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A NEW FIREFLY, *LUCIOLA (PYGOLUCIOLA) KINABALUA*, NEW SPECIES (COLEOPTERA: LAMPYRIDAE), FROM MALAYSIA, WITH OBSERVATIONS ON A POSSIBLE COPULATION CLAMP

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ABSTRACT. – *Luciola (Pygoluciola) kinabalua*, new species (Coleoptera: Lampyridae) is described from males and females; a key to males of the five known species of this subgenus is presented; morphology of the male and female terminal abdomen is described and it is suggested that a copulation clamp may function here. Continued cladistic analysis including this new species, which resembles the type *P. stylifer* Wittmer, 1939, continues to place *Luciola (Pygoluciola)* in a medial clade between *Luciola* and *Atyphella.*

KEY WORDS. – Lampyridae, Luciolinae, *Pygoluciola*, new species, copulation clamp.

INTRODUCTION

This rare subgenus of fireflies (*Pygoluciola*) is known from a handful of specimens and is restricted to the Malaysian states of Sabah and Sarawak; Haneda (1966) misidentified specimens of *Atyphella obsoleta* from New Guinea as *Pygoluciola* sp. *Pygoluciola* was described for a single species, *stylifer*, possessing unusual modifications to abdominal ventrite seven and tergite eight (Wittmer, 1939). McDermott (1966) regarded *Pygoluciola* as a subgenus of *Luciola* and Ballantyne (1968) redescribed the subgenus, keyed four species (two of them new), and assigned *Luciola hamulata* Olivier to *Luciola* (*Pygoluciola*). Aspects of the morphology of the genus were figured by Ballantyne & McLean (1970). Further, Ballantyne (1987b) described presumed sexual characters of certain species (e.g. curved legs, and terminal abdomen structure) and suggested uses in a reproductive context.

In an attempt to determine relationships within the Luciolinae, and to place the subgenus *Pygoluciola*, Ballantyne & Lambkin (2000) scored *Luciola (P.) stylifer* Wittmer in what was the first cladistic analysis of the Luciolinae, using 43 species. Because of many missing features, their analysis, while supporting the retention and extension of the genus *Atyphella* Olliff, revealed a confusing and problematic situation within the genus *Luciola*. Using *L. (P.) kinabalua*, new species, with its possession of a possible copulation clamp as a second examplar for this subgenus, with no missing adult characters, and '?' for larval characters only, Lambkin reran the analysis. Two near taxonomic equivalent taxa (Wilkinson, 1995) (*Atyphella brevis* Lea and *A. flammulans* Ballantyne), with many missing characters were removed to allow the analysis to complete (Ballantyne & Lambkin, 2000). Relationships were inferred from 42 taxa in four genera of the Luciolinae with polymorphic characters retained. These two analyses are the only ones undertaken on the Luciolinae. As neither offered unequivocal indications for directions the taxonomy should take *Luciola* (*Pygoluciola*) spp. are presented in the form devised by McDermott (1966) (see discussion).

Here we describe the new species and refine the cladistic analysis.

MATERIALS AND METHODS

The list of characters and states used in Ballantyne & Lambkin (2000) is repeated here for convenience, as is their data matrix (Table 1). Additional states occur with characters 6, 22, 68, and 82. Male abdominal sternites are called ventrites and are referred to by their actual number, which is one more than their visible number.

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Table 1. Data matrix describing 104 characters for 45 taxa including polymorphic coding. The minority state is indicated by placement in a separate row beneath the majority state for that particular taxon.

