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A PHYLOGENETIC REASSESSMENT OF THE RARE S. E. ASIAN FIREFLY GENUS *PYGOLUCIOLA* WITTMER (COLEOPTERA: LAMPYRIDAE: LUCIOLINAE)

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ABSTRACT. – Cladistic analysis supports the return of the rare Malaysian (Bornean) firefly genus *Pygoluciola* Wittmer to generic status; it is redescribed from the five species included, and keys to males and known females presented. The number of reliably identified specimens in published accounts increases from 21 (in five species) to 28. Females of *P. guigliae* and *P. wittmeri* are described including morphology of the female abdomen and aspects of reproductive system anatomy which may be of significance in female identification. Discussion addresses different preservation techniques relative to interpretation of taxonomic characters and conjecture about function, association of males and females, functional morphology of the terminal abdomen of both sexes, and the value of colouration characters. *Luciola undulata* (Pic) is reassigned to *Atyphella* Olliff.

KEY WORDS. – *Pygoluciola*, taxonomy, female morphology, female reproductive anatomy, colour characters, preservation methods, *Atyphella undulata*.

INTRODUCTION

The Luciolinae present a most interesting array of opportunities for observation and study. They are apparently exclusively flashing fireflies, and a species of *Pteroptyx* undertakes the spectacular synchronous rhythmic flashing on the Selangor River at Kampong Kuantan, Malaysia (Ballantyne, 2001). Their importance to the tourism industry of other Asian countries is being belatedly recognised.

For the taxonomist the variety of male terminal abdomen modifications has excited speculation about their function (Ballantyne, 1987b), and some resolution (the copulation clamp in *Pteroptyx valida* Wing et al., 1983). Such external abdominal structures were used to erect new genera (e.g. *Pteroptyx* Olivier, 1902, based on the deflexed elytral apices and 'trilobed' abdominal V 7). These subdivisions of the Luciolinae, as listed by McDermott (1966), are unsatisfactory and not representative (Ballantyne & Lambkin, 2000, 2001). The early taxonomy was thus male based, there being no distinctive features of the female abdomen until now.

That distinctive features could occur externally on the female abdomen of any Lucioline firefly was unsuspected until Ballantyne & Lambkin (2001), describing *L.* [*P.*] *kinabalua*, highlighted aspects of the female abdomen, which, coupled with male abdomen structure, indicated to them the possibility of a copulation clamp. The dried pinned specimens precluded any investigation of internal anatomy.

A recent collection of seven alcohol preserved specimens, which includes both males and females of two species (*Pygoluciola wittmeri* and *P. guigliae*) permits an investigation and reinterpretation of male and female terminal abdomen morphology, and for the first time an investigation for this group of female reproductive anatomy.

Until this collection, which was killed, fixed and preserved by immersion directly into 70% alcohol, the rare group was represented by five species known from published records of 11 males and 10 females [*Pygoluciola guigliae* (male, female), *P. hamulata* (three males), *P. kinabalua* (five males, eight females), *P. stylifer* (male, female) and *P. wittmeri* (male)] (Olivier, 1885; Ballantyne, 1968; Ballantyne & Lambkin, 2001; Wittmer, 1939). Unusual in the Luciolinae, four of the five species are now known from both sexes. Rarity of occurrence of fireflies when they are obvious by their light and easy to net, usually relates to their occurrence in difficult or dangerous terrain, or in largely uncollected territory. The recent collecting activities in Borneo are thus most welcome.

Pygoluciola Wittmer, a rare group of fireflies with unusual male terminal abdomen modifications, and restricted to the Malaysian states of Sabah and Sarawak, was considered a subgenus of *Luciola* (McDermott, 1966; Ballantyne, 1968; Ballantyne & Lambkin, 2001). Ballantyne & Lambkin (2000) scored *Luciola* (*Pygoluciola*) *stylifer* Wittmer in a cladistic analysis of 43 species of Luciolinae. Because of many missing features their analysis did not give unequivocal directions for its taxonomic position. The analysis was rerun by Lambkin using *L. (P.) kinabalua* as a second exemplar for this subgenus, with no missing adult characters, and '?' for larval characters only (Ballantyne & Lambkin, 2001), but again did not yield unequivocal directions for the taxonomy of this group, thus Ballantyne & Lambkin (2001) continued to address *Pygoluciola* as a subgenus of *Luciola* as had McDermott (1966). The specimens described here, together with a re-examination of the type species (*Pygoluciola stylifer* Wittmer), permit a re-evaluation of their findings.

The position of *Pygoluciola* is addressed with a third cladistic analysis and revised. The genus is redescribed and keyed from known males and females. Males and females of two species of *Pygoluciola* are described or redescribed from features of freshly collected specimens, with detail of the terminal abdomen of each including aspects of the female genitalia and reproductive tract.

MATERIALS AND METHODS

Taxonomic characters are based on Ballantyne & Lambkin (2001), which in turn were described in detail in Ballantyne & Lambkin (2000); changes or emendations to these characters are described following the character description; characters are numbered thus: 9 (8) indicating that character 9 in this paper was character 8 in Ballantyne & Lambkin (2001). Characters and states are included in the descriptions e.g. 'head moderately exposed 4 (1)' = character 4, state 1; '92 (0&1)' indicates that character 92 is polymorphic, equal numbers of specimens show either states 0 or 1; 92(0, 1) indicates for a polymorphic character that state 1 is the majority state. Visible male abdominal sternites are referred to by their actual number, which is one more than their visible number (= ventrites). The ventral plate of the concealed 9th abdominal segment is referred to as a sternite. Ballantyne (1968) refers the terminal abdominal tergite to tergite 7; abdominal segmentation was reviewed in Ballantyne (1987a) and this tergite referred to abdominal segment 8. The degree of head exposure/coverage (characters 4, 5) was expanded to indicate the differing mechanisms by which the head can be concealed (able to be retracted into a pronotal cavity vs. covered by the anterior expansion of the pronotum). Branham and Wenzel (2003) interpreted this (on many more genera than used here) as a capacity to retract between the hypomera, thus effectively characterising the size of a pronotal cavity. Distortion affects absolute dimensions (Ballantyne, 1987a), and most dimensions here are given as absolute and on a comparative basis e.g. GHW as a function of SIW.

Specimens were scored by LB from types, and specimens compared to types, with these exceptions, which were scored from published work and/or identified specimens (authority for identification indicated): *Luciola dejeani* Ballantyne & Lambkin, 2000; *Curtos costipennis* specimens identified by N. Ohba, in ANIC, Jeng et al. (1998); *Luciola pedemontana* specimens identified by F. Papi, in ANIC, Jeng et al. (2003); *Colophotia praeusta* identified by LB in comparison with specimens in Olivier collection at Museum National d'Histoire Naturelle, Paris, specimens in National Museum of Natural History in Washington, D. C.**;** 'Sisiak' undescribed specimens, code named '*Luciola* 12' in Lloyd (1973), work in progress, in LB's collection to be deposited in ANIC; 'Mt. Missim' is an undescribed species based on two males and two females from high elevation in New Guinea, in ANIC; *Pteroptyx malaccae* Ballantyne, 2001; *Lampyroidea syriaca* identified specimens in BMNH London; *Atyphella marginipennis* work in progress (Ballantyne) (Ballantyne & Lambkin, 2000).

Abbreviations for taxonomic characters are: ASW, antennal socket width; FS, antennal flagellar segments, referred to by number e.g. FS 3, 4; GHW, greatest head width; ML, median lobe aedeagus; MN, mesonotal plates; MPP, median posterior projection of ventrite 7; MS, mesoscutellum; LL, lateral lobe aedeagus; PLP, posterolateral projections of ventrite 7; SIW, smallest interocular width; T7, T8, abdominal tergite seven, eight; V followed by a number, abdominal ventrite/s.

Abbreviations for repositories of specimens are:

ANIC	Australian National Insect Collection CSIRO, Canberra
BBM	Bernice Bishop Museum, Hawaii
BORN	Borneensis, Sabah
CMG	Museo Civico di Storia Naturale Giacomo Doria', Genoa
BMNH	Natural History Museum, London
RMNH	National Museum of Natural History Naturalis, Leiden

TAXONOMY

Pygoluciola Wittmer, 1939

Pygoluciola Wittmer, 1939:21.
Luciola (*Pygoluciola*) – McDermott, 1966: 115; Ballantyne, 1968: 119; Ballantyne & McLean, 1970: 233; Ballantyne & Lambkin, 2000: 82; Ballantyne & Lambkin, 2001: 363.

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

Redescription of genus. – *Male*. Body elongate slender, 2.9 – 3.3 times as long as wide.

Pronotum Width/length 1.6 – 2.0; 1/5 – 1/7 as long as whole body length; always wider across posterior 1/3 than anterior 1/3; median anterior margin gently rounded, or slightly medianly emarginate, scarcely projecting beyond anterolateral corners if at all; anterolateral corners defined, rounded and narrowly obtuse or angulate acute, and may project anteriorly beyond anteromedian margin; lateral margins diverging posteriorly along their length, sometimes with some slight sinuousity at mid point; posterolateral corners broadly rounded, acute, and projecting either a little beyond median posterior margin or not at all, and delimited from rest of posterior margin by shallow emarginations which do not follow the anterior margin of the elytral humeral angle; lateral margin near posterolateral corners not indented; lateral margin (viewed from beneath) with anterior 'hypomeral' area developed and distinct from the posterior area, which is flattened in posterior $^2/_3$, slightly more widely so in posterior half than in anterior area, such that the dorsal and ventral surfaces are adpressed to each other in dried pinned specimens and closely approach in 'wet' preserved specimens; dorsal surface smooth, barely convex, except for depressed area of median sulcus and narrow depressed area running along posterior margin; lacking pronounced ridges running obliquely from posterolateral areas to median area of disc, convexity over the posterior margins of the eyes, and a conspicuous flattening of the dorsal surface in median posterior area; irregular small low tubercles present in posterolateral areas in four of five species; punctures small, shallow, fairly inconspicuous, some contiguous, some separated by their width.

Elytra punctation not conspicuously larger than pronotal punctation, not linear; apex not deflexed ; with four barely elevated apunctate interstitial lines, delimited at their sides by punctures which are linear along the side of the interstitial line; epipleuron and sutural ridge extending to rounded apex, with neither thickened in apical half; preapical sutural ridge not downturned; lateral margins not strongly explanate; epipleuron only slightly expanded; elytra at least five times as long as wide, subparallel-sided or tapering posteriorly.

Head in dorsal view is moderately exposed in front of pronotum; vertex shallowly to moderately depressed; lacking posterolateral eye excavation; eyes moderately to widely separated above labrum; GHW 3 – 4.8 X SIW; labrum transverse (wider than long); antennal sockets separated by ASD up to twice but not three times ASW; frons vertex junction not defined; eyes moderately separated behind mouthparts ventrally. *Mouthparts* well developed, especially fleshy lobes of maxillae, and assumed functional; apical segment of labial palpi laterally flattened, with the longest, inner edge bearing a number of slender finger like projections which may differ from one palp to the other; apical segment of maxillary palpi ovoid, not much longer than wide, and as long as apical segment of labial palpi, with an acutely rounded tip. *Antennae* length two to three times GHW; 11 segmented, all segments elongate slender (at least three times as long as wide), simple, apical FS never conspicuously shortened or club like, no FS produced laterally or flattened.

Legs femora and tibiae straight, not swollen, not curved in three of five species; tibiae of all legs curved in *P. guigliae* and *P. stylifer*; all basitarsi simple, not excavated on their inner margins. MFC absent.

Abdomen with six ventrites belonging to segments two – seven; (remnants of segment one may be represented by cuticularisation in the intersegmental membrane anterior to V2); posterior margin of V 3 and V4 not recurved. *Light organs*: occupying all of V 6 except sometimes for some irregular erosion along anterior margin; LO in V 7 occupying at least half the area of V 7, anterior margin often slightly emarginate and not reaching anterior margin of V 7; lateral and posterior margins of LO gently curved, posterior margin may be gently emarginate, no margins reaching to sides or posterior margin of V7; no area posterior to LO in V7 greatly expanded or swollen. *Ventrite seven* (V7): no hairy lobes or pointed projections along posterior margin of V7; posterolateral processes absent, (MPP in pinned specimens tends to be engulfed behind by the downturned apex of tergite 8); posterolateral corners rounded; dorsal face posterior to LO (i.e. MPP) lacking muscle attachments; no median longitudinal groove, carina or dimple; MPP longer than wide, or at least as wide as long, symmetrical, curving strongly dorsally (at about a 90º angle) towards its apex which may be truncate and expanded, or flattened and gently or strongly emarginate, and in dried pinned specimens engages against the downturned apex of tergite eight; if the apex of the MPP is truncate and expanded, the flat posterior surface makes an approximately 90º angle to the horizontal). *Tergite seven*: wider than long or about as wide as long, with strongly depressed lateral areas beneath which dorsoventral muscles attach, and an elevated rounded median area covering the anterior prolongation of tergite eight and the aedeagal complex; median posterior margin recurved. *Tergite eight*: elongate, narrower than tergite seven, if viewed from above is about twice as wide in anterior half as in posterior half (widest at point of lateral angulations), lateral margins narrowing posteriorly in posterior half, most of apex not visible from above, and strongly deflexed ventrally and in dried pinned specimens enveloping the MPP of V7 from behind (in freshly killed specimens preserved in ethanol these structures do not approach closely); anterior margin of tergite eight bifurcate into two elongate slender apically rounded projections; angulate margins at point where tergite eight narrows posteriorly may be slightly asymmetrical; narrowed apex of tergite eight may be entire or gently emarginate; ventral surface in posterior (narrowed) half lacking median longitudinal grooves, lateral ridges, depressed troughs, flanges or any asymmetrical projections; ventral surface in anterior half with a median longitudinal groove separating two thickened surfaces in *P. wittmeri*; ventral surface in anterior half lacking such developments, and lacking longitudinal ridges, flanges lateral ridges in *P. guigliae*, *P. kinabalua* and *P. stylifer*.

Aedeagal sheath (not extracted in *P. stylifer, P. hamulata*; significance of this structure not realised until Ballantyne, 1987a, b); about twice as long as wide, much narrower in anterior half; anterior half of sheath sternite symmetrical and very narrow, narrowed abruptly at about the mid point of its length, or slightly less; posterior half of sheath symmetrical, sheath sternite and tergite equally wide; tergite lacks swollen lateral protuberances but lateral margins of tergite may be visible very narrowly at sides of posterior half of V 9 (seen only in dried pinned specimens of *P. kinabalua*); median anterior margin of tergite 9 evenly emarginate, lateral margins anteriorly prolonged at the sides of the sheath sternite and joining the narrowed anterior prolongation of this ventrite in two species, and visible from beneath; posterior margin of sternite narrowing gently, level with or projecting slightly posteriorly beyond tergite.

Aedeagus Length/Width 2.5 – 4.0; LL and ML symmetrical, basal piece and dorsal base of LL asymmetrical; basal piece in two narrow halves, not sitting symmetrically above ML, left half slightly more ventral than right; ML tapering to a rounded acute apex, shorter than LL, sometimes just longer than half the length of the aedeagus; LL visible to either side of ML when viewed from above or below, separate along almost all their length dorsally, inner dorsal margins always divergent at least in basal fourth, and often closely approximate in apical half; apical half of LL subequal in width, apices no wider than preceding half, and sometimes out-turned; LL lacking leaf like lobes on their outer (lateral) margins, bearing hairs along at least half of their outer margin.

Female macropterous, and assumed capable of flight; similar to male differing in these aspects: pronotum about twice as wide as long, with lateral margins diverging posteriorly, but median anterior margin often projecting beyond rounded obtuse anterolateral corner; head of winged female form, smaller than that of male; abdomen with eight visible ventrites. *Light organ* occupying the whole of V 6 only; V7 with accessory external developments (transverse ridge, lateral mounds) in two of five species; tergite seven with anteromedian mound in one of five species; V7 usually quite deeply emarginate across posterior margin, V8 narrower than V7, sides tapering posteriorly and median posterior margin slightly indented. *Female genitalia* (known from two species) with styli longer than wide, parallel sided and apically rounded, and visible beyond end of V8; coxites not well differentiated, partly sclerotised and lateral margins converging posteriorly; valvifers elongate, slender, well sclerotised and rod like, extending in front of coxites for about $^{7}/_{10}$ of the total length of the complex.

