Present **(1)**.

392 (314). Mandibles with inner teeth: Absent **(0)**; One tooth **(1)** (Fu *et al*. 2012a Fig. 26); Two teeth **(2)** (Fu & Ballantyne 2008 Fig. 27).

392 modified to accommodate mandibles with either one or two teeth; 392 1 is state 2 here.

393. Position of sensory organs on apical palpomere: Terminal **(0)**; Ventral **(1)**.

394. Length/width apical maxillary palpomere: Subequal **(0)**; L>W **(1)**.

395 (315). Tergal plates sclerotised or at least coloured to lateral margins: No **(0)**; Yes **(1)**. Descriptor modified to include "or at least coloured". No change to scoring.

396. Tergal plates heavily sclerotised: No **(0)**; Yes **(1)** (e.g. Fu & Ballantyne 2008 Fig. 2).

397. Ventral body lacking membranous areas (Fu & Ballantyne 2009 Fig. 1d): No **(0)**; Yes **(1)**.

398 (316). Posterolateral corners of penultimate tergite broadly produced posteriorly: No **(0)**; Yes **(1)** (Jeng *et al.* 2003 Fig. 41).

399 (317). Mode of life: Terrestrial **(0)**; Semiaquatic **(1)**; Aquatic **(2)**.

400 (318). Tracheal gills: Absent **(0)**; Present in some stages **(1)**; Present in all stages **(2)** (Fu et al. 2010 Figs 25, 26).

401 (319). Presence of tergum 8 spiracles (Jeng *et al.* 2003 Fig. 41; Fu & Ballantyne 2009 Figs 2c, 3e, 4a, 5): Absent **(0)**; Present **(1)**.

402. Presence of glands at sides of abdomen on eversible sacs (e.g. Fu et al 2010 Figs 48, 49): Absent **(0)**; Present **(1)**.

403 (320). Presence of laterosternal plates to either side of median sternal plate in abdominal segments 1–8 (e.g. Fig. 54): Present **(0)**; Absent **(1)**.

404 (321). Filaments along posterior margins most terga: Absent **(0)**; Present **(1)**.

405. Ventral surface abdomen, posterior margin sternite with paired projections (Fig. 54): No **(0)**; Yes wide **(1)**; Yes narrow **(2)**.

406. Ventral surface abdomen, posterior margin laterosternites narrowly prolonged (Fig. 54): No **(0)**; Yes **(1)**.

407. Ventral surface abdomen, posterolateral areas of laterotergites prolonged (Fig. 54): No **(0)**; Yes **(1)**.

<u>COLOURATION 408–436.</u>

<u>MALE.</u>

408. Dorsal colouration male: Concolourous **(0)**; Not concolourous **(1)**.

409. Nature of concolourous dorsal colour: Pale **(0)**; Dark **(1)**.

410 (322). Elytral colour, concolourous: Yes **(0)**; No **(1)**. Character 322 states 0, 1 score 1 here.

411 (322). Elytral colour, nature of concolourous elytra: Pale **(0)**; Dark **(1)**.

412 (336). Colour of pronotum. Concolourous **(0)**; Not concolourous **(1)**.

413. Nature of concolourous pronotum: Pale **(0)**; Dark **(1)**.

414. Nature of colour on non concolorous pronotum: dark colour in middle area **(0)**; dark colour along lateral margins **(1)**.

415 (323). Elytra dark with paler randomly scattered spots (Ballantyne & Lambkin 2009 Figs 137, 138): No **(0)**; Yes **(1)**.

416 (324). Elytra striped (pale stripes in otherwise dark elytra) (Ballantyne & Lambkin 2009 Figs 11, 122, 123, 124, 150, 151, 153): No **(0)**; Yes **(1)**.

417 (325). Number of pale interstitial lines in striped elytra: <3 **(0)**; 3 **(1)**; >3 **(2)**.

418 (326). Extent of pale lateral margin in striped elytra: narrow does not extend to line 4 **(0)**; wide covers line 4 **(1)**.

419 (327). Fat body contributes to pale line colour in striped elytra (Ballantyne & Lambkin 2009 Fig. 150): No **(0)**; Yes **(1)**.

420 (328). Striped elytra with additional stripes due to lines of fat body (lines between interstitial lines): No **(0)**; Yes **(1)**. "lines between interstitial lines" added to descriptor.

421. Base of largely pale elytra with dark area over humerus: No **(0)**; Yes **(1)**.

422 (330). Extent of dark elytral marking adjacent to MS (Ballantyne & Lambkin 2009 Figs 23, 69, 70, 166, 167, 169): restricted to base of elytron, not a wide triangle **(0)**; wide triangular **(1)**.

423 (329). Base of elytra with dark area adjacent to MS (Ballantyne & Lambkin 2009 Figs 23, 69, 70): No **(0)**; Yes **(1)**.

424. Base of largely pale elytra with dark area extending across base from humerus to MS: No **(0)**; Yes **(1)**.

425. Pale elytra with single apical dark area: No **(0)**; Yes **(1)**.

426 (331). Elytra with pale margin/s (different colour) (Ballantyne & Lambkin 2009 Figs5, 12, 17, 66, 67, 128): No **(0)**; Yes **(1)**.

427 (332). 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)**; sutural margin excluding apex **(5)**. Additional state 5 added.

428 (333, 335). Presence of pale basal area of dark elytra (Ballantyne & Lambkin 2000 Fig. 19 g, h): No **(0)**; Yes **(1)**.

429 (337). Colour T8: as dark as preceding tergites **(0)**; paler **(1)**.

FEMALE 430–432.

430 (338). Colour elytra: Concolourous **(0)**; Not concolourous **(1)**.

431. Elytra with base much paler than rest: Concolourous **(0)**; Not **(1)**.

432 (339). Nature of colour on non concolourous pronotum: Dark area in middle **(0)**; Dark colour along lateral margins **(1)**. Character 339 state 1 is 1 or 2 here.

NATURE OF CRYPSIS/MIMICRY.

433 (340). Nature of dorsal colouration female: crypsis **(0)**; mimicry **(1)**.

434 (341). Type of crypsis female: Background matching **(0)**; Disruptive colouration **(1)**.

435 (342). Nature of dorsal colouration male: Crypsis **(0)**; Mimicry **(1)**.

436 (343). Type of crypsis male: Background matching **(0)**; Disruptive colouration **(1)**.