	10	20	30	40	50	60	70	80	90	100	
Photuris sp.	0001000410	0000211000	0100001011	0000000021	0000000000	0000000000	0000000000	0001001010	0001132100	0111102100	0000
Atyphella aphrogeneia	1011000300	0010000110	1100010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000100100	1100002100	00?1
Atyphella atra *	1011000300	0000000110	2010010100	0000000000	0000010102	1000000000	0000000001	0001001010	0000100102	1111012100	0000
										00	
Atyphella brevis *	1011000300	0000001110	2010010?00	0000000000	0000010102	1000000000	0000000001	0001001010	00001321??	??????????	????
Atyphella carolinae	1011000300	000000?110	?100010?00	0000000010	0000010102	1000000000	0000000001	0001001010	000100???	??????????	????
Atyphella conspicua *	1011000300	0000000110	2111010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000100132	111111????	????
			1								
Atyphella costata	1111000300	0000000110	1100010010	0000000010	0000010102	1000000000	0000000001	0001001010	0000061100	101000????	????
	0										
Atyphella ellioti *	1011000300	0000000110	2100010?00	0001000000	0000010102	1000000000	0000000001	0001001010	0000111??	??????????	????
Atyphella flammans *	1011000300	0000001110	2000010?00	0000000010	0000010102	1000000000	0000000001	0001001010	0000132101	1110012100	0001
Atyphella flammulans *	1011000300	0000001110	2010010?00	0000000010	0000010102	1000000000	0000000001	0001001010	00001321??	??????????	????
Atyphella immaculata *	1011000300	0000000110	2100010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000001??	??????????	????
Atyphella inconspicua *	1111000300	0000000110	2110010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000100132	111101????	????
	0								1		
Atyphella leucura	1011000300	0000000110	1100010000	0000000010	0000010102	1000000000	0000000001	0001001010	0000151l??	??????21??	????
Atyphella lewisi *	1011000300	0000001110	2000010100	0000000000	000010??2	1000000000	0000000001	0001001010	0000132142	100111????	????
Atyphella lychnus *	1012000300	0000000110	2100010100	0000000000	0000010102	1000000000	0000000001	0001001010	0000131102	1110012110	0101
									2		
Atyphella marginipennis	1011000300	0000000110	1100010010	0000000010	0000010102	1000000000	0000000001	0001001010	0000030100	1011002110	0011
Atyphella majuscula *	1011000300	0000001110	1100010000	0000000010	0000010102	1000000000	0000200001	0001001010	0000000100	1000002110	1011
Atyphella monteithi *	1012000300	0000001110	2100010000	0000000000	0000010102	1000000000	0000000001	0001001010	00001001??	??????????	????
Atyphella olivieri *	1011000300	0000001110	1000010?00	0000000010	0000010002	1000000000	0000000001	0001001010	0000130101	1110002111	0101
Atyphella scintillans *	1012000300	0000000110	2100010000	0001000000	0000010102	1000000000	0000000001	0001001010	0000100122	1100012111	0111
Atyphella similis *	1011000300	0000000110	2110010000	0000000000	0000010102	1000000000	0000000001	0001001010	0000100132	1101012100	0011
									1		
Atyphella wolfi	1011000300	0000001110	?100010000	0000000010	0000010102	1000000000	0000000001	0001001010	0000030100	101010????	????
Atyphella huonensis	1012011300	0000000110	1000010000	0000000010	0000011103	3100010000	0000300001	0001001010	0000151100	111100????	????
Atyphella obsoleta	1012011300	0000000110	1100010000	0000000010	0000010102	3100010000	0000300001	0001001010	0000151100	111100????	????
Bourgeosia hypocrita	1111000300	0002111121	2000010000	0000000010	000001???0	0000000000	0000000000	0000121000	0200000112	1001001010	2010
			1								
Colophotia praeusta	1011100200	0002100110	1100000020	0010100000	0000012204	3010103320	0010401000	1102003120	0010061100	101100????	????
Curtos costipennis	1011000201	0001000110	1100000010	0000000010	0000010202	0000000000	000000010?	0011001010	0000061100	101100????	????
Lampyroidea syriaca	1311100200	0002100111	1100010010	0000001000	0000010202	2000000000	0000000000	0000121010	0200120122	110111????	????
Luciola (Luciola) australis *	1111100200	0002110110	1100000010	0000000000	0000010103	1000000000	0000400000	0002001020	0010000100	1001000000	0001
	3										
Luciola (Luciola) cowleyi *	1110100300	0000100121	2000010000	0000000000	0000010200	0000000000	0000000000	0000000021	01001101??	??????????	????
	3										
Luciola (Luciola) dejeani *	1111000200	0002100110	1100000010	0000000010	0000010000	0000000000	0000000000	0000121000	0200061l??	??????????	????
Luciola (Luciola) flavicollis *	1111100200	0002100110	1100000010	0000000000	0000010203	1000000000	0000400000	0002001020	0010020000	1011000000	0001
	3					3			41		
Luciola (Luciola) italica	1011000200	0002110110	1100010010	0000000010	0000010000	0000000000	0000000000	0000121000	0200000100	100100????	????
Luciola (Luciola) nigra *	1111100200	0002100110	1100000010	0000000000	0000010203	1000000000	0000400000	0002001020	0010000000	1001000000	0001
	3				1	2					
Luciola (Luciola) orapallida *	1111100200	0002100110	1100000010	0000000000	0000010201	1000000000	0000400000	0002001020	0010020100	1011000000	0001
	3										
Luciola (Hotaria) parvula	1011000200	0002100110	1100010?10	0000000010	0000010100	0000000000	0000000000	0000121000	0200100112	110101????	????
Luciola (Pygoluciola) stylifer	1231300?00	000???01?0	01?00000??	0000000010	0000110201	3200000000	00?0???01?	00?1000010	0000161l??	??????????	????
Luciola (Pygoluciola) kinabalua	1231320100	0002000110	0300010020	0000000010	0000010204	1200000000	0000000310	0001000010	0300171100	100100????	????
					1					1	
Pyrophanes beccarii *	1111100200	0002110100	1100000010	1000000000	1111112103	1001001111	1001400000	0102002120	1010000100	100110????	????
										1	
Pteroptyx cribellata *	1111100200	1102010110	1100000010	0000000000	0000010103	1000001210	0110400000	0002001020	0010000000	100100????	????
Pteroptyx macdermotti	1111100200	11020?0010	1100000020	1100000100	1000012214	1000003111	1001400200	0102002120	0010061100	1011?0????	????
Pteroptyx malaccae	1111100200	1102010100	1100000010	1000000000	1001012103	1000002210	0000400000	0102001120	0010061100	100100????	????
						1					
Pteroptyx platygaster *	1111100200	1202010110	1100000010	0000000000	0000010103	1000001210	0110400000	0002001020	0010000000	100100????	????
Sisiak	1211210300	0000000110	1000010000	0000000010	0000012102	3001000000	0000010001	0002002020	1010171100	110100????	????
Mtmissim	1221400100	0000000100	02001?2020	0000010010	0000010202	3100001110	0000100000	0001111010	0200071100	100100????	????

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 sternite 7; MS, mesoscutellum; LL, lateral lobe aedeagus; PLP, posterolateral projections of ventrite seven; SIW, smallest interocular width; T7, T8, abdominal tergite seven, eight; V 3-7, abdominal ventrites three-seven.

Character Analysis. – In the following discussion the characters are numbered according to sequence in the data matrix and the designated states are numbered to the right. The matrix of taxa and assigned character states is given in Table 1.