Larva unknown.

Remarks. - Wittmer (1939) misinterpreted the abdominal segmentation and recorded seven ventrites. His third last segment, a light organ, is actually V 6, and he interpreted the light organ on V 7 as a separate segment surrounded at the sides and behind by the last abdominal sternite. This is one segment, V 7, only. Ballantyne (1968) briefly redescribed *Luciola* (*Pygoluciola*) from four species, two of which were known from three specimens only. There is inconsistency between that description and this because of the redefinition of abdominal segmentation by Ballantyne (1987a,b) (tergite seven there becomes tergite eight here; visible abdominal sternites are referred to as ventrites and given their actual segmentation number), and certain other characters which are redefined here (e.g. interstitial lines), and that redescription should be replaced by the current one. Ballantyne (1968) did not distinguish the curved legs on the holotype of *P. stylifer*, and Ballantyne & Lambkin (2001), without a re-examination, erroneously keyed *P. stylifer* using the character of straight tibiae. This is corrected below.

List of species of Pygoluciola *Wittmer*

1. *Pygoluciola guigliae* (Ballantyne, 1968)
2. *Pygoluciola hamulata* (Olivier, 1885)
3. *Pygoluciola kinabalua* (Ballantyne & Lambkin, 2001)
4. *Pygoluciola stylifer* Wittmer, 1939
5. *Pygoluciola wittmeri* (Ballantyne, 1968)

Key to species of *Pygoluciola* using males

1. All tibiae curved; lateral margins of elytra tapering posteriorly 2
– No tibiae curved; lateral margins of elytra usually sub-parallel sided 3
2. Apex of median posterior projection of tergite 8 no wider than rest and rounded; pronotum with large median darker area; lateral margins of pronotum slightly sinuate .... *P. guigliae*
– Apex of median posterior projection of tergite 8 wider than rest and medianly emarginate; lateral margins of pronotum not slightly sinuate .... *P. stylifer*
3. Median posterior projection of abdominal ventrite 7 bifurcate at apex 4
– Median posterior projection of abdominal ventrite 7 not bifurcate at apex .... *P. hamulata*
4. Apex of median posterior projection of abdominal ventrite 7 deeply emarginate, laterally ensheathing the downturned apex of tergite 8 and projecting laterally beside it .... *P. wittmeri*
– Apex of median posterior projection of abdominal ventrite 7 shallowly emarginate, not laterally ensheathing the downturned apex of tergite 8 and not projecting beside it ..... *P. kinabalua*

Key to species of *Pygoluciola* using females

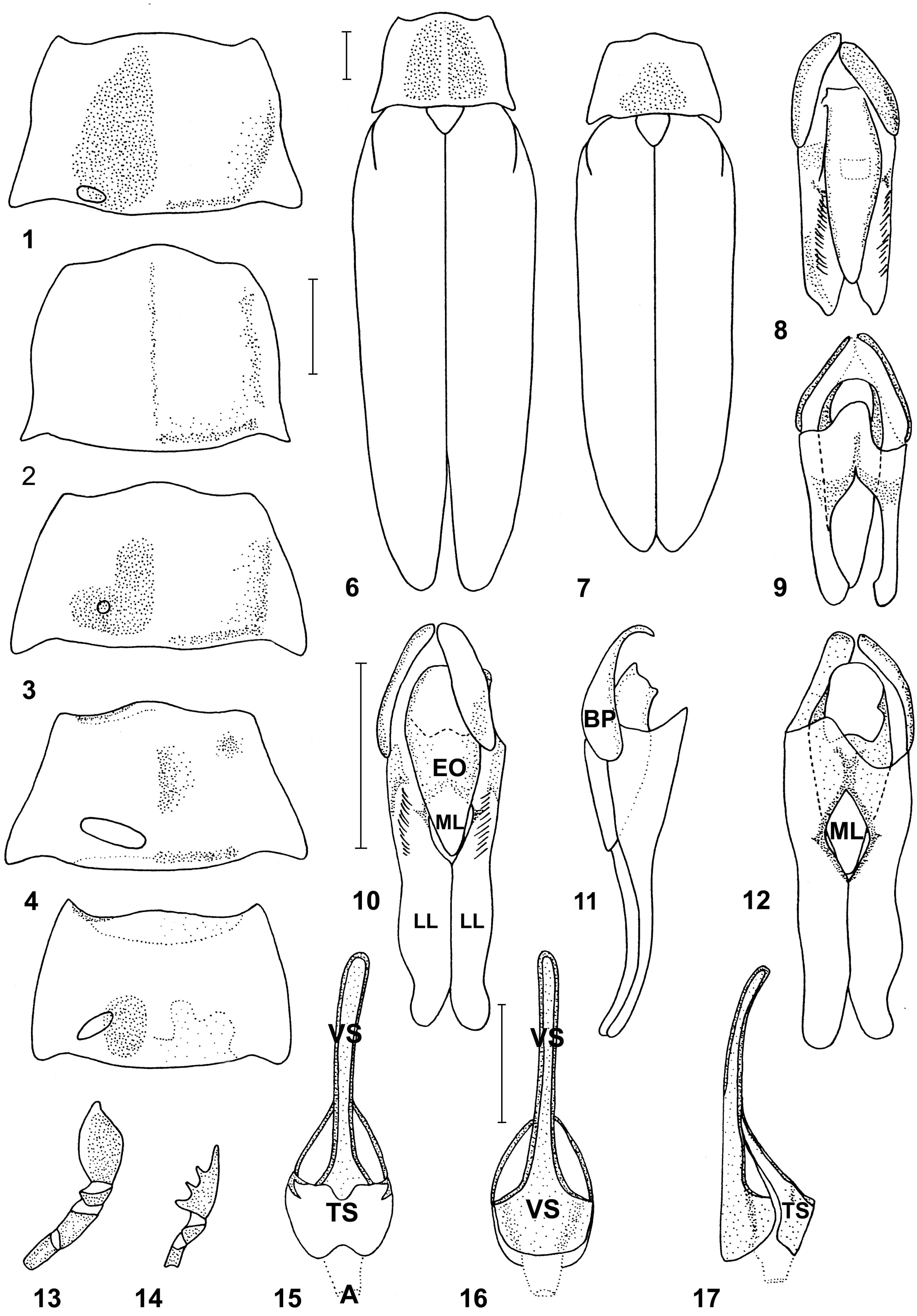
1. All tibiae curved .... *P. guigliae*
– No tibiae curved 2
2. Posterior margin of Ventrite 7 deeply emarginate; bearing a small ridge anterior to median area of deepest emargination; ventrite 8 with anteromedian prolongation not any more sclerotised than remainder of ventrite 8; tergite 7 with anteromedian area rounded and elevated, lateral areas not flattened .... *P. kinabalua*
– Posterior margin of Ventrite 7 shallowly emarginate, lacking an anteromedian ridge; ventrite 8 with anteromedian prolongation well sclerotised and visibly separated from remainder of ventrite 7; tergite 7 lacking a rounded and elevated anteromedian area, with lateral areas flattened .... *P. wittmeri*

Pygoluciola guigliae (Ballantyne)

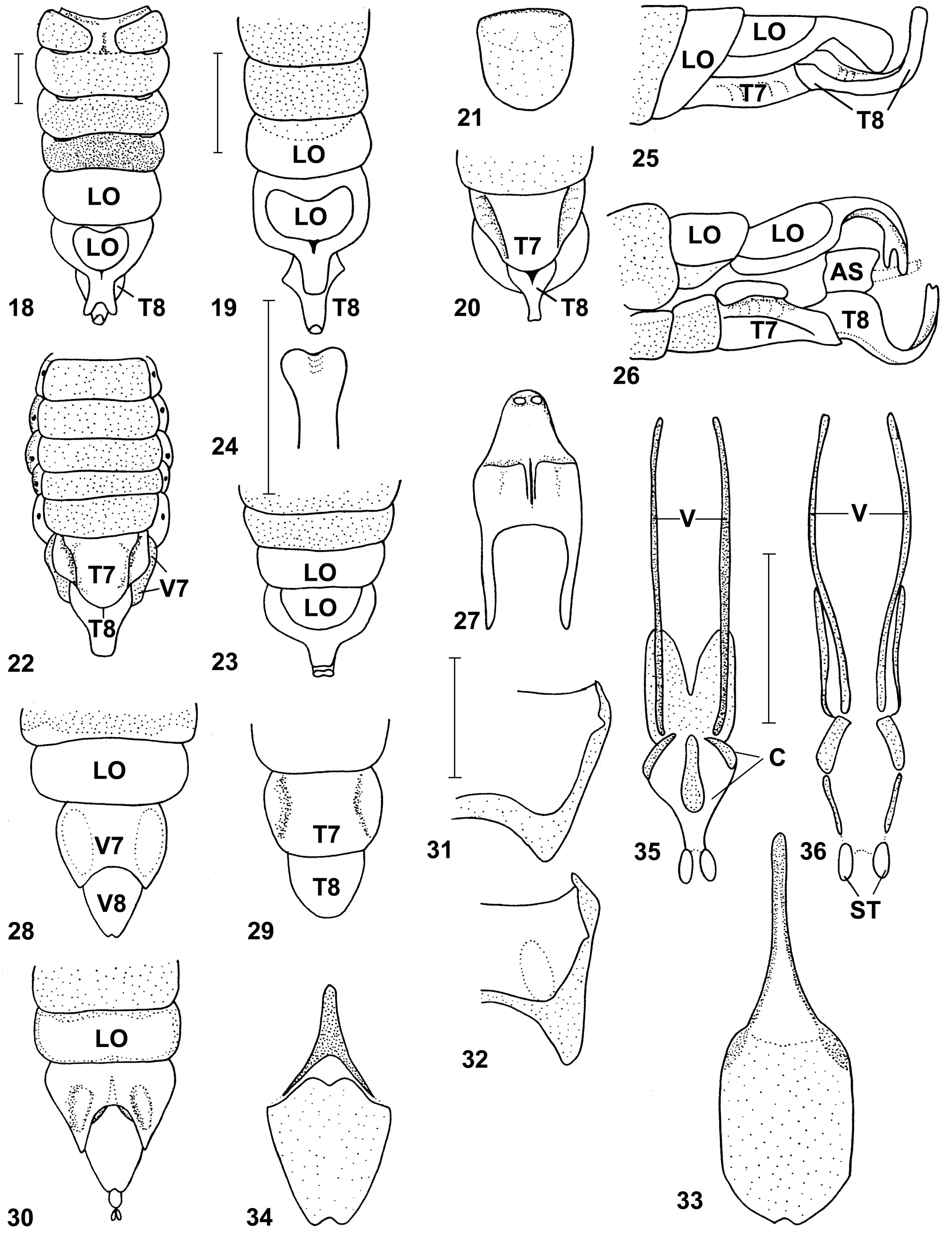
(Figs. 1, 6, 13-17, 19, 21, 27, 30, 32, 34, 35, 38-40)

Luciola (*Pygoluciola*) *guigliae* Ballantyne, 1968: 120 [*Holotype male* British North Borneo, Bundu Tukan (BBM)].

Diagnosis. – Both sexes with strongly curved tibiae on all legs; males elongate, slender, 3.2 times as long as wide, with elytra tapering towards their apices, most similar to *P. stylifer*, distinguished by the darker pronotal colour, the forwardly



Figs. 1-17. Features of male *Pygoluciola*. 1, 6, 13-17: *P. guigliae*; 2: 'Mt Missim' male; 3, 7: *P. kinabalua* holotype male; 4, 10-12: *P. stylifer* holotype male; 5, 8-9: *P. wittmeri*. 1-5: dorsal, male pronota (left side shows colour pattern, right side sculpturing; solid line indicates extent of irregular tubercles, dotted lines retraction of fat body): 6,7: dorsal , whole body; aedeagi (8; 10 ventral; 9, 12 dorsal; 11, left lateral); 13: maxillary palp, ventral surface; 14: labial palp, ventral surface; 15-17: aedeagal sheath, dorsal, ventral, and lateral. These figures share scale lines: 1-5; 6-7; 8-14; 15-17. Figure legend: A, anus; BP, basal piece; EO, ejaculatory orifice; LL, lateral lobe; ML, median lobe; TS, tergite aedeagal sheath; VS, ventrite aedeagal sheath.



Figs. 18-36. Features of female *Pygoluciola*: Figs. 18-27; Features of female *Pygoluciola*: Figs. 28-36. 18, 22, 26, 27-29, 31, 33, 36 (*P. wittmeri*); 19, 21, 27, 30, 32, 34, 35 (*P. guigliae*); 20, 23-25 (*P. stylifer* holotype male). 18, 19, 23, 28, 30, ventral terminal abdominal segments [29 stippled outline in V 7 = fat body, in 30 = lateral elevations of V7]; 20, 22, 29, dorsal, terminal abdominal segments; 21, vertical face of apex of MPP of ventrite 7, dorsal face uppermost; 24, posterior face apex of tergite 8; 25, 26, lateral terminal abdominal segments, ventrites uppermost [26 anus, stippled, protrudes through MPP of V7]; 27, dorsal face abdominal tergite 8; 31, 32, dorsal surface abdominal ventrite 7 [right side only; stippling = dorsally reflexed cuticle; in 32 dotted oval = position of elevation]; 33, 34, ventral face, abdominal ventrite 8; 35, 36, ventral female genitalia. These figures share scale lines: 18, 20, 22, 23, 28-30; 19, 25-27; 31-34; 35-36.
Figure legend: AS, aedeagal sheath complex; C, coxite; LO light organ; ST, stylus; T7, T8 tergite 7, 8; V, valvifer, female genitalia.

projecting anterolateral pronotal angles, the slight narrowing in the lateral pronotal margin, and the shape of the apex of abdominal tergite 8; female with posterior margin of V 7 deeply and broadly emarginate, with lateral projections apically acute and longer than broad, and smoothly raised elevations present in lateral areas; tergite 8 lacking any median mound; anterior prolongation of V9 not as long as posterior (wider) portion of this ventrite, well sclerotised, and membranous separation from the rest of the ventrite in posterior area only.

***Material Examined.* –** Three males, one female, Malaysia, Sabah: 5.48°N 116.26°E, Mahua, 1045 m, coll. Mahadimenakbar bin Mohamed Dawood, 19 Mar.2004, 20.45 – 22.00 hrs. (BORN). Specimens of both *P. guigliae* and *P. wittmeri* were collected "at night by a river where some individuals formed a group of about 10, perching and flashing on branches of trees. Some were collected while flying. They are quite common here" (pers. comm. Collector). That there was more than one species was not recognised at the site, and it is not known whether one or both species aggregated in the trees or whether one or both were taken in flight. No observations on light production patterns were made.

***Redescription.* –** *Male*. Body 11.1 – 11.9 mm long; 3.2 times as long as wide (Fig. 6). Pronotum yellow, semitransparent, marked extensively in dark brown in median area (Fig. 1); pubescence pale; underlying fat body clustered closely under cuticle in all areas except around margin; MS, MN yellow; elytra pale brown semitransparent; both suture and lateral margins are semitransparent until apex, which is very narrowly darker brown (when elytron is viewed separate to underlying hind wing); elytral punctures very dark brown, interstitial lines pale brown and margined by a single row on each side of dark punctures; head between eyes, antennae and palpi dark brown except for pale under half of FS 4 – 9 and inner half of apical segment of maxillary palpi; labrum brown, semitransparent; ventral surface of pro and mesothorax light brown, of metathorax dark brown, darker in median area; legs 1, 2, dark brown except for pale brown coxae and trochanters and ventral surface of basal $^1/_6$ of femora; legs 3 dark brown except for pale trochanters and narrow basal area of femora; basal abdominal ventrites dark brown, V 6 pale semitransparent [underlying fat body shows through cuticle] along anterior margin where pale yellow light organ is broadly and shallowly emarginate; V7 pale semitransparent in areas not occupied by light organ, with underlying fat body visible especially in anterior areas, and a small, short, very dark median line just behind posterior margin of light organ; MPP pale, semitransparent; dorsal surface of tergites 2 – 6 brown, dorsally reflexed margins of ventrites 2-5 brown; tergite 7 mottled brown in median (raised area) mainly pale in lateral areas with a small median brown spot, posterior margin pale semitransparent; tergite 8 pale semitransparent with a slightly darker median line; dorsally reflexed margins of V6, V7 pale.

Pronotum (Fig. 1) 2.8 – 3.0 mm (2) wide; 1.8 (2) - 1.9 mm long; width/length 1.6; pronotum $^1/_6$ as long as whole body; median anterior margin not indented, projecting only slightly

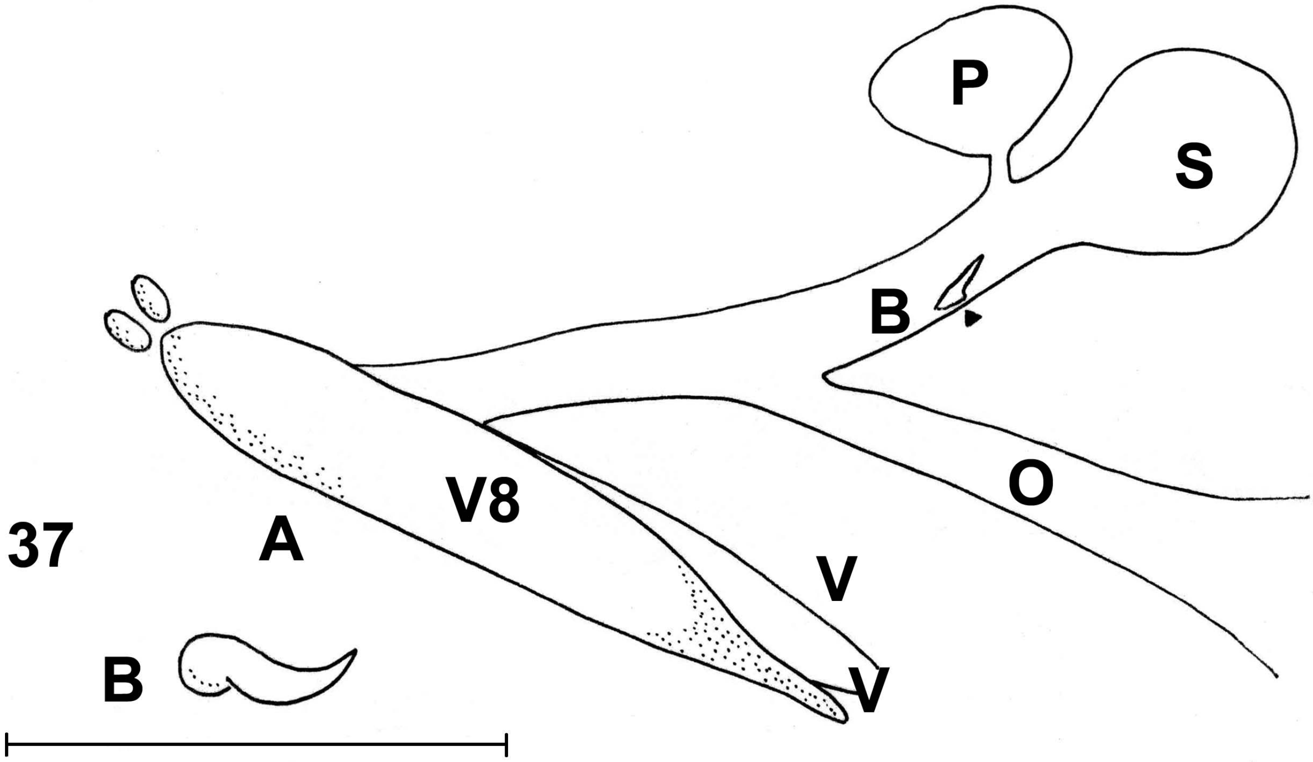


Fig. 37. Female reproductive system. A, diagrammatic representation of ventrite 8, part of female genitalia, bursa and spermatheca and gland [bursa is shown to side of spermatheca] Figure not to scale, dimensions represented relatively; B, internal aspect, hook in bursa; scale line is 1 mm. Figure legend: B, bursa (arrow indicates hook); O, median oviduct; S, spermatheca; P, gland; V8, ventrite 8; V, valvifers female genitalia.

beyond anterolateral corners and separated from them by rounded shallow emarginations; anterolateral corners angulate, (anterior and lateral margins subtend approximately a right angle between them); lateral margins divergent posteriorly with a slight narrowing at posterior half, then diverging evenly until posterolateral corner; posterolateral corners angulate, acute, not projecting posteriorly as far as median posterior margin, which is entire, and separated from it by shallow emarginations. *Elytron* (Fig. 6) 9.2 - 10 mm long; lateral margins diverge in anterior $^{2}/_{9}$ and converge in posterior $^{7}/_{9}$; maximum width across elytra, measured in anterior third, 4 mm; elytra 2.5- 3.0 mm wide (at $^{2}/_{9}$ of their length from tip).

Head gently depressed between eyes; GHW 1.7 - 1.8mm; SIW 0.5 - 0.6 mm; ASD = ASW or just slightly >; apical segments of labial palpi (Figs. 13, 14) with 3 teeth on each (1); 4 on R and 3 on L (1), 4 on each (1); antennal length almost 3 X GHW, pedicel slightly narrowed near base; with FS 1-6 subequal in length, about 4 times as long as wide, and FS 6 - 9 subequal in length slightly narrower than 1 - 6.

Legs with all tibiae curved, stouter at apices than at base (maximum width of apex/maximum width at base of hind tibiae =1.2 - 1.7) and all femora stout, not curved (maximum width hind femora 0.5 – 0.6 mm).

Abdomen (Figs. 19, 21) with V2 lacking faint median 'carina' between bases of coxae 3. *Light organs*: entire in V6 with a broad emargination along anterior margin; entire in V7, with a shallow anteromedian emargination, not posteromedially emarginated. *Ventrite 7*: MPP 1.2 X longer than wide, not expanded at its tip when viewed from beneath; when viewed from side, tip expanded in posterior $^{2}/_{3}$, such that the ventral margin of the MPP is continuous with the more anterior margin of V7, there being no change of angle, and the dorsal surface expands such that the posterior half of the MPP is twice as deep as the anterior half; posterior margin of MPP not emarginated dorsally (Fig. 21), rounded ventrally, with ventral half of posterior half clothed in short fine hairs and dorsal half slightly depressed, paler than rest; dorsal surface of anterior part of MPP with narrow short longitudinal depression corresponding to external dark marking; apex of tergite 8 (Fig. 27) narrows gradually towards tip, rounded, entire.

Aedeagus in the aedeagal sheath (Figs. 15 – 17) protrudes behind the posterior margin of the MPP of V7 in the median line, lateral lobes splay to each side of the downturned tip of tergite 8. Aedeagus with ML much shorter than LL, which are widely divergent along their dorsal, inner margins in basal 2/7 of their length and closely approximate along their apical 4/7 with apices touching then diverging to each side; LL in 'wet' preserved specimens white, plump (about as high as wide), becoming dorsoventrally flattened and darker after immersion in 20% KOH for about 20 minutes.

Description. – *Female.* 12.0 mm long; body 4.3 mm wide across widest point of closed elytra; macropterous, and observed in flight; dorsal colouration as for male except for paler brown markings on pronotum (extent is confused by retraction of underlying fat body in the coloured areas); ventral colouration as for male except for all legs which have very dark brown apices of femora, dark brown tibiae and tarsi, and pale golden brown coxae, trochanters and basal $^{2}/_{3}$ of femora; basal abdominal ventrites moderately dark brown; pale light organ in V6, and V7 and 8 shiny light brown; abdominal tergites brown except for golden brown tergite 8.

Pronotum 1.8 mm long; 3.3 mm wide; pronotum $^{1}/_{7}$ as long as whole body; median anterior margin not indented, not projecting either beyond or behind anterolateral corners and separated from them by rounded shallow emarginations; anterolateral corners angulate obtuse; lateral margins divergent posteriorly with a slight narrowing at posterior half, then diverging evenly until posterolateral corner; posterolateral corners angulate, acute, not projecting posteriorly as far as median posterior margin, which is entire, and separated from it by shallow emarginations.

Elytra 10.2 mm long; elytral lateral margins divergent in anterior $^{2}/_{7}$, subparallel in next $^{1}/_{7}$, then convergent in apical $^{4}/_{7}$; maximum width across elytra 4.3 mm (measured at $^{3}/_{10}$ their length from front); maximum width across elytra 3.2 mm (measured at $^{2}/_{10}$ their length in front of apices).

Head completely concealed beneath pronotum at rest; GHW 1.8 mm, SIW 0.6mm; ASD subequal to ASW; head barely depressed between eyes; mouthparts well developed, functional; apical segments of maxillary and labial palpi shaped as for male, except the right apical segment of the labial palpi has 4 elongate slender evenly spaced projections on the longer inner margin while the left palp has 4 with the middle two fused at their bases.

Legs with all tibiae curved, stouter at apices than at base (maximum width of apex/maximum width at base of hind tibiae = 1.3) and all femora moderately stout, not curved (maximum width hind femora 0.5 mm).

Abdomen (Figs. 30, 32, 34) with posterior margin of V7 evenly and quite deeply emarginate, posterolateral corners apically acute and longer than wide, projecting posteriorly beyond the median posterior margin of V7 by more than their width; ventral surface with posterolateral elongate rounded protuberances, but lacking any troughs, or ridges; anterior half of V8 narrowed, and linearly prolonged beneath V7, prolonged portion shorter than wider posterior portion of V8, all of anterior prolongation well sclerotised; dorsal surface of tergite 7 evenly rounded.

Genitalia similar to *P. wittmeri* (Figs. 35, 36), with some sclerotisation between coxites, and valvifers long, slender and not diverging in anterior half.

Reproductive system (Fig. 37). The junction of the 'vagina', the median oviduct, and the duct leading to the bursa and spermatheca occurs just above the anterior prolongation of V8 and the anterior tips of the valvifers of the female genital complex (2.5 mm from the posterior margin of V8). Muscles run from the anterior narrow portion of abdominal V8 and attach onto the anterior portions of the valvifers. The presumed spermatheca is about 1/10 the size of the spermathecal gland, both appear quite muscular and neither has any obvious internal cuticularisation. Paired anteriorly directed hooks, attached to the sides of the median duct [the bursa] at their bases only, occur just in front of the junction of the median oviduct to the vagina, and a half empty presumed spermatheca was found here. These hooks are above the narrowed anterior prolongation of V8.

Remarks. – Ballantyne (1968) describe the pronotal colour on a pinned specimen as red-brown and the elytral with an apical brown area, and the single (pinned) female as lacking curvature on the anterior tibiae.

Pygoluciola hamulata (Olivier)

(Figs. 38-40)

Luciola hamulata Olivier, 1885: 367; 1902: 80; 1907: 52; 1913: 59 [*Holotype* male Borneo, Sarawak (CMG)].
Luciola (*Luciola*) *hamulata* – McDermott, 1966: 105.
Luciola (*Pygoluciola*) *hamulata* – Ballantyne, 1968: 121

Diagnosis. – Most similar to *P. stylifer*, distinguished by the non curved legs and the apex of abdominal tergite 8 being entire (that of *stylifer* is emarginate).

Pygoluciola kinabalua (Ballantyne)

(Figs. 3, 7, 38-40)

Luciola (Pygoluciola) kinabalua Ballantyne & Lambkin, 2001: 371 [Holotype male Malaysia, Sabah: Mt Kinabalu (BMNH)].

Diagnosis. – Males elongate slender (Figs. 3, 7), about three times as long as wide, with elytra subparallel sided; one of two species of *Pygoluciola* with the apex of the MPP of V7 emarginate, gently so in this species; distinguished from *P. wittmeri*, which has a deeply emarginate apex; female with posterior margin of V7 deeply and broadly emarginate, with a small transverse ridge just anterior to this emargination, lateral projections moderately broad and apically rounded; tergite 7 with strongly sclerotised median 'mound'; lateral margins of anterior prolongation of V8 not well sclerotised nor well defined.

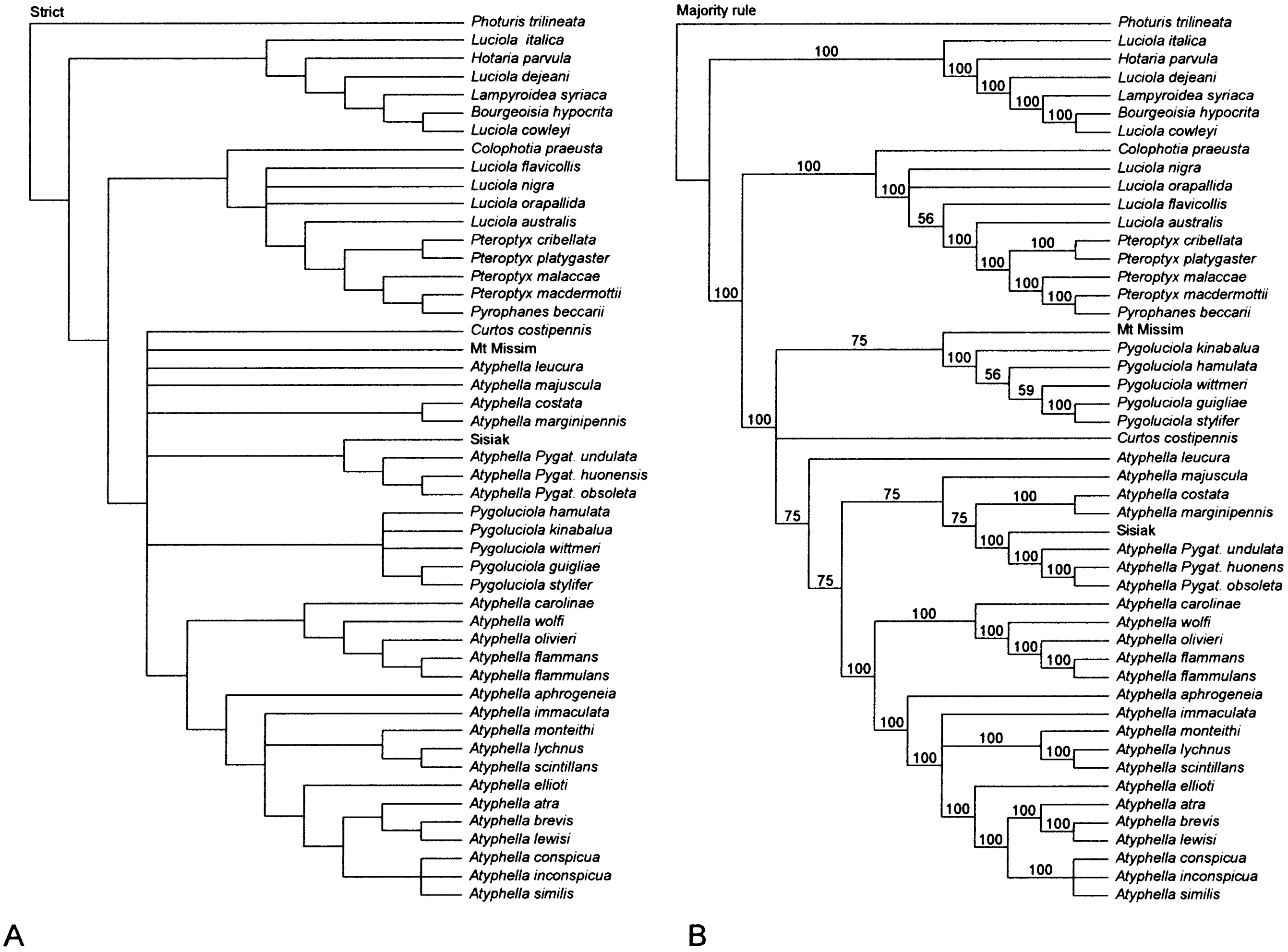


Figure 38. (A). The strict consensus of the 2992 MPT for 49 taxa of the Luciolinae found with phylogenetic analysis of 115 characters, excluding 10 colour and mimicry characters. (B). The majority rule consensus of the 2992 MPT for the Luciolinae, showing above the branch the percentage of MPT retaining that node. 153 of the MPT were compatible with the majority rule consensus.