ADULT MALE MORPHOLOGY (CHARACTERS 1-88)

Pronotum (1-9)

1. hypomera
   - open 0
   - closed in front 1

2. lateral pronotal margins
   - diverging along anterior half or more with some convergence in posterior area (Ballantyne & Lambkin, 2000: Figs. 1a-d, f, g, i-l) 0
   - subparallel or wider across middle with slight convergence anteriorly and posteriorly 1
   - diverging along their length (Ballantyne & McLean, 1970: Fig. 4c) 2
   - converging posteriorly along their length (Ballantyne & Lambkin, 2000: Fig. 19a) 3

In states 0 and 2 the pronotum is wider across the base than across the middle; in state 1 it is wider across the middle than across the base.

3. Anterolateral corners of pronotum
   - obliterated (McDermott & Buck, 1959: Fig. 38) 0
   - rounded obtuse (Ballantyne & Lambkin, 2000: Figs. 1, 19a-e) 1
   - pointed (Ballantyne, 1968: Fig. 130) 2
   - acutely rounded (Ballantyne, 1968: Fig. 120) 3

4. Degree of head exposure in front of pronotum
   - greatly exposed 0
   - scarce to moderately exposed 1
   - completely concealed 2

The head is either greatly exposed in front of the pronotum (when the head cannot be retracted beneath the pronotum), slightly exposed (when at least some of the posterior section of the head is retracted beneath the pronotum at rest) or completely concealed (not visible from above).

5. Posterolateral corners of pronotum
   - rounded obtuse (Ballantyne & Lambkin, 2000: Figs. 1a-c, d, f-g, I, j-l) 0
   - right angled or angulate obtuse (Figs. 19c-e; Ballantyne & McLean, 1970: Fig. 4h) 1
   - rounded acute 2
   - broadly pointed (Ballantyne, 1968: Fig. 120) 3
   - narrowly pointed (Ballantyne, 1968: Fig. 130) 4

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 emargination 2

7. Lateral margin of pronotum near posterolateral corner
   - not indented 0
   - slightly indented 1

8. Lateral margin of pronotum
   - 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

9. Anterior margin of pronotum
   - not explanate 0
   - narrowly explanate 1

Elytron (10-17)

10. Punctation
    - not conspicuously larger than pronotal punctation 0
    - conspicuously larger than pronotal punctation 1

11. Apex
    - not deflexed 0
    - deflexed with apex rounded (Ballantyne & Lambkin, 2000: Figs. 20j, k) 1

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

13. Development of epipleuron and sutural apex in apical half of elytron
    - no thicker than rest 0
    - considerably thicker than anterior portions 1

14. Interstitial lines
    - 2-4 well defined lines 0
    - one only defined line (line 3) 1
    - no lines well defined 2

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

16. Sutural ridge
    - extending to apex of elytron 0
    - evanescent before elytral apex 1

17. Margins
    - parallel sided 0
    - convex sided 1

Head (18-39)

18. Depression of vertex
    - minimal 0
    - moderate - deep 1

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

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.

21. Antenna length
    - much longer than twice GHW 0
    - > GHW - 2 x GHW 1
    - subequal to GHW 2

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

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

24. Median area of frons vertex junction
    - not elevated or indented 0
    - elevated and/or indented (Ballantyne & Lambkin, 2000: Figs. 2f, g) 1

25. Anterior margin of head
    - not prolonged 0
    - prolonged in front of eye for about its width (Ballantyne, 1968: Figs. 132, 134) 1

26. Labrum
    - approximately twice as wide as long 0
    - about as long as wide 1

27. Clypeolabral suture
    - flexible 0
    - inflexible, visible 1
    - inflexible and invisible (Ballantyne, 1968: Figs. 132, 134) 2

John Lawrence (ANIC Canberra) interpreted the nature of the labrum and clypeus on specimens of *Photuris* and "Mt Missim'.

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.

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

30. Antennal flagellar segment 1
    - as long as or longer than pedicel 0
    - shorter than pedicel 1

31. Apex of antennal flagellar segment 1
    - not expanded at its outer apex 0
    - expanded at its outer apex 1

32. Median area of antennal flagellar segment 1
    - not produced 0
    - produced (Ballantyne & McLean, 1970: Fig. 18b) 1

33. Flagellar segments 7-9
    - not conspicuously shorter than rest of FS 0
    - conspicuously shorter than rest of FS 1

34. Number of segments
    - 11 — 0
    - < 11 — 1

35. Flagellar segment 9
    - apically rounded — 0
    - apically pointed — 1

36. Flagellar segments 2-8
    - not expanded — 0
    - expanded at anterior apical angle — 1

37. Antennal segments
    - not flattened — 0
    - flattened — 1

38. Pedicel
    - not produced at outer apex — 0
    - produced at outer apex — 1

39. Shape of labial palpi
    - fusiform or about as wide as long with inner margin entire — 0
    - dentate, laterally flattened — 1
    - lunate, inner margins entire — 2

Legs (40-45)

40. Inner tarsal claw of each leg
    - not split — 0
    - split — 1

41. Metafemoral comb (Ballantyne, 1987a: Fig. 1j)
    - absent — 0
    - present — 1

42. Femora 3 (Ballantyne & McLean, 1970: Fig. 4p)
    - not swollen — 0
    - swollen — 1

43. Curvature of femora 3
    - not curved — 0
    - curved along their length (Ballantyne & Lambkin, 2000: Fig. 26h) — 1