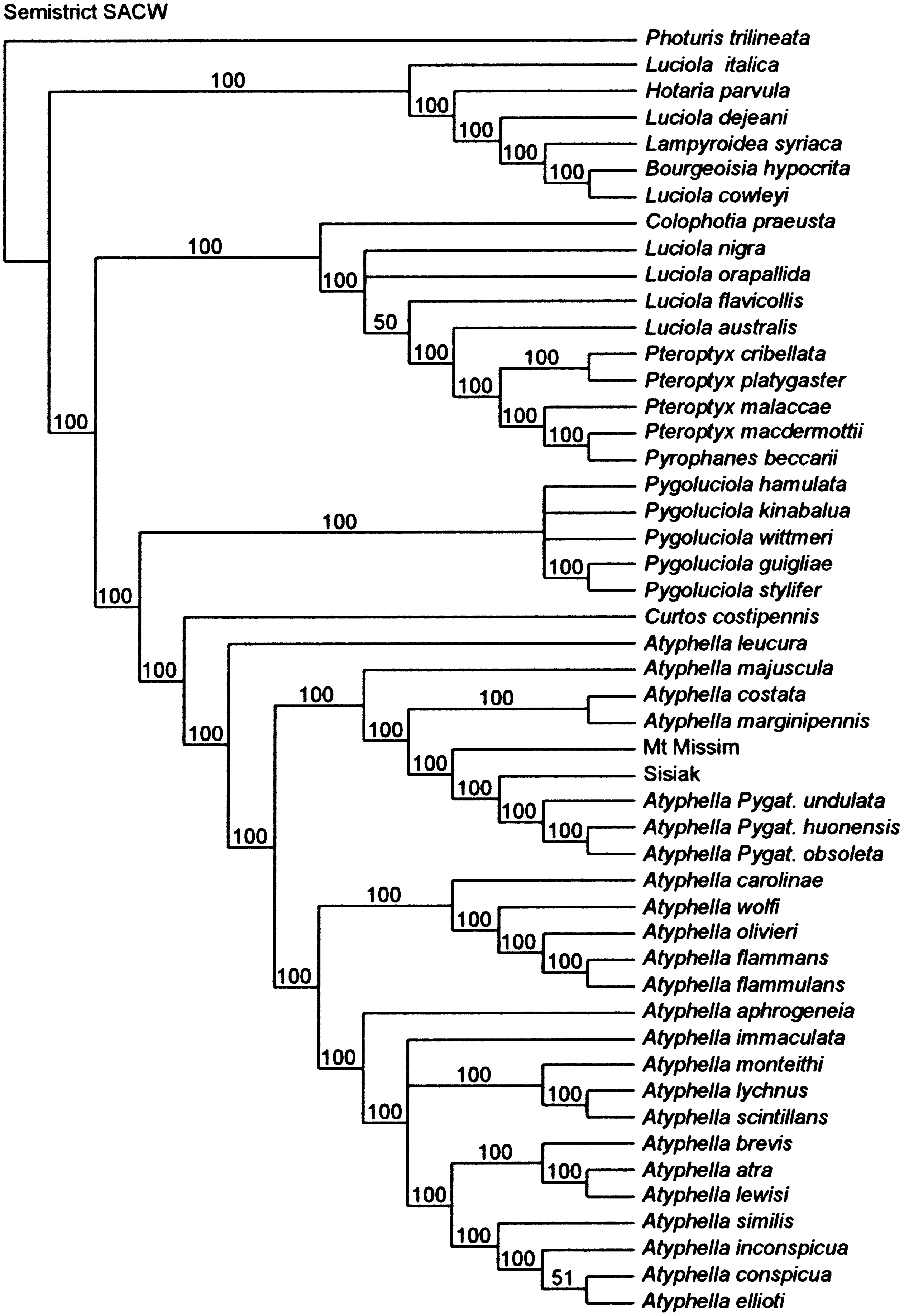


Figure 39. Semistrict consensus of 195 successively weighted trees. Percentage of successively weighted trees with this resolution shown above the branch. None of the MPT was compatible with the semistrict consensus successively weighted trees.

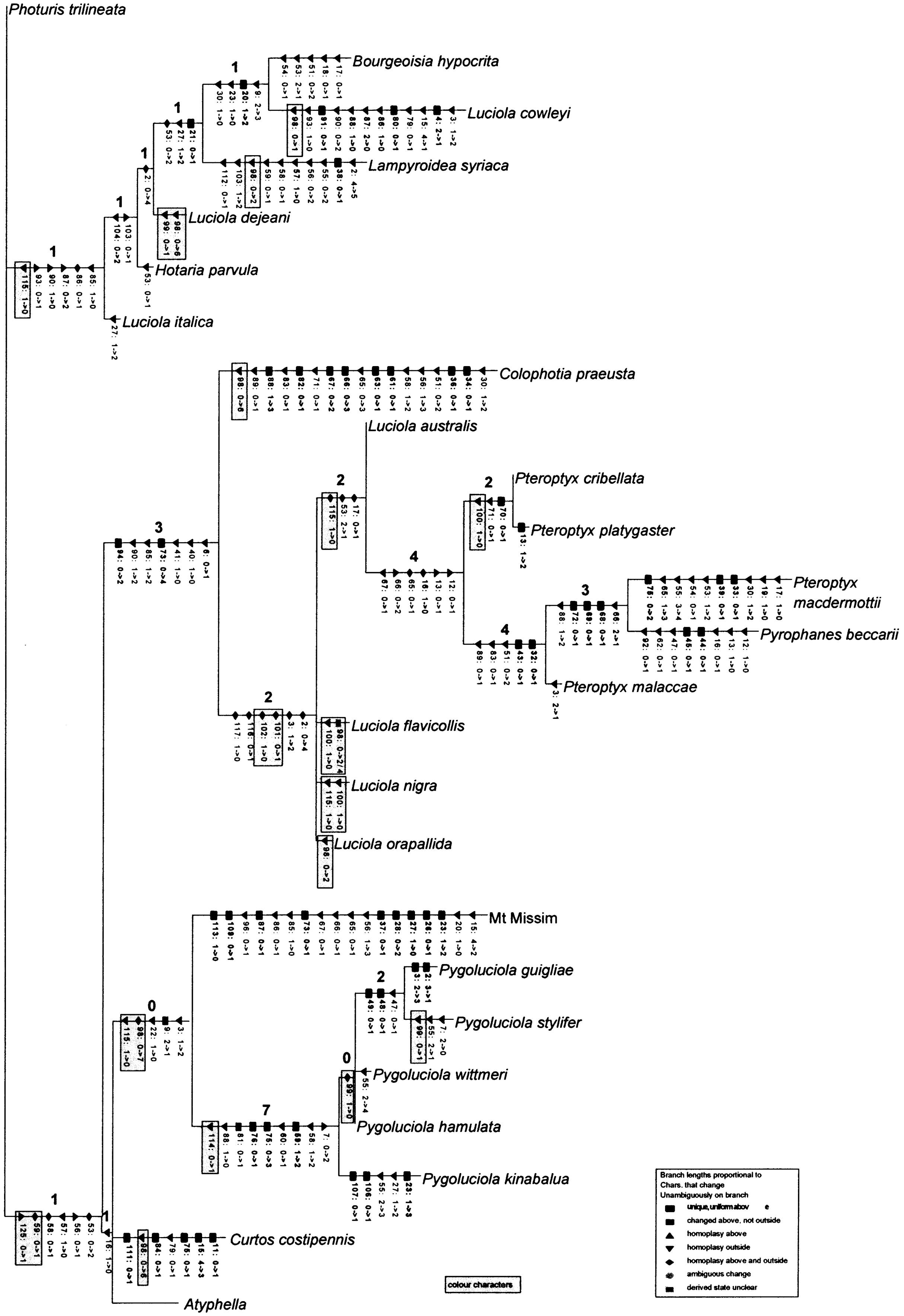


Figure 40. Preferred MPT from 153 filtered MPT compatible with the majority rule consensus of the 2992 MPT, Part 1, without *Atyphella* clade. Unambiguous character and state changes were mapped using MacClade. Colour and mimicry characters, not used in the phylogenetic analysis, are enclosed in boxes. Bremer support values shown above nodes.

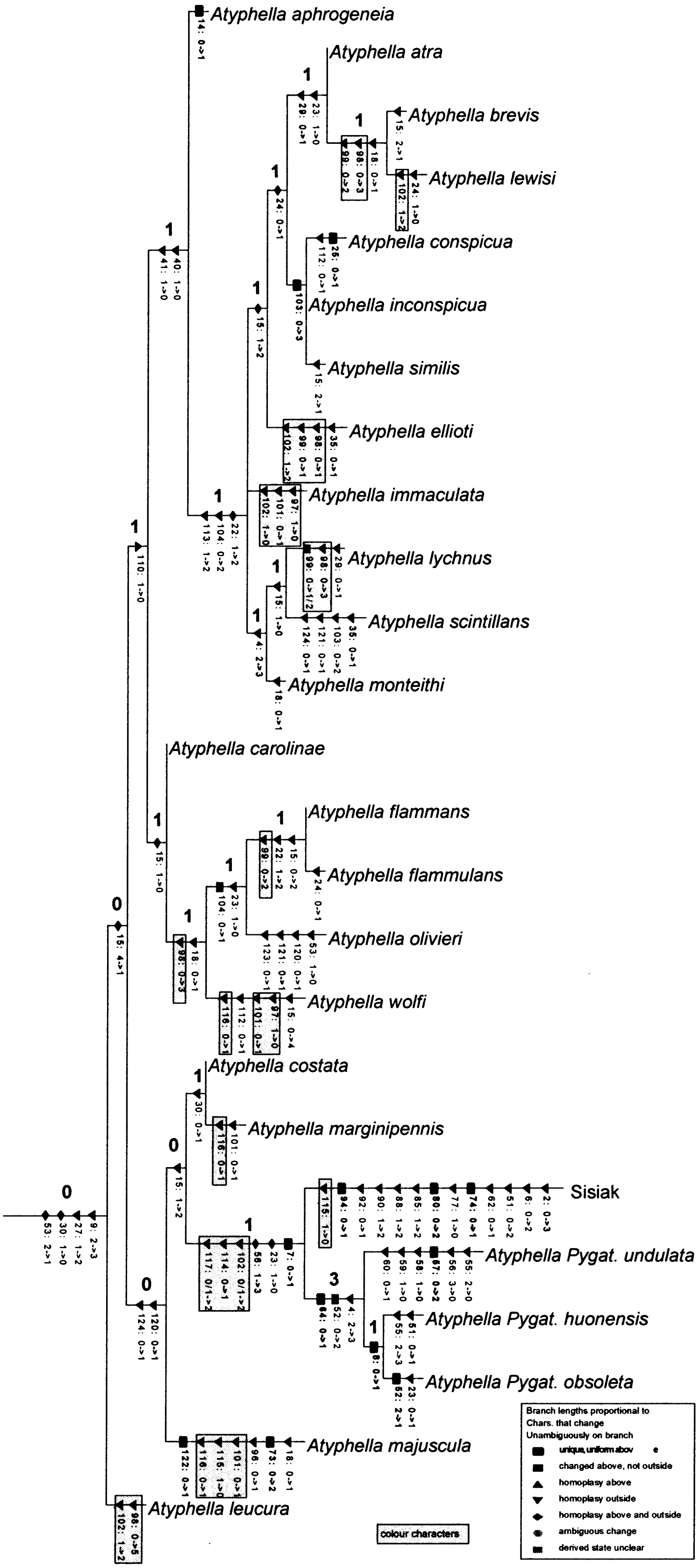


Figure 41. Preferred MPT from 153 filtered MPT compatible with the majority rule consensus of the 2992 MPT, Part 2, *Atyphella* clade. Unambiguous character and state changes were mapped using MacClade. Colour and mimicry characters, not used in the phylogenetic analysis, are enclosed in boxes. Bremer support values shown above nodes.

***Pygoluciola stylifer* Wittmer**

(Figs. 4, 10 – 12, 20, 23 – 25, 38-40)

Pygoluciola stylifer Wittmer, 1939: 22 [Holotype male Borneo (RMNH). Labelled 1. hand written *Pygoluciola stylifer* Wittm.; printed det. W. Wittmer. 2. orange typed 'Holotype'. 3. hand written 'TYPUS'. 4. Printed 'H. C. Siebers/M. O. Borneo Exp./ 120 M. bij L. Petak/1925 viii – ix.'].

Luciola (Pygoluciola) stylifer – McDermott, 1966: 115; Ballantyne, 1968:119.

Diagnosis. – Most similar to *P. hamulata*, distinguished by the curved tibiae of all legs, and the emarginate apex of abdominal tergite 8.

Redescription of Holotype Male. – Elongate slender, three times as long as wide; elytra tapering towards their apices. 11.2 mm long. Pronotum light golden brown with no apparent darker markings on the dorsal surface except for very narrow dark brown markings along anterior margin to either side of mid line; fat body is retracted along anterior and posterior margins and these areas appear paler brown; MS, MN paler brown than pronotum; elytra light golden brown, slightly darker than the pronotum, and apical 1/6 a little darker than rest; elytral punctures dark brown; head and maxillary palpi very dark brown, labial palpi mid brown; antennae dark brown, left antenna (R is incomplete) with dorsal surface of FS 6 – 9 paler brown than preceding segments, and very pale whitish yellow beneath; ventral surface of pro and meso thorax light brown; legs 1 with coxae and femora light brown, tibiae darker brown, tarsi very dark brown; ventral surface of metathorax dark brown ; legs 2 and 3 yellowish except for dark brown tibiae and tarsi 2, and tarsi 3; basal abdominal ventrites dark brown, V6 creamy yellow (light organ), V7 yellowish (light organ is torn from surface of V7); tergites 7 and 8 pale.

Pronotum (Fig. 4) 3.1 mm wide; 1.8 mm long; width/length = 1.7; pronotum $^1/_5$ as long as whole body length; lateral margins smoothly divergent along their length; median anterior margin rounded, not emarginate, projecting a little beyond anterolateral corners, which are narrowly rounded and obtuse, but do not project anteriorly; posterolateral corners rounded, acute (60 - 70°), not projecting beyond posterior margin; dorsal surface of pronotum mainly fairly smooth and flat except for slight depressions in median and anterolateral areas and narrowly across the posterior margin, and with irregular low elevations in posteromedian areas.

Elytra 9.4 mm long, apparently tapering toward their apices; left elytron lateral margin divergent in anterior $^1/_4$, subparallel sided in next $^1/_4$, and convergent in posterior $^1/_2$; right elytron similar but more strongly convergent in posterior $^1/_2$ (this may be a post-mortem effect).

Head gently depressed between eyes; GHW 1.9 mm; SIW 0.5 mm; GHW/SIW 3.8; ASD subequal to ASW; apical segments of both labial palpi with three elongate projections on their inner surface; antennae slightly longer than twice GHW; FS 1-5 subequal in length (about three times as long as wide and slightly shorter than scape); FS 6 – 9 more slender than preceding FS.

Legs with all tibiae curved.

Abdomen (Figs. 20, 23 – 25) MPP of V7 expanded at its tip as described for *P. guigliae*; tergite 8 narrowed before its apex which is expanded with posterior margin shallowly emarginate.

Aedeagus (Figs. 10 – 12) with ML about half as long as LL; inner dorsal margins of LL strongly divergent in basal half, converging level with tip of ML and closely approximate until apical 1/6, where they diverge slightly.

Pygoluciola wittmeri **(Ballantyne)**

(Figs. 5, 8-9, 18, 22, 26-29, 31, 33, 36, 38-40)

Luciola (*Pygoluciola*) *wittmeri* Ballantyne, 1968: 121; Ballantyne & Lambkin, 2001: 371 [Holotype male, 'British North Borneo' (BBM)].

Diagnosis. – Male distinguished from *P. kinabalua* see above; female with posterior margin of V7 shallowly emarginate and posterolateral corners apically rounded and moderately broad; ventral surface of V7, 8 smooth; anterior prolongation of V8 longer than posterior (wider) portion, and lateral margins well sclerotised in posterior half.

Material examined. – One male, two females, Malaysia, Sabah, 5.48°N 116.26°E, Mahua, by the Mahua River, 1045 m, coll. Mahadimenakbar bin Mohamed Dawood, 19 Mar.2004, between 2045 – 2200 hrs. Malaysian time (Borneensis).