44. Swelling of tibiae 3
    - not swollen — 0
    - swollen at least at their apices (Ballantyne & Lambkin, 2000: Fig. 26h) — 1

45. Curvature of tibiae 3
    - not curved — 0
    - curved (Ballantyne & Lambkin, 2000: Fig. 26h) — 1

Abdominal sternites (46-62)

46. Sternite 8
    - present — 0
    - absent — 1

47. Light organ in sternite 7
    - entire (e.g. Ballantyne & Lambkin, 2000: Fig. 4a) — 0
    - posterior medial division short - long1 (Ballantyne, 1968: Figs. 42, 91) — 1
    - bipartite (Ballantyne & Lambkin, 2000: Fig. 26a) — 3

48. Light organ in sternite 7
    - reaching sides and posterior margin of sternite 7 — 0
    - reaching sides but not posterior margin — 1
    - not reaching sides or posterior margin — 2

49. Size of light organs
    - occupying at least half of the area of sternite 7 or more — 0
    - restricted to very small paired anterolateral plaques that occupy less than 10% of the area of sternite 7 (Ballantyne & McLean, 1970: Fig. 18c) — 1

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

51. Length/ width of MPP of sternite 7
    - not produced — 0
    - about as long as broad or shorter; narrower than half the width of sternite 7 — 1
    - about as long as broad; at least half as wide as sternite 7 — 2
    - at least twice as long as wide — 3

52. MPP of sternite 7
    - not engulfed (e.g. Ballantyne & Lambkin, 2000: Fig. 4a) — 0
    - partially engulfed and surrounded laterally by the slightly downturned apex of tergite 8 (Ballantyne, 1968: Figs. 5, 9, 26, 91) — 1
    - engulfed by the down turned apex of tergite 8 completely (Ballantyne, 1968: Figs. 18, 107-109, 111, 113) — 2

53. Median longitudinal carina in sternite 7
    - absent — 0
    - present (Ballantyne & McLean, 1970: Figs. 3d, f) — 1

54. Median longitudinal trough in sternite 7
    - absent — 0
    - present — 1

55. Median longitudinal trough on ventral surface of MPP
    - absent — 0
    - present (Ballantyne & McLean, 1970: Figs. 3d, f) — 1

56. All of sternite 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

57. Length of PLP of sternite 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: Figs. 2a, b) 3

58. Width of PLP of sternite 7
    - not developed 0
    - narrower than MPP (Ballantyne & Lambkin, 2000: Fig. 26a) 1
    - as wide as MPP (Ballantyne & McLean, 1970: Figs. 9a, b) 2
    - broader than MPP (Ballantyne, 1987b: Figs. 2a, b) 3

59. Inclination of PLP of sternite 7
    - not developed 0
    - horizontal 1
    - oblique - vertical (Ballantyne & McLean, 1970: Figs. 3d, f; Ballantyne, 1968: Figs. 11, 13) 2

60. Incurving hairy lobes along posterior margin of sternite 7 (Ballantyne & Lambkin, 2000: Fig. 26a)
    - absent 0
    - present 1

61. Pointed projection of sternite 7 posterior margin (Ballantyne & Lambkin, 2000: Fig. 26a)
    - absent 0
    - present 1

62. Dimple on sternite 7 (Ballantyne & Lambkin, 2000: Fig. 20k)
    - absent 0
    - present 1

Abdominal tergites (63-70)

63. Ventral face of tergite 8
    - lacking flanges 0
    - with symmetrical flanges (Ballantyne & Lambkin, 2000: Fig. 20l) 1
    - with asymmetrical flanges (Ballantyne, 1987a: Fig. 13r) 2

64. Ventral face of tergite 8 with depressed lateral troughs (Ballantyne & Lambkin, 2000: Figs. 26c, d)
    - absent 0
    - present 1

65. 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 longt trough 1
    - slightly thickened barely elevated ridges margining a median longt trough 2
    - low barely elevated ridges present in posterior half of ventral surface only 3
    - longt. raised well developed ridges delimiting a median longitudinal trough 4

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.

67. Bifurcate anterior margin of tergite 8
    - about as long as or no longer than entire posterior (visible) part of tergite 0
    - at least 3 times as long as entire posterior visible part of tergite 1

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

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 (70-73)

70. Symmetry of aedeagal sheath sternite
    - symmetrical in posterior half (Ballantyne & Lambkin, 2000: Figs. 21b, d, e) 0
    - asymmetrical in posterior half (Ballantyne & Lambkin, 2000: Fig. 21i) 1

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

72. Lateral margins of aedeagal sheath
    - lacking paraprocts (Ballantyne & Lambkin, 2000: Figs. 21c, d) 0
    - with paraprocts (Ballantyne & Lambkin, 2000: Figs. 21a, b) 1
73. Length/width of tergite 9 of aedeagal sheath
    - about as long as wide 0
    - much wider than long 1

Aedeagus (74-84)

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) 1
    - narrow (less than 2/1) (Ballantyne & Lambkin, 2000: Figs. 21o, r, u; 26e) 2
75. Inclination of apex of median lobe
    - not curving ventrally 0
    - curving ventrally (Ballantyne, 1968: Figs. 164, 168) 1
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
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
78. Separation of lateral lobes of aedeagus
    - separated for > half their length 0
    - separated for less than half their length (Ballantyne & Lambkin, 2000: Figs. 26e-g) 1
79. Width of lateral lobes of aedeagus
    - much wider and flatter at their apices than widest point of ML (Ballantyne & Lambkin, 2000: Figs. 21l, 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: Figs. 21p, s, u, v, 26e-g) 2
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
81. Aedeagal symmetry
    - symmetrical 0
    - asymmetrical (Ballantyne & Lambkin, 2000: Figs. 26e, f) 1
82. Fleshy lobes on lateral lobes
    - absent 0
    - present as short rounded projections (Ballantyne & Lambkin, 2000: Fig. 21k) 1
    - present as elongate leaf like lobes (Ballantyne & Lambkin, 2000: Figs. 21l, n) 2
    - present as elongate flat hair bearing structures 3
83. Extent of ventral face of apices of lateral lobes
    - extending to either side of ML and visible frombeneath (Ballantyne & Lambkin, 2000: Figs. 5, 21k, l, m) 0
    - not extending to either side of ML and not visible from beneath (Ballantyne & Lambkin, 2000: Figs. 21o, p, r, s, u, v, 26e-g) 1
84. Lateral appendages of lateral lobes
    - absent 0
    - present (McDermott & Buck, 1959: Figs. 62a-c) 1

Male colour patterns (85-88)

85. Colour of pronotum
    - pronotum concolourous 0
    - pronotum with dark markings 1
86. Colour of elytral margins compared to rest of elytra
    - elytra concolourous (dark – light 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 only 6
    - elytra concolourous (Pale) 7
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
88. Colour of terminal abdominal tergum
    - As dark as or darker than preceding terga 0
    - Pale (as pale as preceding terga or paler) 1

ADULT FEMALE MORPHOLOGY (89-96)

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.

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
91. Extent of female light organ
    - occupying sternites 6 and 7 0
    - restricted to sternite 6 1
92. Colour of pronotum
    - pronotum concolourous 0
    - pronotum with coloured markings 1
93. Colour of elytra
    - elytra concolourous 0
    - elytra not 1
94. Number of elytral interstitial lines
    - four 0
    - less than 4 1
95. Nature of pronotal punctures
    - contiguous in at least lateral areas 0
    - not contiguous in any area 1
96. Head form
    - of winged female form (Ballantyne & Lambkin, 2000: Fig. 6b) 0
    - of wingless female form (Ballantyne & Lambkin, 2000: Figs. 6d, e) 1

LARVAL MORPHOLOGY (97-104)

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
98. Length/width of pronotum
    - longer than wide 0
    - about as long as wide 1
99. Nature of tergal margins
    - not ridged 0
    - ridged 1
100. Paired dorsal and ventral tubercles on protergum
    - absent 0
    - present (Ballantyne & Lambkin, 2000: Figs. 15a, c) 1
101. Shape of posterolateral corners of protergum
    - rounded (Ballantyne & Lambkin, 2000: Fig. 15a-c) 0
    - acute (Ballantyne & Lambkin, 2000: Fig. 12c) 1
    - narrowly produced 2
102. Margins of median line on terga 1-10
    - not ridged 0
    - ridged 1
103. Size of punctures in anterior half of terga 2-10
    - no larger than rest 0
    - larger than rest 1
104. Extent of posterolateral corners of tergum 11
    - not produced (Ballantyne & Lambkin, 2000: Figs. 7a, 15b) 0
    - produced (Ballantyne & Lambkin, 2000: Figs. 12a-c, 15a, c) 1

TAXONOMY

Luciola subgenus *Pygoluciola* (Wittmer)

Pygoluciola Wittmer, 1939: 21.

Luciola (Pygoluciola) (Wittmer). McDermott, 1966:115; Ballantyne, 1968: 119; Ballantyne & McLean, 1970: 233; Ballantyne & Lambkin, 2000:82.

Type species. – *Pygoluciola stylifer* Wittmer, 1939, monobasic.

Key to species of *Luciola* (*Pygoluciola*) using males

1. All tibiae curved .... *guigliae* (Ballantyne)
– No tibiae curved 2

2. Median posterior projection of abdominal sternite 7 bifurcate at apex 3
– Median posterior projection of abdominal sternite 7 not bifurcate at apex 4

3. Median posterior projection of abdominal sternite 7 widely bifurcate, laterally ensheathing the downturned apex of tergite 8 and projecting laterally beyond it .... *wittmeri* (Ballantyne)
– Median posterior projection of abdominal sternite 7 narrowly bifurcate, not laterally ensheathing the downturned apex of tergite 8 and not projecting beyond it .... *kinabalua*, new species

4. Apex of abdominal tergite 8 entire .... *hamulata* (Olivier)
– Apex of tergite 8 emarginate .... *stylifer* (Wittmer)

Luciola (Pygoluciola) kinabalua, new species
(Figs. 1-19; Table 1)

Material examined. – Types – MALAYSIA: SABAH. 6.10°N, 116.40°E, Mt Kinabalu, Mesialu (camp): 5000ft, 13-15 Mar.1964, coll. S. Kueh, three males, three females; two males, five females, coll. J. Smart (31 Jan.1964, female; 2 Feb.1964, female; 6 Feb.1964, male, female; 19 Feb.1964, male, two females). Mt Kinabalu, Kundasan: 20-26 Feb.1964, coll. J. Smart, male. All specimens in Natural History Museum, London.

Male. – 10.6-11.3 mm long.

Pronotum light brown, semitransparent and appearing paler in some areas because of underlying fat body; with median brown markings (Fig. 1) which are difficult to discern in some males because of age and underlying fat body (85, 1); MS and MN light brown; elytra uniformly pale brown (86, 7; 87, 1); head, mouthparts, venter of thorax, and all legs dark reddish-brown except for paler basal half of femora; antennae dark red-brown at base, FS 5-7 are paler in four of six males; basal abdominal tergites dark brown, T 7, 8 yellow (88, 1); abdominal ventrites 2-4 pale brown in median area and darker at sides; V 5 moderately brown, darker at sides; light organs in V 6 and V 7 yellowish, rest of V 7 is brown.