Redescription. – *Male*. 10.1 mm long. Pronotum pale creamy yellow and semitransparent, marked faintly in pale brown in posteromedian areas; pubescence pale; underlying fat body clustered closely under cuticle in all areas except two anteromedian areas and narrowly across most of the anterior margin; MS, MN pale creamy yellow, fat body dense under MN and restricted to posterior half of MS; elytra pale brown semitransparent; both suture and lateral margins are semitransparent until apex, which is very narrowly darker brown (when elytron is viewed separate to underlying hind wing); elytral punctures very dark brown, interstitial lines pale brown and margined by a single row on each side of dark punctures; head between eyes, antennae and palpi dark brown except for pale under half of FS 7 – 9 and inner half of apical segment of maxillary palpi; labrum brown, semitransparent; ventral surface of pro and mesothorax light brown, of metathorax very dark brown in median area with metepisterna and metepimera paler brown; legs 1, 2 with pale creamy yellow coxae, trochanters and femora, except for brown inner margins of coxae and trochanters, and brown apical $^2/_3$ of femora; tibiae and tarsi of all legs dark brown; legs 3 with ventral surface of coxae very dark brown except for narrow pale basolateral areas; trochanters and femora pale yellow; tibiae very light brown; tarsi dark brown, not as dark as tarsi 1, 2; V2 light brown with dusky cream lateral areas;

V3 with median brown area more extensive than that of 2, and small anterolateral paler areas which are outlined posteriorly in dark brown; V4 moderately brown except for paler anterolateral areas; V5 similar, more darkly marked; V6 wholly occupied with light organ; V7 pale semitransparent in areas not occupied by light organ, with underlying fat body visible especially in posterolateral areas, and a small very dark median triangular mark just behind posterior margin of light organ; MPP pale, semitransparent, fat body clustered in anterior $^{2}/_{3}$; dorsal surface of tergites 2 – 6 brown, darkening progressively towards tip of abdomen; dorsally reflexed margins of ventrites pale; tergites 7 and 8 pale, 8 with a fine dark median line.

Pronotum (Fig. 5) 1.6 mm long, 2.8 mm wide, width/length = 2; $^{1}/_{7}$ as long as whole body; anterior margin rounded, slightly indented in median line, not projecting beyond anterolateral corners and separated from them by slight emarginations; anterolateral corners pointed, acute; lateral margins divergent posteriorly with no convergences; posterolateral corners rounded acute, not projecting beyond median posterior margin and separated from it by shallow emarginations; dorsal surface smooth, mainly flat; slight irregularities of the surface on either side of the median area in posterior half of dorsal surface.

Elytron 8.6 mm long; lateral margins subparallel for half their length, converging posteriorly in posterior $^{3}/_{8}$.

Head shallowly depressed between eyes; GHW 1.7 mm; SIW 0.35mm;ASD > ASW but not 2 X ASW; antennal length approximately twice GHW, with FS 1-6 subequal in length, about 4 times as long as wide, and FS 7-9 subequal in length but slightly shorter than 1 - 6; apical segment of labial palpi with 4 slender evenly spaced projections on both palpi.

Legs with no segments swollen or curved; width of hind femora at widest area 0.4 mm.

Abdomen (Figs. 18, 22, 26, 27) with V2 with faint median 'carina' between bases of coxae 3. *Light organs*: entire in V6; entire in V 7, with a shallow anteromedian emargination (not visible in this specimen unless abdomen is manipulated); not posteromedially emarginated. *Ventrite 7*: with small anterolateral depressions but no obvious signs of strong D-V muscle blocks; MPP much longer than wide, apically widely emarginate and curving dorsally where in the single male examined the emargination engulfs the end of the alimentary canal; lateral arms of emarginate apex apically rounded, about as wide at base as at apex; median posterior margin of tergite 7 rounded and projecting backwards over the anterior margin of tergite 8; apex of tergite 8 narrowly and shallowly medianly emarginate.

Aedeagus (Figs. 8, 9) in the aedeagal sheath protrudes behind the posterior margin of the LO in V7 in the median line and the rectum is engulfed by the emarginate MPP. Aedeagus with ML a little shorter than LL, which are widely divergent along their dorsal, inner margins and closely approximate but not contiguous at their apices.

Description. – *Female*. 11.5 - 12.0 mm long; body 5.5 mm wide across widest point of closed elytra; macropterous, and observed in flight; dorsal colouration as for male except for extensive median dark brown markings on pronotum; ventral colouration as for male except for brown anterior ventrites which are marked in posterolateral areas with small irregular pale brown markings, pale light organ in V6, and V7 and 8 shiny light brown; abdominal tergites light brown.

Pronotum 2.0 mm long; 4 mm wide; pronotum $^{1}/_{6}$ as long as total body; median anterior margin smoothly rounded, projecting a little beyond the rounded, obtuse anterolateral angles which are not produced; lateral margins diverge posteriorly; median sulcus prominent, dark, and depressed in its posterior half; dorsal surface narrowly depressed along posterior margin; pronotal surface smooth lacking any irregular tubercles; posterior area of median sulcus bearing a cluster of long white posteriorly directed hairs; a line of hairs extends along posterior margin [hairs only visible when specimen dried]; punctures small mainly separated by their width.

Elytra 10.5 - 11 mm long; elytra slightly convex sided lateral margins diverge along anterior half, subparallel for next $^{2}/_{8}$ then converge in posterior $^{3}/_{8}$.

Head completely concealed beneath pronotum at rest; GHW 2.0 mm, SIW 0.7mm; ASD < ASW; head barely depressed between eyes; mouthparts well developed, functional; apical segments of maxillary and labial palpi shaped as for male, except the apical segments of the labial palpi have three elongate slender projections on their longer inner margin in one female, and four on left and three on right in second female (the male has four on both).

Abdomen (Figs. 28, 29, 31, 33) with posterior margin of V7 evenly and shallowly emarginate, posterolateral corners apically acute and moderately broad, projecting posteriorly beyond the median posterior margin of V7 by a little more than their width; ventral surface lacking any troughs, elevations or ridges; anterior half of V8 acutely narrowed, and linearly prolonged beneath V7, prolonged portion longer than wider posterior portion of V8, lateral margins of anterior prolongation well sclerotised in posterior half; dorsal surface of tergite 7 laterally flattened, median area evenly and linearly rounded; tergites 7, 8 and V 7, 8 more heavily sclerotised than preceding segments.

Genitalia (Fig. 36) similar to *P. guigliae*, lacking any median sclerotisation between coxites, valvifers long slender and diverging in anterior half.

Reproductive system as described for *P. guigliae*; two females were dissected, in both the two structures arising anterior to the bursa are well developed, thick walled and equal in size, and assumed to be a gland and a spermatheca.

Remarks. – The width between the high points on V8 of the female could accommodate the apex of the male MPP between them. In this alcohol preserved male the MPP and tergite 8 apex are widely divergent, and the aedeagus, still partly contained in the aedeagal sheath, protrudes towards the tip of tergite 8. In the (pinned) holotype the apex of tergite 8 is contained between the apical emargination of the MPP. Because of its disposition in this specimen, there seems no reason to expect the aedeagus to be extracted laterally, despite the downturned apex of tergite 8 and upturned apex of V 7.

PHYLOGENETIC ANALYSIS

Our earlier phylogenetic analyses of the Lampyridae (Ballantyne & Lambkin, 2000, 2001) were expanded to include 49 taxa, with the addition of another four species: *Atyphella undulata*, *P. guigliae*, *P. hamulata*, and *P. wittmeri*. A full list of exemplar taxa is given in Table 1, the Data Matrix. One hundred and twenty-five morphological characters were scored comprising 315 states in the analysis. Most are binary, but 30 characters were coded as multistate characters each with three states, while characters 4, 5, 56, 65, 66, and 75 were coded with four states, characters 9, 11, 55, 73, and 103, with five states, character 2 with six states, and character 98 with eight states. The six characters (97-100, 114-115) that describe colour, and four characters (101-2, 116-7) that describe mimicry or colour patterns were not used in the phylogenetic analysis but mapped onto the resultant trees to examine patterns of evolution.

Character analysis

Phylogenetic analyses presented here do not prejudge the relative informativeness of characters (Larson & Dimmick, 1993; Kallersjö *et al.*, 1999). 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, not in binary form (Meier, 1994), and treated as unordered (non-additive). Cladistic analyses completed 1000 random step-wise addition heuristic searches, with TBR branch swapping, MULPARS, and branches having maximum length zero collapsed to yield polytomies using PAUP*4.0b10 (Swofford, 2002).

Initial searches indicated that there were most parsimonious trees (MPT) of length 312, but searches tended to become stuck in suboptimal tree space. Therefore 10000 random step-wise addition heuristic searches were completed, saving no more than 3000 MPT of length greater than or equal to 313, and abandoning the replicate if that limit was hit.

Successive approximations character weighting (successive weighting) is a method of choosing between MPT (Farris, 1969; Carpenter, 1988). It is an iterative character weighting procedure in which the weights are assigned, based on their observed level of homoplasy. Initial weights are derived from the MPT under equal weighting, and heuristic searches completed based on the Rescaled Consistency Index (Farris, 1989). The procedure is repeated until the weights (and the trees) remain stable over iterations. Successive weighting of the MPT was computed using PAUP*.

Strict (Schuh & Farris, 1981), semistrict (Bremer, 1990), and majority-rule consensus (Margush & McMorris, 1981) of MPT were computed using PAUP*. The 50% majority rule consensus shows all nodes that are found in more than 50% of the trees. Groups are preserved in the majority rule consensus tree even if there are some MPT that support conflicting groups (Margush & McMorris, 1981). Bremer support (Bremer, 1988; Kallersjö *et al.*, 1992; Bremer, 1994) values were calculated with TreeRot v.2 (Sorenson, 1999) with 20 heuristic searches of the data. The command line (nchuck=10000 chuckscore=322 abortrep=yes) was added for each heuristic search to prevent prolonged searches of suboptimal tree space.

Phylogenetic Results

Analysis of 115 characters (excluding the colour and mimicry characters) in the data matrix in Table 1 produced 2992 MPT of length 312, consistency index (Kluge & Farris, 1969) 0.56, consistency index without uninformative characters (Kluge & Farris, 1969) 0.50, retention index (Farris, 1989) 0.75, and rescaled consistency index (Farris, 1989) 0.42. The strict (Fig. 38A) and 50% majority rule (Fig. 38B) consensus trees were calculated. Successive weighting of the 2992 MPT produced 195 trees for which the semistrict consensus (Fig. 39) was calculated and saved. A tree filter, created in PAUP*, found none of the 2992 MPT was compatible with the semistrict consensus of the successively weighted trees. Therefore the successive weighting was unable to aid in choice of MPT. However, a second filter found 153 of the 2992 MPT were compatible with the 50% majority rule consensus of the 2992 MPT. One of these 153 MPT (Figs. 40-41) was chosen as the preferred MPT, and Bremer supports calculated and shown above the nodes. Unambiguous character and state changes, including the 10 colour and mimicry characters not used in the phylogenetic analysis, were mapped onto the preferred MPT (Figs. 40-41) in MacClade (Maddison & Maddison, 2001).

Characters

Characters and states are numbered to reflect their number in Ballantyne & Lambkin (2001) [e.g. 6(5) = character 6 here was character 5 previously], and are as described therein with these exceptions which are described following the appropriate character– **1**. **Modified**: 2(2), 3(3), 4(4), 6(5), 15(14), 18(17), 22(21), 279260, 28(27), 40(39), 41(39), 51(47), 71(63), 77(70), 93(82), 94(83), 98(86), 99(87), 113(96); **2. New**: 5, 48, 49, 52, 57-60, 78-81, 96, 101-2, 106-9, 111, 116, 117.

Pronotum (1-10)

1.	Hypomera:	
	Open	0
	Closed in front	1
2.	Inclination of lateral pronotal margins:	
	Diverging along anterior half or more with some convergence in posterior area which is not sinuate (Ballantyne & Lambkin 2000, Fig. 1a-d, f, g, i-l)	0

Diverging along all their length except for a slight sinuousity at about the mid point of the lateral margin 1
Diverging along anterior half or more (widest across posterior margin) with posterior $^{1}/_{4}$ sinuate (gentle convergence followed by gentle divergence) 2
Diverging along their length (Ballantyne & McLean, 1970, Fig. 4c) 3
Subparallel or wider across middle with slight convergence anteriorly and posteriorly 4
Converging posteriorly along their length (Ballantyne & Lambkin, 2000, Fig. 19a) 5

New states 1 and 2 accommodate slight sinuousity of the lateral margin; old state 1 becomes 4, and 3 becomes 5. In states 0-3 the pronotum is wider across the base than across the middle; in 4 it may be wider across the middle than across the base; in 5 it is wider across the anterior margin than the base.

3. Anterolateral corners of pronotum:
Obliterated (there is a smooth even transition from the middle of the anterior margin to the lateral margins; no anterolateral corner is defined) (Lloyd & Ballantyne, 2003, Figs. 5-10,19) 0
Broadly rounded, obtuse (Ballantyne & Lambkin, 2000, Fig. 1, 19a-e) (smooth fairly even transition from middle of the anterior margin to the lateral margins, anterolateral corner discernable but not well defined, rounded and widely obtuse) 1
Narrowly rounded, obtuse (corner defined, rounded, and narrowly obtuse) 2
Angulate acute (corner defined, not smoothly rounded, acute 3

Old state 2 is submerged into 3, and a new state 2.

4 (4). Degree of head exposure in front of pronotum (governed by retraction into pronotal cavity):
Concealed but not retracted into the cavity beneath the pronotum (outgroup) 0
Greatly exposed (slightly retracted into the cavity beneath the pronotum) 1
Scarce to moderately exposed (moderately retracted into the cavity beneath the pronotum) 2
Completely concealed (fully retracted into the cavity beneath the pronotum) 3

See explanation following 5; a new state 1 is necessary.

5. Degree of head exposure as covered by expanded anterior and lateral margins of the pronotum:
Covered (*Photuris*) 0
Not so covered 1

In the Luciolinae the head is concealed by retraction into the cavity beneath the pronotum; and this concealment relates to the size of both head and pronotal cavity; lateral pronotal margins even if explanate do not contribute to this concealment. The head is either greatly exposed in front of the pronotum (when the head cannot be retracted within and beneath the pronotum), slightly exposed (when at least some of the posterior section of the head is retracted within and beneath the pronotum at rest) or completely concealed (not visible from above). In *Photuris* spp. (outgroup) the wide head cannot be retracted into the pronotal cavity and both the explanate anterior and lateral margins contribute to head concealment, from above. Characters 4 and 5 make this distinction.

6(5). Posterolateral corners of pronotum (shape and angle):
Rounded obtuse (Ballantyne & Lambkin, 2000, Fig. 1 a-c, d, f-g, I, j-l) 0
Right angled or angulate obtuse (Ballantyne & McLean, 1970, Fig. 4h) 1
Rounded acute 2
Pointed acute (Ballantyne, 1968, Fig. 130) 3

States 2, 3 are combined and state 4 becomes state 3.

7(6). Posterolateral corners of pronotum:
Scarcely projecting beyond posterior margin nor delimited by a deep emargination of the posterior margin 0
Projecting considerably beyond posterior margin and often delimited by an emargination of the Posterior margin (Ballantyne, 1968, Figs. 20, 33, 38, 51, 62, 70) 1
Projecting beyond posterior margin but not delimited by a wide pronounced emargination 2

8(7). Lateral margin of pronotum near posterolateral corner:
Not indented 0
Slightly indented 1

The indentation is slightly irregular and small, contrasting with the evenly sinuate posterior margin of character 2 state 2.

9(8). Lateral margin of pronotum (viewed from beneath):
Not flattened 0
Flattened only in posterior half 1
All of lateral margin narrowly flattened but not more so in posterior half 2
All of lateral margin narrowly to widely flattened but more so in posterior half of pronotum 3
Lateral margin widely flattened along its length and anterior area as wide as or wider than posterior area 4

10(9). Anterior margin of pronotum:
Not explanate 0
Narrowly explanate 1

Elytron (11-18)

11(10). Punctation:
Not conspicuously larger than pronotal punctation 0
Conspicuously larger than pronotal punctation 1

12(11). Apex:
Not deflexed 0
Deflexed with apex rounded (Ballantyne & Lambkin, 2000, Fig. 20 j, k) 1

13(12). Apex:
Not deflexed 0
Deflexed with sides A, B, C equal (Ballantyne & Lambkin, 2000, Fig. 20k) 1
Deflexed with sides A, B longer than C (Ballantyne & Lambkin, 2000, Fig. 20j) 2

14(13). Development of epipleuron and sutural apex in apical half of elytron:
No thicker than rest 0
Considerably thicker than anterior portions 1

15(14). Interstitial line development as elevation similar to that of sutural ridge:
4 well defined lines (1, 2, 3, 4 including the humeral carina, line 3 arising at or near the humerus) 0
3 well defined lines (lines 1, 2, and 3 or 4) 1
2 well defined lines (lines 1, 2 closest to the suture) 2
Only one line well defined 3
No lines well defined 4

This character is amplified to reflect the development of all the possible interstitial lines which may be visible (e.g. paler in colour than rest, or often delimited by punctures along their sides), but not elevated comparable to the elevation of the sutural ridge, in which case they are classed as state 4.