Pronotum (Fig. 1) 2.9-3 mm wide; 1.6-1.8 mm long; width/length = 0.5-0.6; lateral pronotal margins diverge along their length (2, 2); median anterior margin rounded, barely projecting beyond anterolateral corners; anterolateral corners angulate, acutely rounded, and project slightly anteriorly (3, 3); head only slightly exposed in front of pronotum (4, 1); posterolateral corners broadly pointed (5, 3); posterolateral corners project beyond posterior margin and delimited from rest of posterior margin by shallow emarginations (6, 2); lateral margin near posterolateral corner not indented (7,0); lateral margin seen from beneath is flattened in posterior 2/3, more widely so in posterior half than in anterior area (8, 1); dorsal surface of pronotum smooth and flat; punctures small, shallow, fairly inconspicuous, some contiguous, some separated by their width;

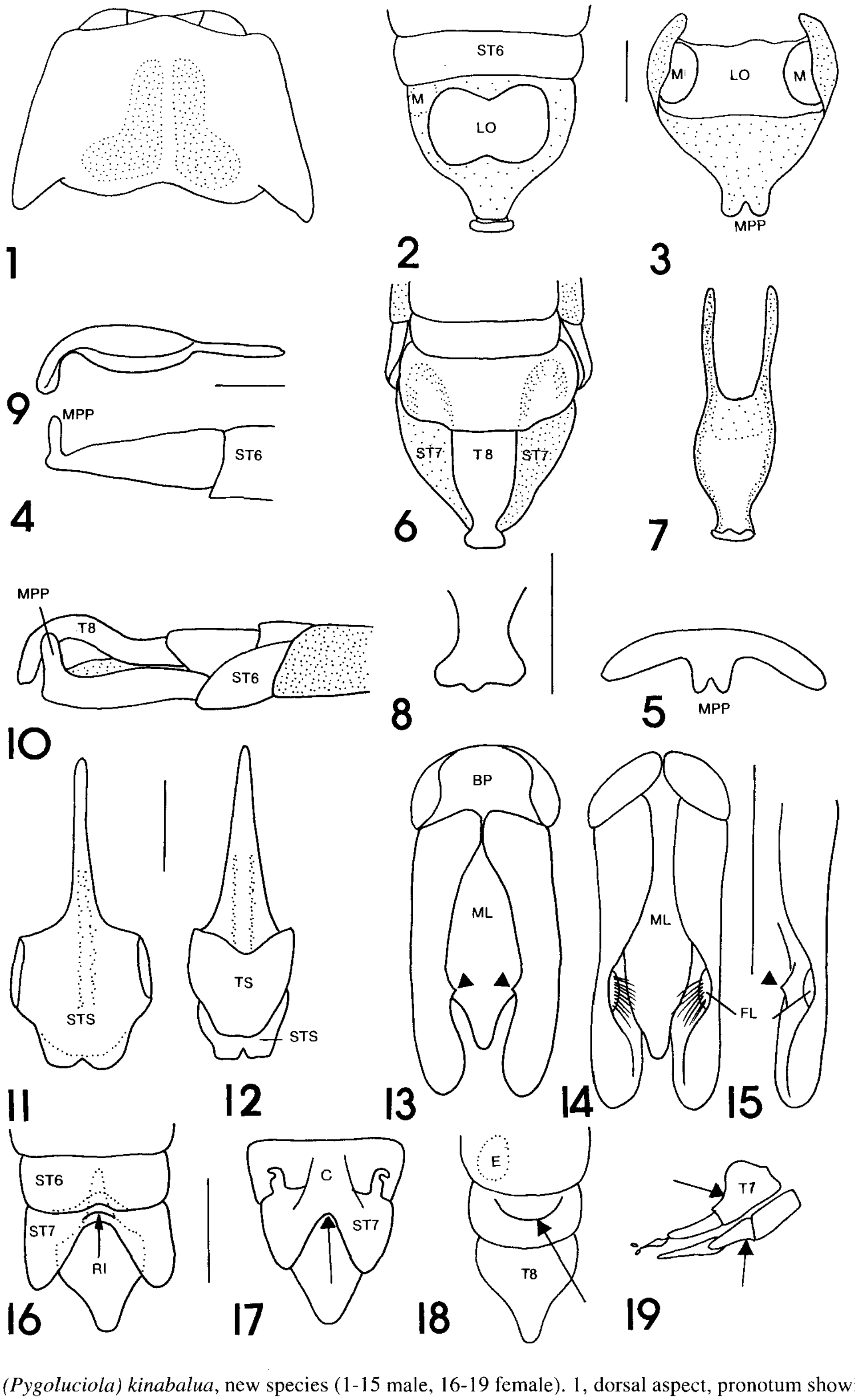
Elytron 9.2-9.2 mm long; punctation not conspicuously larger than pronotal punctation (10, 0), not linear; four interstitial lines delimited by punctures but scarcely elevated (14, 2); apex not deflexed (11, 0; 12, 0); epipleuron and sutural ridge extending to apex (15, 0; 16, 0), but neither thickened in apical half (13, 0); preapical sutural apex not downturned; lateral margins not strongly explanate; elytral epipleuron not strongly expanded; margins parallel-sided (17, 0).

Head with GHW 1.75mm; SIW 0.5-0.57 mm; SIW/GHW 1/3 (29, 2); antennal sockets separated by more than twice but not three times ASW (22, 3); vertex moderately depressed (18, 1); eye separation on ventral surface just behind mouthparts/GHW 0.2 (19, 1); posterolateral eye excavation absent (20, 0); frons-vertex junction rounded (23, 0), median area not elevated or indented (24, 0); anterior head margin not prolonged in front of eye for its width (25, 0); labrum about as long as wide (26, 1); clypeolabral suture flexible (27, 0). *Mouthparts* functional (28, 0); apical segment of labial palpi laterally flattened and inner margin dentate (39, 1). *Antennae* 11 segmented (34, 0); about three times as long as GHW (21, 0); no segments flattened, expanded or laterally produced (31, 0; 32, 0; 36, 0; 37, 0; 38, 0); FS 1 longer than pedicel (30, 0); all FS elongate slender, four to five times as long as wide, FS 7-9 not conspicuously shortened (33, 0), 7, 8 as long as preceding segments, FS 9 about 2/3 as long as FS 8 and apically acutely rounded (35, 0). *Legs* lacking metafemoral comb (41, 0); no segments swollen or curved (42-45, 0); inner tarsal claw not split (40, 0).

Abdomen (Figs. 2-10): posterior margins of ventrites 3, 4 not recurved. Light organ in V 7 entire, occupying more than half its area (49, 0), posterior margin of light organ with short medial emargination in five of six males (47, 0, 1) (Fig. 2); V 7 light organ not reaching anterior margin or sides (48, 2), median anterior margin broadly emarginate; strong dorso-ventral muscle blocks occur at anterolateral corners of V 7 to the sides of the light organ (Figs. 2, 3); V 7 posterior to light organ not expanded or swollen (56, 0); no hairy lobes or pointed projections along posterior margin of V 7 (60, 0; 61, 0); posterolateral processes of V 7 absent (57-59, 0); dorsal face of V 7 posterior to light organ is smoothly sclerotized and lacks muscle attachments (Fig. 3); no median longitudinal groove, carina, or dimple on V 7 (53, 0; 54, 0; 55, 0; 62, 0); MPP of V 7 (Figs. 2-4, 10) not visible from beneath, arising just before the posterior dorsal margin and inclining dorsally; about as wide as long (51, 1), symmetrical, apex emarginate (50, 4), and engulfed wholly or partially by the downturned apex of T 8 (52, 2); T 7 (Figs. 6-10) wider than long, with strong depressed areas laterally which attach to the dorsoventral muscles arising in V 7; median longitudinal area of T 7 elevated over the anterior prolongation of T 8; T 8 (Figs. 6-10) elongate slender, half as wide as T 7 (68, 3), narrowed in posterior 1/4 (69, 1), inclining ventrally and enveloping the MPP of V 7; anterior margin of T 8 (Fig. 7) bifurcate into two elongate slender apically rounded projections (67, 0); posterior margin asymmetrically biemarginate (Fig. 8); ventral surface smooth, lacking any median longitudinal groove, lateral ridges, depressed troughs, flanges, or any asymmetrical projections (63-66, 0) (Fig. 7).

Aedeagal sheath (Figs. 11-12) symmetrical especially in posterior half (70, 0), lacking paraprocts (72, 0) although tergite 9 may be narrowly visible laterally; sternite 9 with anterior half elongate slender and rounded anteriorly, posterior half broad (71, 0), about as wide as long with posterior margin medially emarginate; anterior margin of sheath tergite emarginate; tergite 9 about as wide as long (73, 0).

Aedeagus (Figs. 13-15) symmetrical (81, 0), moderately wide (74, 1); ML shorter than LL (77, 0) and apex narrowed,



Figs. 1-19. *Luciola (Pygoluciola) kinabalua*, new species (1-15 male, 16-19 female). 1, dorsal aspect, pronotum showing anterior margin of head. 2-5, 16-17, terminal abdominal ventrites (2, ventral surface of ventrites 5-7(dorsoventral muscle block shown on left only); 3, dorsal, ventrite 7 showing anterolateral areas of dorso-ventral muscle attachment; 4, left lateral ventrites 6, 7, dorsal face uppermost; 5, posterior margin of ventrite 7, ventral face uppermost, viewed along longitudinal body axis); 16, ventral, ventrites 5-8 (outline of anterior prolongation of ventrite 7 stippled; hole at base of ventrite 7 occurs just below arrow indicating ridge); 17, dorsal face, ventrites 6-8 (arrow indicates hole at base of ventrite 7). 6-9, 18, terminal abdominal tergites (6, dorsal aspect segments 4-7; 18, dorsal aspect segments 6-8; 7, 9, ventral, and left lateral tergite 8, tergite 9 with dorsal face uppermost; 8, ventral apex of tergite 8). 10, 19, terminal abdomen, left lateral, dorsal surface uppermost (in 19 arrows show positions of posterior margin of elevation of tergite 8 surface, and median anterior ridge on ventrite 7). 11, 12, aedeagal sheath, ventral and dorsal. 13-15, aedeagus (13, dorsal, 14 ventral,15 ventral, detail left lateral lobe, hairy lobe drawn without hairs); arrows on 13, 15 indicate pointed projection of inner dorsal surface of lateral lobes. Scale lines are 1 mm; scale lines shared by 1, 4-7, 9, 10; 2-3; 11-12; 13-15; 16-19. Figure Legend: BP basal piece aedeagus; E outline of egg; C cuticle prolongation of Ventrite 7; FL hair bearing lobe; M Muscle; MPP median posterior projection ventrite 7; RI ridge; ST 6-8 ventrites 6-8; STS sternite aedeagal sheath; T 7-8 tergites 7, 8; TS tergite aedeagal sheath.

rounded, not curving ventrally (75, 0) and preapical ventral area not produced (76, 0); LL separated for most of their length dorsally (78, 0); apices of LL about as wide as base of ML (79, 1); ventral faces of apices of LL extend to either side of ML and are visible from beneath (83, 0); LL bearing small elongate flattened hair bearing lobes on their inner ventral surface (82, 3), and small short pointed projections along inner dorsal margin at apical third (Figs. 13, 15 arrowed).