16(15). Epipleuron:
Extending to apex of elytron 0
Extending past mid point of elytron but not to apex 1
Extending no further than mid point of elytron 2

17(16). Sutural ridge:
Extending to apex of elytron 0
Evanescent before elytral apex 1

18(17). Margins:
Parallel sided (may converge in posterior 1/3) 0
Convex sided 1

Head, antennae, mouthparts (19-41)

19(18). Depression of vertex:
Minimal 0
Moderate - deep 1

20(19). Approximation of eyes on ventral surface of head (measured as eye separation taken just behind mouthparts/GHW measured ventrally):
Wide separation(0.5 or greater) 0
Close to moderate separation (0.4 or less) 1
Contiguous or almost so 2

21(20). Posterolateral eye excavation (Ballantyne, 1968, Figs. 144, 147-150):
Absent; if slightly developed not visible when head is retracted 0
Well developed and usually visible even when head is evenly retracted 1

A well developed posterolateral eye excavation is at least as wide as long when viewed from the side.

22(21). Antenna length:
Longer than twice GHW 0
> GHW - 2 x GHW 1
Subequal to GHW 2

Amplification 'much' eliminated from state 0.

23(22). Proximity of antennal sockets:
Contiguous 0
Separated by < 2 x ASW but not contiguous 1
Separated by at least 3 x ASW 2
Separated by > twice but not 3 x ASW 3

24(23). Frons-vertex junction:
Not acute (Ballantyne & Lambkin, 2000, Fig. 2 a, d, h) 0
Acute (Ballantyne & Lambkin, 2000, Fig. 2 c, f, g, I) 1

25(24). Median area of frons vertex junction:
Not elevated or indented 0
Elevated and/or indented (Ballantyne & Lambkin, 2000, Fig. 2f, g) 1

26(25). Anterior margin of head:
Not prolonged 0
Prolonged in front of eye for about its width 1

See Ballantyne, 1968, Figs. 132, 134.

27(26). Length width of labrum:
Posterior margin of labrum not defined (clypeolabral suture absent) 0
Posterior margin of labrum defined (clypeolabral suture present); labrum wider than long 1
Posterior margin of labrum, defined by clypeolabral suture present; labrum about as long as wide 2

A new state 0 defines the situation where, in the absence of a clypeolabral suture, the posterior margin of the labrum cannot be accurately determined and it is not possible to measure L/W of labrum.

28(27). Clypeolabral suture:
Present, clypeus and labrum not fused, and junction between clypeus and labrum flexible 0
Present, clypeus and labrum fused, and junction between clypeus and labrum inflexible 1
Absent, clypeus and labrum fused with no defined junction between the two (Ballantyne, 1968, Figs. 132, 134) 2

John Lawrence (ANIC Canberra) determined the extent of the labrum and clypeus, and the position of the clypeolabral suture on specimens of *Photuris* and "Mt Missim'. The states are elaborated here; scoring remains the same as in Ballantyne & Lambkin (2001).

29(28). Mouthparts:
Functional 0
Non functional 1

Non functional mouthparts have very small apical segments of labial and maxillary palpi, mandibles often do not cross in the median line and the antennal sockets are contiguous.

30(29). Proximity of eyes above labrum (SIW/GHW):
Close (1/6 - 1/15) 0
Moderately separated > 1/6 1
Widely separated 1/3 – 1/2 2

31(30). Antennal flagellar segment 1:

As long as or longer than pedicel	0
Shorter than pedicel	1

32(31). Antennal flagellar segment 1:

Not expanded at its outer apex	0
Expanded at its outer apex	1

33(32). Median area of antennal flagellar segment 1:

Not produced	0
Produced (Ballantyne & McLean, 1970 Fig. 18b)	1

34(33). Flagellar segments 7-9:

Not conspicuously shorter than rest of FS	0
Conspicuously shorter than rest of FS	1

35(34). Number of segments:

11	0
< 11	1

36(35). Flagellar segment 9:

Apically rounded	0
Apically pointed	1

37(36). Flagellar segments 2-8:

Not expanded	0
Expanded at anterior apical angle	1

38(37). Antennal segments:

Not flattened	0
Flattened	1

39(38). Pedicel:

Not produced at outer apex	0
Produced at outer apex	1

40(39). Shape of apical segment of labial palpi:

Fusiform, or about as wide as long	0
Laterally flattened	1

41(39). Nature of inner margin of apical segment of labial palpi:

Entire (margin rounded, convex)	0
Dentate	1
Lunate	2

Character 39 has been split into two to reflect the shape of the apical segment of the labial palp and the nature of its inner margin.

Legs (42-49)

42(40). Inner tarsal claw of each leg:

Not split	0
Split	1

43(41). Metafemoral comb (Ballantyne, 1987a, Fig. 1j):

Absent	0
Present	1

44(42). Femora 3 (Ballantyne & McLean, 1970, Fig. 4p):

Not swollen	0
Swollen	1

45(43). Curvature of femora 3:

Not curved	0
Curved along their length (Ballantyne & Lambkin, 2000, Fig. 26h)	1

46(44). Swelling of tibiae 3:

Not swollen	0
Swollen at least at their apices (Ballantyne & Lambkin, 2000, Fig. 26h)	1

47(45). Curvature of tibiae 3:

Not curved	0
Curved (Ballantyne & Lambkin, 2000 Fig. 26h)	1

48. Curvature of tibiae 2:

Not curved	0
Curved	1

49. Curvature of tibiae 1:

Not curved	0
Curved	1

Abdominal segments – ventrites (50 - 70)

50(46). Ventrite 8:

Present	0
Absent	1

51(47). Light organ in ventrite 7:

Entire (e.g. Ballantyne & Lambkin, 2000, Fig. 4a)	0
Posterior medial division short - long (Ballantyne, 1968, Fig. 42, 91)	1
Bipartite (Ballantyne & Lambkin, 2000 Fig. 26a)	2

State 2 was erroneously listed as 3 in Ballantyne & Lambkin (2001).

52. Intrusion of swollen posterior half of ventrite 7 into light organ posterior margin:

Posterior half of ventrite 7 not swollen	0
Posterior half of ventrite 7 swollen but not reaching into posterior half of light organ	1
Posterior half of ventrite 7 swollen and reaching into emarginate posterior border of light organ	2

53(48). Light organ in ventrite 7:

Reaching sides and posterior margin of ventrite 7	0
Reaching sides but not posterior margin	1
Not reaching sides or posterior margin	2

54(49). Size of light organs:

Occupying at least half of the area of ventrite 7 or more	0
Restricted to very small paired anterolateral plaques that occupy less than 10% of the area of ventrite 7 (Ballantyne & McLean, 1970, Fig. 18c)	1

55(50). Apex of MPP of ventrite 7:
MPP not developed 0
Apex truncate 1
Apex rounded 2
Apex gently emarginate (e.g. Ballantyne & Lambkin, 2000 Fig, 20 d, f, j, k, i) 3
Apex deeply emarginate (Ballantyne & Lambkin, 2000 Fig. 3 d, e, g, j; Ballantyne, 1968 Fig. 13) 4

56(51). Length/ width of MPP of ventrite 7:
Not produced 0
About as long as broad or shorter; narrower than half the width of ventrite 7 1
About as long as broad; at least half as wide as ventrite 7 2
At least twice as long as wide 3

57. Relation of posterior margin of ventrite 7, to apex of tergite 8:
MPP developed 0
MPP not developed, posterior margin of Ventrite 7 not enveloped by strongly ventrally deflexed apex of tergite 8 1
MPP not developed, posterior margin of ventrite 7 engulfed by the strongly ventrally deflexed apex of tergite 8 2

58. Dorsal inclination of MPP:
MPP not developed 0
MPP developed, not strongly reflexed dorsally 1
MPP developed, strongly reflexed dorsally 2

59. Relationship of MPP to tergite 8:
MPP not developed 0
MPP developed but not engulfed at its posterior margin by the strongly downturned tergite 8 apex 1
MPP developed and engulfed at its posterior margin by tergite 8 apex 2

60. Inclination of apex of tergite 8:
Apex of tergite 8 not strongly inclined ventrally 0
Apex of tergite 8 strongly inclined ventrally 1

Character 52 is replaced by 57 – 60, to distinguish the situation where the apices of tergite 8 and the MPP of ventrite 7 are narrowed and approach each other by being strongly inclined (at approximately a 90° angle) in either a ventral or dorsal direction; it eliminates species such as *A. obsoleta, A. huonensis* and 'Mt. Missim', where both tergite 8 and ventrite 8 may curve slightly towards each other, but are not bent at a pronounced angle.

61(53). Median longitudinal carina in ventrite 7:
Absent 0
Present (Ballantyne & McLean, 1970, Fig. 3 d, f) 1

62(54). Median longitudinal trough in ventrite 7:
Absent 0
Present 1

63(55). Median longitudinal trough on ventral surface of MPP:
Absent 0
Present (Ballantyne & McLean, 1970, Fig. 3 d, f) 1

64(56). All of ventrite 7, especially in posterior half:
Flat, not arched or swollen (e.g. Ballantyne & Lambkin, 2000, Fig. 4a) 0
Arched and often swollen (Ballantyne, 1968, Figs. 56, 89) 1

65(57). Length of PLP of ventrite 7:
Not developed 0
Slightly produced (Ballantyne & Lambkin, 2000, Fig. 26a) 1
Moderately produced, may extend beyond the tip of the MPP 2
Considerably produced (Ballantyne, 1987b Fig. 2 a, b) 3

66(58). Width of PLP of ventrite 7:
Not developed 0
Narrower than MPP (Ballantyne &Lambkin, 2000, Fig. 26a) 1
As wide as MPP (Ballantyne & McLean, 1970, Fig. 9 a, b) 2
Broader than MPP (Ballantyne, 1987b, Fig. 2 a, b) 3

67(59). Inclination of PLP of ventrite 7:
Not developed 0
Horizontal 1
Oblique - vertical 2

See Ballantyne & McLean, 1970, Fig. 3 d, f; and Ballantyne, 1968, Figs. 11, 13.

68(60). Incurving hairy lobes along posterior margin of ventrite 7 (Ballantyne & Lambkin, 2000, Fig. 26a):
Absent 0
Present 1

69(61). Pointed projection of ventrite 7 posterior margin (Ballantyne & Lambkin, 2000, Fig. 26a):
Absent 0
Present 1

70(62). Dimple on ventrite 7 (Ballantyne & Lambkin, 2000, Fig. 20k):
Absent 0
Present 1

Abdominal segments - tergites (71-76)

71(63). Flanges on ventral face of tergite 8:
Lacking flanges 0
With flanges (Ballantyne & Lambkin, 2000, Fig. 20l) 1

State 2 is eliminated and state 1 modified.

72(64). Ventral face of tergite 8 with depressed lateral troughs (Ballantyne & Lambkin, 2000 Fig. 26c, d):
Absent 0
Present 1

73(65). Posterior half of ventral face of tergite 8 with elongate longitudinal symmetrical developments margining a median longitudinal trough:
Absent 0
Fine transparent barely elevated ridges margining a median longitudinal trough 1
Slightly thickened barely elevated ridges margining a median longitudinal trough 2
Low barely elevated ridges present in posterior half of ventral surface only 3
Longitudinal raised well developed ridges delimiting a median longitudinal trough 4

74(66). Ventral face of tergite 8 with asymmetrical projections (other than flanges), and/or transverse ridges and/or hooks:
Absent 0
Present (Ballantyne, 1987b, Fig. 2f) 1

Ballantyne (1987b) termed all the narrowed ventral projections of tergite 8 ‘flanges’. Flanges are here interpreted as the narrowed anterior projections often of lateral longitudinal ridges on the ventral surface of tergite 8.

75(68). Width of tergite 8:
About as wide as long 0
Very short 1
Much longer than wide and projecting considerably beyond MPP 2
Longer than wide but not projecting considerably beyond MPP 3

76(69). Width of posterior half of tergite 8:
Not narrowed, or lateral margins converging posteriorly but not abruptly 0
Abruptly narrowed (Ballantyne, 1968, Figs. 17,110,112,114) 1

Aedeagal sheath (77- 84)

77 (70). Aedeagal sheath ventrite <u>symmetry</u> in posterior area i.e. posterior to point of articulation with the sheath tergite, as distinct from symmetry or otherwise of posterior margin of ventrite 9:
Symmetrical (Ballantyne & Lambkin, 2000, Fig. 21 b, d, e) 0
Asymmetrical in posterior area (Ballantyne & Lambkin, 2000, Fig. 21 i) 1

Undescribed specimens ‘<u>Sisiak</u>’ were scored state 1 in Ballantyne & Lambkin, 2000; the posterior margin of the sheath ventrite is asymmetrical; state 1 is modified above and new characters 77-79 address this inconsistency.

78. Width of posterior area of ventrite 9 (posterior to point of articulation with sheath tergite):
As wide as tergite of sheath and symmetrical; if narrower than tergite of sheath then symmetrical 0
About half as wide as tergite of sheath and asymmetrical (right side of ventrite is evenly emarginate along its length 1

79. Length of posterior area of ventrite 9 (posterior to point of articulation with sheath tergite):
About as long as tergite of sheath 0
Shorter than tergite of sheath but not less than half its length 1
Shorter than half the length of tergite of sheath 2

80. Symmetry or asymmetry of posterior margin of sheath ventrite:
Posterior margin of sheath ventrite entire, rounded 0
Posterior margin of sheath ventrite emarginate,symmetrical 1
Posterior margin of sheath ventrite emarginate, asymmetrical 2

81. Width of aedeagal sheath ventrite in anterior half:
Broad; if narrowed then this is a gradual narrowing anteriorly 0
Abruptly narrowed, anterior prolongation much narrower than posterior half of ventrite 1

82(71). Length/width of aedeagal sheath:
Never more than about 4 times as long as wide 0
Very long and narrow (about 7 times as long as wide) 1

83(72). Lateral margins of aedeagal sheath:
Lacking paraprocts (Ballantyne & Lambkin, 2000, Fig. 21 c, d) 0
With paraprocts (Ballantyne & Lambkin, 2000, Fig. 21 a, b) 1

84(73). Length/width of tergite 9 of aedeagal sheath:
About as long as wide 0
Much wider than long 1

Aedeagus (85-96)

85(74). Maximum width across lateral lobes/ maximum width of median lobe:
Wide (4 – 6/1) (Ballantyne, 1968, Fig. 171) 0
Moderate (2/1) (Ballantyne & Lambkin, 2000, Fig. 5)
Narrow (less than 2/1) (Ballantyne & Lambkin, 2000, Fig. 21 o, r, u; 26e) 2

86(75). Inclination of apex of median lobe:
Not curving ventrally 0
Curving ventrally (Ballantyne, 1968, Figs. 164, 168) 1

87(76). Extent of preapical ventral area of median lobe:
Not produced 0
Produced and rounded 1
Produced and pointed (Ballantyne, 1968, Figs. 162, 164, 168) 2

88(77). Length of median lobe of aedeagus relative to lateral lobes:
Much shorter than LL 0
Subequal in length to lateral lobes or slightly longer 1
Longer than LL but less than twice their length 2
Much longer than LL i.e. more than twice their (separated) length 3

89(78). Separation of lateral lobes of aedeagus:
Separated for > half their length 0
Separated for less than half their length (Ballantyne & Lambkin, 2000, Fig. 26 e-g) 1

90(79). Width of lateral lobes of aedeagus:
Much wider and flatter at their apices than widest point of ML (Ballantyne & Lambkin, 2000, Fig. 21 l, m) 0
About as wide at apices as widest point of ML (Ballantyne & Lambkin, 2000 Fig. 5) 1
Much narrower at apices than widest point of ML (Ballantyne &Lambkin, 2000 Fig. 21 p,s,u,v; Fig. 26 e-g) 2

91(80). Separation of lateral lobes into broad basal section and narrowed widely separated apical section:
No such separation 0
Present (Ballantyne & Lambkin, 2000, Fig. 21k) 1

92(81). Aedeagal symmetry:
Aymmetrical 0
Asymmetrical (Ballantyne & Lambkin, 2000, Fig. 26e, f) 1

93(82). Fleshy leaf like lobes arising from lateral margins of lateral lobes:
Absent 0
Present (Ballantyne & Lambkin, 2000, Fig. 21l, n) 1

This modification eliminates states 1 and 3, those species with various, non leaf like lobes supporting in some cases dense hair bearing areas.

94(83). Extent of ventral face of apices of lateral lobes:
Extending to either side of ML and both visible from beneath (Ballantyne & Lambkin, 2000, Fig. 5, Fig 21 k, l, m) 0
Almost extending to sides of LL but both apices may not be visible in the same plane 1
Not extending to either side of ML and not visible from beneath except in basal half or less (Ballantyne & Lambkin, 2000, Fig. 21) 2

A new state 1 is included.

95(84). Lateral appendages of lateral lobes:
Absent 0
Present (McDermott & Buck, 1959, Fig. 62a-c) 1

96. Shape of basal piece of aedeagus:
Not hooded 0
Hooded 1

Male colour patterns (97 – 102)

97(85). Colour of pronotum:
Pronotum concolourous 0
Pronotum with dark markings 1

98(86). Colour of elytral margins compared to rest of elytra:
Elytra concolourous (dark – light, pale brown) 0
If elytron dark then only lateral margin pale 1
Lateral and sutural margins pale at least in basal half 2
Lateral and sutural margins pale with base of elytron dark 3
Lateral sutural and apical margins pale, base of elytron pale 4
If elytron pale then darker markings scattered at base and apex 5
If elytron pale then dark markings at apex only6
Elytra concolourous (Pale, usually yellow) 7

States 1 and 7 are amplified to avoid confusion.

99(87). Colour of interstitial lines 1, 2 as distinct from basal elytron colour or colour of its margins:
No paler than dark area between lines 1 and 2 0
About as pale as this area or slightly paler 1
Distinctly paler than this area so I lines appear as stripes 2

Where interstitial lines traverse differing colours on the elytra this character is scored according to the dominant colour of these lines.

100(88). Colour of terminal abdominal tergum:
As dark as or darker than preceding terga 0
Pale (as pale as preceding terga or paler) 1

101. Dorsal colouration pattern:
Dorsal colouration crypsis 0
Dorsal colouration mimicry 1

102. Dorsal colouration pattern:
Mimicry 0
Crypsis – background matching 1
Crypsis – disruptive colouration 2

In background matching, cryptic colour patterns randomly resemble the visual background in shape, size and colour at the time and place of highest predation risk (Endler, 1978). Because edges and boundaries are the primary features used in visual recognition, a mechanism often used to attain crypsis is disruptive coloration (Cott, 1957) where the organism's shape, or even number, is obliterated (Oxford & Gillespie, 1998). The animal blends into the background as the surface is broken into meaningless shapes or the attention of the predator is drawn to nonessential patterns (Merilaita, 1998).

Adult female morphology (103 – 113)

103(89). Development of fore wings of female:
Fully developed (or covering all but two terminal abdominal segments) 0
Elytra longer than pronotum but shortened such that they cover approximately $^{1}/_{2}$ - $^{2}/_{3}$ of the abdomen 1
Elytra shorter than pronotum (more than half as long as pronotum) and contiguous in the median line 2
Elytra shorter than half pronotal length and often contiguous or closely approaching in the median line 3
Elytra shorter than half pronotal length and widely separated in the median line 4

Macropterous gravid females may have one to two abdominal segments protruding beyond the elytral apices.

104(90). Development of hind wings of female:
Fully developed 0
Hind wings about 2/3 as long as macropterous state 1
Hind wings vestigial or absent 2

105(91). Extent of female light organ:
Occupying ventrites 6 and 7 0
Restricted to ventrite 6 1

106. Developments of dorsal face of abdominal tergite 8:
Tergite 8 lacking dorsal elevation 0
Tergite 8 with dorsal elevation 1

107. Developments of median ventral face of abdominal ventrite 7:
Ventrite 7 lacking median ridge 0
Ventrite 7 with median ridge (Ballantyne & Lambkin, Fig. 16) 1

108. Developments of lateral areas of ventral face of ventrite 7:
Ventrite 7 lacking lateral developments 0
Ventrite 7 with lateral developments 1

109. Depressed lateral areas on ventrite 7 ventral face (corresponding to dorsoventral muscles):
Absent 0
Present 1

110(94). Number of well defined elytral interstitial lines:
Four 0
Less than four 1

111. Elytral carina:
Absent 0
Present 1

112(95). Nature of pronotal punctures:
Contiguous in at least lateral areas 0
Not contiguous in any area 1

113(96). Head form:
Of same form as male 0
Of winged female form (Ballantyne & Lambkin, 2000, Fig. 6b) 1
Of wingless female form (Ballantyne & Lambkin, 2000, Fig. 6d, e) 2

A new state 0 is necessary.

Adult female colour patterns (114 – 117)

114(92). Colour of pronotum:
Pronotum concolourous 0
Pronotum with coloured markings 1

115(93). Colour of elytra:
Elytra concolourous 0
Elytra not concolourous 1

116. Dorsal colouration mimicry or crypsis:
Dorsal colouration crypsis 0
Dorsal colouration mimicry 1

117. Dorsal colouration pattern:
Mimicry 0
Crypsis – background matching 1
Crypsis – disruptive colouration 2

Larval Morphology (118 – 125)

118(97). Production of lateral margins of terga:
Lateral margins not explanate (Ballantyne & Lambkin, 2000, Fig. 22) 0
Lateral margins narrowly explanate especially at posterolateral corners (Ballantyne, 1968, Figs. 158-160) 1
Lateral margins widely explanate (Ballantyne & Lambkin, 2000, Figs. 12, 15) 2

119(98). Length/width of pronotum:
Longer than wide 0
About as long as wide 1

120(99). Nature of tergal margins:
Not ridged 0
Ridged 1

121(100). Paired dorsal and ventral tubercles on protergum:
Absent 0
Present (Ballantyne & Lambkin, 2000, Fig. 15a, c) 1

122(101). Shape of posterolateral corners of protergum:
Rounded (Ballantyne & Lambkin, 2000, Fig. 15 a-c) 0
Acute (Ballantyne & Lambkin, 2000, Fig. 12 c) 1
Narrowly produced 2

123(102). Margins of median line on terga 1-10:
Not ridged 0
Ridged 1

123(103).	Size of punctures in anterior half of terga 2-10:	
	No larger than rest	0
	Larger than rest	1
125(104).	Extent of posterolateral corners of tergum 11:	
	Not produced (Ballantyne & Lambkin, 2000, Fig. 7a, 15b)	0
	Produced (Ballantyne & Lambkin, 2000, Fig. 12a-c, 15 a, c)	1

DISCUSSION

Taxonomy

This study supports the return of *Pygoluciola* to generic status, and the general trends shown in previous analyses (Ballantyne & Lambkin, 2000, 2001) while indicating directions for further resolution within the Luciolinae. Taxonomic features that permit reliable identification of certain females occur on the external female abdomen and within the reproductive tract. This is a useful development as Luciolinae taxonomy until now has been male based, and there have been no reliable external or internal features of females to permit identification to species.

However there are also indications of problems with firefly taxonomy that could have wider application to other soft bodied insects. The method and state of preservation confuses interpretation of certain taxonomic characters, and influences conjecture about the function of various structures. Certain artefacts identified on the female abdomen are a consequence of dehydration. The use of colour by early taxonomists in fireflies was widespread, but colour is of limited value in cladistic analyses. These aspects are explored below.

Phylogeny

Pygoluciola is clearly distinct and separate from *Luciola.* The genus *Pygoluciola* is found in all MPT, and therefore in the strict consensus (Fig. 38A), in all successively weighted trees (Fig. 39), and receives the highest Bremer support of any group in this analysis of the Luciolinae (Fig. 39).

The relationships between *Pygoluciola* and other taxa are less clear. The majority rule consensus (Fig. 38B), like our previous analyses (Ballantyne & Lambkin, 2000, 2001), indicates that 'Mt Missim' is more closely related to *Pygoluciola* than any other taxa. 'Mt Missim' is more closely related to *Pygoluciola* in 75% of the MPT, and 25% of the MPT would place 'Mt Missim' elsewhere. Close inspection of the character mapping on the preferred MPT (Figs. 40, 41) shows that the undescribed species, 'Mt. Missim', is highly apomorphic, having many characters that are not shared with any other taxon. Unlike our previous analyses (Ballantyne & Lambkin, 2000, 2001) the successively weighted semi-strict consensus (Fig. 39) suggests that 'Mt Missim' is more closely related to 'Sisiak' and the sub-genus *Pygatyphella*. The placement of 'Mt Missim' remains unresolved.

The position of *Curtos costipennis* is also problematical, as it is unresolved in both the strict and majority rule consensus (Fig. 38), and the preferred MPT (Fig. 40). The successively weighted semi-strict consensus (Fig. 39) suggests that *Curtos costipennis* is closely related to *Pygoluciola,* as in our previous analyses; however *Curtos costipennis* now falls between *Pygoluciola* and *Atyphella.* Future studies including more members of *Curtos* will address the placement of this genus.

The clade of *Atyphella,* found in our previous analyses, is retained in the successively weighted semi-strict consensus (Fig. 39). However the majority rule consensus (Fig. 38B) indicates that the clade *Atyphella* is present in only 75% of the MPT. The preferred MPT (Figs. 40, 41) shows the very low support values for the internal nodes of the clade. Future studies including more members of *Atyphella* will address relationships in this genus.

The basal (*L. italica-L. cowleyi*) and (*Colophotia praeusta-Pyrophanes beccarii*) clades found in our previous analyses are retained, not as sister clades but paraphyletic with low support, in the strict and majority rule consensus (Fig. 38), the successively weighted semi-strict consensus (Fig. 39), and the preferred MPT (Fig. 40).

That the Luciolinae might be a monophyletic group united by the possession of a reduced number of abdominal segments, is under investigation. While it appears that it is abdominal ventrite 8 in the male that is missing (Ballantyne 1987a, b), and this can be interpreted by counting the abdominal spiracles to confirm segmentation, it has not been determined whether the ventrite is lost or fused with 7. Branham and Wenzel (2001) established a monophyletic concept of the Lampyridae in which a Luciolinae clade was represented by 8 species (5 of which were scored here). Although we continue to use the same set of species (Ballantyne & Lambkin, 2000, 2001), decisions about further revisions of taxonomic categories in the Luciolinae await work in progress (Ballantyne, unpub.). However with few exceptions, the same categories arise from this analysis as in the previous two (Ballantyne & Lambkin 2000, 2001):

1. The type species of *Luciola, L. italica* (= *pedemontana*), and *L. dejeani*, *L. cowleyi*, *L.* (*Hotaria*) *parvula*, *Lampyroidea syriaca* (the type species of *Lampyroidea*), and *Bourgeoisia hypocrita.* Kawashima et al. (2003) submerged *Hotaria* into *Luciola* without a cladistic analysis. A distinctive aedeagal pattern of wide flaring lateral lobes which are visible from beneath, and a small leaf like lobe on their outer margins and aedeagal sheath broad and symmetrical. Both patterns are repeated in *Luciola satoi* Jeng et Yang, *L. terminalis* Olivier, and *L. praeusta* Kiesenwetter (Jeng Yang & Lai, 2003).

2. Species of four existing genera: *Pteroptyx* (4 species), *Pyrophanes* (1), Australian *Luciola* (4), and *Colophotia praeusta*. The aedeagus is elongate and slender, with the apices of lateral lobes narrow and not visible from below, and variously shortened. The aedeagal sheath is long , narrow and symmetrical. Ballantyne (1987a,b) distinguished 2 subgroups of *Pteroptyx,* (which are split

here), based on the presence/absence of lateral protuberances on the aedeagal sheath and the metafemoral comb.

3. *Atyphella* Olliff, distinguished by Ballantyne & Lambkin (2000). The aedeagus has lateral lobes visible from beneath and median lobe slightly longer than lateral lobes. The aedeagal sheath is rather broad, with the posterior half asymmetrical. [A similar pattern of 'exposed' lateral lobes, and an asymmetrical posterior half of the sheath ventrite occurs in several aquatic *Luciola* from China (Jeng Lai & Yang 2003)]. In this analysis certain elements are unresolved (three New Guinean species and *A. costata* from Australia) while 'Sisiak' groups with three *Atyphella* species distinguished by Ballantyne (1968) as *Luciola* (*Pygatyphella*). Further analyses should include certain Chinese and Japanese fireflies.

4. *Pygoluciola* Wittmer. The aedeagal sheath has the anterior portion of the ventrite very narrow, the posterior half very broad and symmetrical, a pattern not yet seen elsewhere.

Certain elements are still unresolved and should be addressed again – '<u>Mt Missim</u>' (based on 4 specimens) is an undescribed species from high elevation in New Guinea. The aedeagus is similar to that of *Atyphella,* differing in the very narrow median lobe which curves at its apex. '<u>Mt Missim</u>' differs from all other Luciolinae in lacking a clypeolabral suture. '<u>Sisiak</u>' is based on undescribed New Guinean specimens, where the aedeagal sheath and aedeagus differ from that of *Atyphella* but repeated phylogenetic analyses still place it within *Atyphella*.

The problem of colour

Although morphological characters, especially those of the male terminal abdomen, have been used for grouping in the Luciolinae, early taxonomists, especially Ernest Olivier (see McDermott, 1966), made much use of colour in describing new species, and colour still plays an important part. Species of animals are recognised by combinations of colour and pattern providing taxonomists with a means of identification and categorisation (Brush, 1978).

Colour is not included in many cladistic analyses as it is both difficult to quantify, and has traditionally been considered a character of little phylogenetic value. The poor regard for colour characters in phylogenetic analysis stems, at least partially, from the belief that colour is easily affected by convergent evolution. Selection for crypsis in particular habitat types leads to the convergent evolution of similar colours and colour patterns in unrelated species (Cott, 1957; Oxford & Gillespie, 1998). Such phenotypic similarity reflects similar selection pressures, not shared ancestry, and in phylogenetic analysis gives rise to homoplasy (Givnish & Sytsma, 1998) that can distort the inference of relationships. Previous quantitative phylogenetic studies (unpublished, Lambkin, 2001) combining a data set of over 200 colour characters with over 300 morphological characters in the Exoprosopini (Diptera: Bombyliidae: Anthracinae) found strong evidence for convergent evolution of similar coloration in unrelated species producing a misleading signal.

For these reasons the six characters (97-100, 114-115) that describe colour, and four characters (101-2, 116-7) that describe mimicry or colour patterns were not used in the phylogenetic analysis but mapped onto the preferred MPT (Figs. 40 - 41). The characters that describe mimicry or colour patterns are clearly delineated by a box surrounding them on the preferred MPT (Figs. 40 - 41).

Most of the characters (97-100, 101-2, 114-115, 116-7) that describe colour or mimicry are apomorphic, and therefore only found on branches leading to particular taxa (Figs. 40 – 41). None of the colour or mimicry characters optimized on the preferred MPT is unique.

The '<u>Sisiak'</u>-*Pygatyphella* clade is homoplasiously supported by characters 102, 114, 117; <u>Mt Missim</u>-*Pygoluciola* clade by characters 98, 115; *L. italica-L. cowleyi* clade by character 115, and *L. australis-Pyrophanes beccarii* clade by characters 101-2 (see further discussion above).

Few internal nodes are substantiated by colour or mimicry characters, indicating that phylogenetically, there is little grouping information and a great deal of homoplasy in these characters. Again there is evidence of convergent evolution of similar coloration in unrelated species.

Methods of preservation and interpretation problems

Fireflies are soft bodied insects much given to distortion once pinned. Collecting at least some into ethanol facilitates dissection and manipulation (Ballantyne, 1987b). However, problems occur with colour interpretation (Ballantyne, 1987a, 2001), distortion of shape, determination of the extent of the light organ, especially where the specimen was pinned after first immersion in ethanol, colour fading of larvae, and hardening of specimens preserved for a long period in ethanol (Ballantyne & Lambkin, 2000).

Further problems arise here with 'wet' preserved specimens. The degree of explanation of the lateral pronotal margins, and determination of states for character 9 is more difficult to determine. The lateral lobes of the aedeagus in *P. guigliae* are white and 'plump' (as wide as high) in the freshly preserved specimens, but when dehydrated appear dorsoventrally flattened and slightly brown, as in the very similar *P. stylifer,* suggesting they may have owed their contour to body fluids. Ballantyne (1968) used such features to help distinguish the aedeagi of *P. guigliae* and *P. hamulata*.

A small hook on the inner margins of the lateral lobes in *P. stylifer* may be a result of dehydration; in the very similar, 'wet' preserved *P guigliae,* the same area is not pointed or acutely developed, and is an area of heavier sclerotisation extending from the junction of the lateral lobes and running ventrally to the ventral side of these lobes.

The close approximation of the apices of abdominal tergite 8 and ventrite 7 in dried specimens of *Pygoluciola* is not seen in 'wet' specimens, where they may splay apart (see Functional Morphology below). Presumed distortions of the (pinned) female abdomen (seen in *P kinabalua* between the bases of V7 and 8) are not seen in 'wet' specimens, and no internal developments correspond with this apparent artefact, which probably reflects, indirectly, the muscle attachments onto the anterior prolongation of ventrite 8 and the anterior portions of the valvifers (Ballantyne & Lambkin, 2001).

Female morphology and identification

Lucioline firefly taxonomy is male based until now, and association of the sexes without taking a mating pair was, and in most cases still is, difficult (Ballantyne & McLean, 1970; Ballantyne, 1987a). Ballantyne (1988) associated females by taking them on the wing, flying with males where no other species occurred. Ballantyne (1987b) described features of the female, none of which taken in isolation would have allowed reliable identification to species. Ballantyne & Lambkin (2000, 2001) advocated a more pragmatic approach and made tentative identifications based on similarity of label data.

External abdominal modifications, seen in two species of *Pygoluciola*, fortuitously allow female identification. However their actual function is unknown. The presence of hooks in the bursa of two species of female *Pygoluciola*, and the existence of plates in the bursa of *Pteroptyx valida* female suggests the usefulness of these as taxonomic characters, and an investigation of such plates in female Luciolinae is under *way (Ballantyne, unpub.).*

Functional morphology

In *Pteroptyx valida*, the female abdomen is held in a pincer fashion between the deflexed elytral apices and the MPP of the male ventrite 7 ('copulation clamp'). No obvious external morphology of the female abdomen hints at such an arrangement, but the *valida* female has cuticular plates in the bursa that may prevent damage to the female during mating (Wing et al., 1983). They are absent in the *Pygoluciola* females dissected.

Ballantyne & Lambkin (2001) suggested a type of 'copulation clamp could exist in *P. kinabalua* where the male abdomen can open posteriorly in a pincer like fashion, and may engage against the female, which has a transverse ridge on abdominal ventrite 7, and a dorsal 'mound' on tergite 7. [Such splaying of the male terminal abdomen may nevertheless be nothing more than a deterrent to another male trying to copulate with an already coupled female (Ballantyne, 1987b); see also Methods of Preservation above). That some clamping mechanism could occur in other *Pygoluciola* species is supported by two observations – first, that the male abdomen in 'wet' preserved specimens described here shows a wide divergence between V7 and T 8. Secondly, the dorsoventral musculature is very strong, evidenced by the lateral depressions in abdominal tergite 7, the absence of light organ at the anterolateral corners of V7, where these muscles attach, and where the sides of V7 may be very strongly sclerotised and ridge like. If some clamping mechanism exists, (assuming a tail to tail mating position) the reinforcement for it shows externally, as there is nothing about the female reproductive system to indicate any reinforcement against outside pressure. Any external pressure on the female abdomen of *P. guigliae* (which lacks any obvious external modifications), if such there is, would be exerted between the elevations on V 7 and on the anterior half of V8 where it projects under V7. This coincides internally at least with the attachment of muscles from the valvifers of the female genitalia to the anterior prolongation of V8, and above this, the hooks in the female reproductive system. These hooks in the duct, attached only at their bases, may be under the female's control, and if erected they would probably prevent any backward movement of a spermatophore once it had been inserted, particularly if pressure were exerted from outside (LB squeezed the bursa accidentally during a dissection and found that the spermatophore only moved forward).

However this would seem to be a female modification that on first glance, benefits the male. LB acknowledges Prof James Lloyd for the following suggestions that address the possible function of the hooks in the female vagina: 1. If the copulating male sometimes removes ejaculate after depositing sperm, because it is the presence of nutritive contributions that persuade the female to copulate with him, he might reclaim and reuse the package to gain additional copulations with other females; 2. Males may remove sperm previously inserted by other males; if the female has invested time etc in selecting or waiting for a male and has accepted sperm from him, and then later is forced into copulation with another male, such hooks could reduce the chance that the second male could remove the spermatophore, thus negating her previous decision; 3. If another male tries to push or pry a copulating male away from a female, the intruder will have more difficulty in prising away the coupled male if both the male and the female have a firm grasp on the spermatophore.

The pronotal irregularities are seen in both sexes except for the single 'wet' preserved female of *P. wittmeri*. They may be a cluster of sense organs (no specimens were available for EM study). Curved tibiae of all legs are seen in both sexes of one species. In certain *Pyrophanes* males, curved tibiae 3, and enlarged femora 3 are coupled with a metafemoral comb, and taken together they may have some grasping function (Ballantyne, 1987b: 174). The function of curved tibiae in *Pygoluciola* is unknown.

Ballantyne (1987b) suggested that the surface area of the anterior prolongation of the aedeagal sheath ventrite, which provides area for attachment of these muscles, could indicate some of the complexity of movements the aedeagus can make, but in *Pygoluciola* the anterior prolongation of V9 although very narrow, has muscles from the base of the aedeagus attaching all along its length, thus the width of this surface may not be a good indicator of the extent of this musculature.

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Table 1. Data matrix describing 125 characters for 49 taxa, including polymorphic coding.

```
DATA MATRIX
Character number                      10         20            30         40         50                  60      65    70         80         90             100        110              120   125

Photuris trilineata        0  0 00000041 0000421100 0  0 10001101 1000000001 2100000000   0 000  0   0 1000 0000  0 00000 0000000000 ?000100101 0000101  3   2 1 0100000001 011  1   1 01210 00000
Bourgeoisia hypocrita      1  4 12100030 0000411112 1{12}00002000 0000000001 1000000001   2 011  0   0 1000 0000  0 00000 0000000000 0000012100 0010000  0   0 1 0112100001 001  0   0 01101 02010
Colophotia praeusta        1  0 12110020 0000410011 0  1 10001002 0001010000 0000000001   2 020  4   3 0210 1010  3 32000 1040000000 0110200312 0002000  6   1 1 0100100001 001  0   1 01??? ?????
Hotaria parvula            1  0 12100020 0000410011 0  1 100010?1 0000000001 1000000001   0 010  0   0 1000 0000  0 00000 0000000000 0000012100 0010001  0   0 1 1012100001 002  1   0 10??? ?????
Lampyroidea syriaca        1  5 12110020 0000410011 1  1 10002001 0000000100 0000000001   0 020  2   2 0110 0000  0 00000 0000000000 0000012100 0010001  2   0 1 0122100001 012  1   0 01??? ?????
Luciola australis          1{45}22110020 0000411011 0  1 10001001 0000000000 0000000001   0 010  3   1 0110 0000  0 00000 0040000000 0000200102 0002000  0   0 1 1000100001 001  0   0 10000 00001
Luciola cowleyi            1{45}21110030 0000110012 1  2 00002000 0000000000 0000000001   0 020  0   0 1000 0000  0 00000 0000000011 0000000002 1000001  1   0 1 01???????? ???  ?   ? ????? ?????
Luciola dejeani            1  4 12100020 0000410011 0  1 10001001 0000000001 1000000001   0 000  0   0 1000 0000  0 00000 000000???? ????012100 0010000  6   1 1 01???????? ???  ?   ? ????? ?????
Luciola flavicollis        1{45}22110020 0000410011 0  1 10001001 0000000000 0000000001   0 020  3 {13}0110 0000  0 00000 0040000000 0000200102 0002000{24}{01}0 1000100001 001  0   1 10000 00001
Luciola italica            1  0 12100020 0000411011 0  1 10002001 0000000001 1000000001   0 000  0   0 1000 0000  0 00000 0000000000 0000012100 0010000  0   0 1 1000100001 001  0   0 10??? ?????
Luciola nigra              1{45}22110020 0000410011 0  1 10001001 0000000000 0000000001   0 020{13}{12}0110 0000  0 00000 0040000000 0000200102 0002000  0   0 0 1000100001 001  0   0 10000 00001
Luciola orapallida         1{45}22110020 0000410011 0  1 10001001 0000000000 0000000001   0 020  1   1 0110 0000  0 00000 0040000000 0000200102 0002000  2   0 1 1000100001 001  0   1 10000 00001
Pteroptyx cribellata       1  4 22110020 0110401011 0  1 10001001 0000000000 0000000001   0 010  3   1 0110 0000  1 21001 1040000000 0000200102 0002000  0   0 0 1000100001 001  0   0 10??? ?????
Pteroptyx macdermottii     1  4 22110020 0110400001 0  1 10001002 0110000010 0010000001   2 021  4   1 0110 0000  3 11110 0140200000 0010200212 0002000  6   1 1 0100100001 0?1  0   1 01??? ?????
Pteroptyx malaccae         1  4 12110020 0110401010 0  1 10001001 0100000000 0010010001   2 010  3   1 0110 0000{12}21000 0040000000 0010200112 0002000  6   1 1 0100100001 001  0   0 01??? ?????
Pteroptyx platygaster      1  4 22110020 0120401011 0  1 10001001 0000000000 0000000001   0 010  3   1 0110 0000  1 21001 1040000000 0000200102 0002000  0   0 0 1000100001 001  0   0 10??? ?????
Pyrophanes beccarii        1  4 22110020 0000411010 0  1 10001001 0100000000 0011111001   2 010  3   1 0110 0100  1 11110 0140000000 0010200212 0102000  0   0 1 1000100001 011  0 {01}10??? ?????
Pygoluciola guigliae       1  1 32122010 0000400011 0  0 10001002 0000000001 1000001111   0 020  2   1 0221 0000  0 00000 0000310000 1000100001 0000001  3   0 1 0100100101 011  1   0 01??? ?????
Pygoluciola hamulata       1  3 221220?0 0000???0?? 0  0 ?000?00? 000000000? ?000000001   0 020  2   1 0221 0000  0 00000 000031???? ?000100001 0000000  6   0 1 01???????? ???  ?   ? ????? ?????
Pygoluciola kinabalua      1  3 22122010 0000400011 0  0 30002002 0000000001 1000000001 {01}020  3   1 0221 0000  0 00000 0000310000 1000100001 0000001  7   1 1 0100111001 001  1   0 01??? ?????
Pygoluciola stylifer       1  3 22120010 0000400011 0  0 10001001 0000000001 1000001111   0 020  1   1 0221 0000  0 00000 000031???? ????100001 0000000  6   1 1 010??????? ???  ?   ? ????? ?????
Pygoluciola wittmeri       1  3 22122010 0000400011 0  0 10001001 0000000001 1000000001   0 020  4   1 0221 0000  0 00000 0000310000 1000100001 0000001  3   0 1 0100100001 011  1   0 01??? ?????
Curtos costipennis         1  0 12100020 1000300011 0  1 10001001 0000000001 1000000001   0 020  2   1 0110 0000  0 00000 0000101110 0001100101 0000000  6   1 1 0100100001 101  0   1 01??? ?????
Atyphella aphrogeneia      1  0 12100030 0001100011 0  1 10002000 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0   0 1 0100100000 001  1   0 01210 000?1
Atyphella atra             1  0 12100030 0000200011 0  2 01002010 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0   0 1 0102100001 002{01}{01}01210 00000
Atyphella brevis           1  0 12100030 0000100111 0  2 010020?0 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  3   2 1 01???????? ???  ?   ? ????? ?????
Atyphella carolinae        1  0 12100030 0000000011 0  ? 100020?0 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0   0 ? 01????000? ???  ?   ? ????? ?????
Atyphella conspicua        1  0 12100030 0000200011 0{12}11102000 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0   0 1 0132100001 012  1   1 01??? ?????
Atyphella costata          1{04}12100030 0000200011 0  1 10002001 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000000  6   1 1 0100100001 001  0   1 01??? ?????
Atyphella ellioti          1  0 12100030 0000200011 0  2 100020?0 0000100000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  1   1 1 02???????? ???  ?   ? ????? ?????
Atyphella flammans         1  0 12100030 0000200111 0  2 000020?0 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  3   2 1 0201100000 002  1   1 02210 00001
Atyphella flammulans       1  0 12100030 0000200111 0  2 010020?0 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  3   2 1 02???????? ???  ?   ? ????? ?????
Atyphella immaculata       1  0 12100030 0000100011 0  2 10002000 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000000  0   0 1 10???????? ???  ?   ? ????? ?????
Atyphella inconspicua      1{04}12100030 0000200011 0  2 11002000 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0 {01}1 0132100001 002  1   1 01??? ?????
Atyphella leucura          1  0 12100030 0000400011 0  1 10002000 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  5   1 1 02????000? ???  ?   ? ??21? ?????
Atyphella lewisi           1  0 12100030 0000200111 0  2 00002010 0000000000 0000000001   ? 0??  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  3   2 1 0242100001 012  0   0 01??? ?????
Atyphella lychnus          1  0 13100030 0000000011 0  2 10002010 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  3 {12}1 0102100000 002  1   1 01211 00101
Atyphella majuscula        1  0 12100030 0000100111 0  1 10002000 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0020001100 0000100101 0000010  0   0 1 1000100001 001  0   0 10211 01011
Atyphella marginipennis    1  0 12100030 0000200011 0  1 10002001 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000000  3   0 1 1000100001 001  0   1 10211 00011
Atyphella monteithi        1  0 13100030 0000100111 0  2 10002000 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0   0 1 01???????? ???  ?   ? ????? ?????
Atyphella olivieri         1  0 12100030 0000000111 0  1 000020?0 0000000001 1000000001   0 000  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  3   0 1 0201100000 001  1   1 02211 10101
Atyphella scintillans      1  0 13100030 0000000011 0  2 10002000 0000100000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0   0 1 0122100000 002  1   0 01211 10111
Atyphella similis          1  0 12100030 0000100011 0  2 11002000 0000000000 0000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000001  0 {01}1 0132100001 002  1   0 01210 00011
Atyphella wolfi            1  0 12100030 0000400111 0  1 10002000 0000000001 1000000001   0 010  2   1 0110 0000  0 00000 0000001100 0000100101 0000000  3   0 1 1000100000 011  0   1 10??? ?????
Atyphella Pygat. huonensis 1  0 13101130 0000200011 0  1 00002000 0000000001 1000000001   1 210  3   3 0110 0001  0 00000 0030001100 0000100101 0000001  5   1 1 0200100001 001  1   1 02??? ?????
Atyphella Pygat. obsoleta  1  0 13101130 0000200011 0  1 10002000 0000000001 1000000001   0 110  2   3 0110 0001  0 00000 0030001100 0000100101 0000001  5   1 1 0200100001 001  1   1 02??? ?????
Atyphella Pygat. undulata  1  0 13101030 000020001? 0  1 00002000 0000000001 1000000001   0 210  0   0 2001 0001  0 00000 00?0001100 0000100101 0000001  5   1 1 0200100001 001  1   1 02??? ?????
Sisiak                     1  3 12121030 0000200011 0  1 00002000 0000000001 1000000001   2 010  2   3 0110 0100  0 00000 0001000??2 0000200202 0101001  7   1 1 0200100001 001  1   0 02??? ?????
Mt Missim                  1  2 22130010 0000200010 0  0 20010202 0000001001 1000000001   0 020{12}  3 0110 0000  1 11000 0010001100 0000011101 0000010  7   1 1 0100100011 000  0   0 01??? ?????
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