Female. – 10.9-12 mm long.

Macropterous (89,0; 90,0) and assumed capable of flight; dorsal colouration as for male (93, 0) except dark pronotal markings may be sparse (92, 0, 1), and are lacking in one of six females which has bright yellow pronotum; ventral colouration as for male except antennae all dark brown, abdominal ventrites 2-5 brown, light organ in V6 is dull creamy yellow (91, 1), and V 7 and 8 are clear shiny semitransparent yellow; basal abdominal tergites brown, T 7, 8 pale yellow.

Pronotum 1.6-1.9 mm long, 2.1-3.5 mm wide; outline as for male except anterolateral corners are rounded obtuse, and lateral margins may converge slightly in posterior 1/6 in six of eight females (convergence in two specimens is on right and not left side). Median posterior margin of light organ and ventrite 6 shallowly emarginate. V 7 widely and deeply medianly emarginate, with a median transverse ridge just anterior to the emargination, anterior margin of V 7 with a median prolongation of cuticle and anterolateral corners with short strong curved prolongations; T 7 with strongly sclerotised elevated median mound. In these dried specimens the base of V 7 bends away from that of V 8 and a median hole appears (Figs. 16, 17 arrow shows position; this is probably a postmortem change; it is only visible from behind). It was not possible on these very dry specimens to determine any internal structure apart from the obvious and numerous eggs.

Larva.– Unknown.

A POSSIBLE COPULATION CLAMP IN *LUCIOLA (PYGOLUCIOLA) KINABALUA*, NEW SPECIES

Within the Luciolinae, it is the males which usually display the array of modifications to legs, wings and the terminal abdomen, which have been used as a basis for generic distinction (McDermott, 1966), and assumed to be of sexual significance. Ballantyne (1987b) reviewed these modifications and suggested possible uses in a reproductive context for many of them. However only in *Pteroptyx valida* have modifications of the terminal abdomen and deflexed elytral apices been reliably correlated with sexual behaviour. Here a copulation clamp functions; the female terminal abdomen is wedged between the MPP of abdominal ventrite 7 of the male pressing from below and the deflexed elytral apices from above. The female lacks obvious external modifications, but has internal sclerotisation of the bursa apparently to accommodate this pressure (Lloyd & Wing, 1981; Lloyd et al., 1982; Wing et al., 1983). A wider occurrence of such a clamp in fireflies with deflexed elytral apices is anticipated.

Modifications of the male abdomen (similar to those seen in *Luciola (Pygoluciola) kinabalua*), where the median posterior projection of ventrite 7 engages in some manner against tergite 8, leaving the lateral margins free and open, have been variably interpreted. Ballantyne (1987b) considered that in *Luciola (Pygoluciola)* spp. the additional posterior prolongation and ventral flexion of tergite 8 could contribute a mechanical advantage in physically deterring other males from even attempting to copulate with an already coupled female (assuming male above female).

In *Luciola (Pygoluciola) kinabalua* the female abdomen exhibits external features not known in other female Luciolinae viz. the swelling and hardening of the dorsal surface of tergite 7; the small hard ridge in the anteromedian area of ventrite 7 anterior to the wide and deep emargination of its posterior margin, and the strongly hooked and sclerotized anterolateral prolongations of its anterior margin. The form of the male abdomen and the very strong dorso-ventral muscles of ventrite 7, suggest the possibility that the end of the male abdomen opens in a pincer fashion and engages against the female abdomen in these positions. If the pair were coupled with heads facing in opposite directions then the apex of the male tergite 8 may engage against the hard swollen surface of the female tergite 7, being prevented from doing internal damage or moving further forward by this swelling; the apex of ventrite 7 would abut the median ridge in the anterior portion of ventrite 7. As no determinations of internal structure were possible is it not known what role, if any, the median 'hole' that appears between V7 and V8, other than being a post-mortem change.

CLADISTIC ANALYSIS

Terminal taxa. – For our previous attempt to analyse Luciolinae phylogeny using the methods of cladistics LB examined specimens of 43 taxa of the Luciolinae and coded morphological features which clearly distinguished species, groups of species, or genera. That analysis included all the Australian species plus a wider analysis of the Luciolinae based where possible on the type species of each genus and subgenus as defined in McDermott, 1966. Alternatively genera were scored from a representative species for which specimens were accessible and/or published information exists. LB scored all but *Photuroluciola* Pic which is not reliably identified in collections.

A representative collection of New Guinean species considered by Ballantyne (1992) to be closely related to the Australian fauna was included, and two distinctive but as yet unnamed groups from New Guinea code named 'Sisiak' (= '*Luciola* species 12' in Ballantyne,1987: Figs. 1c-f, page 185), and 'MtMissim'. A single female of the latter was described by Ballantyne (1968: 122, Figs. 130-132, 134) as possibly belonging to *Luciola (Pygoluciola)*; the species is

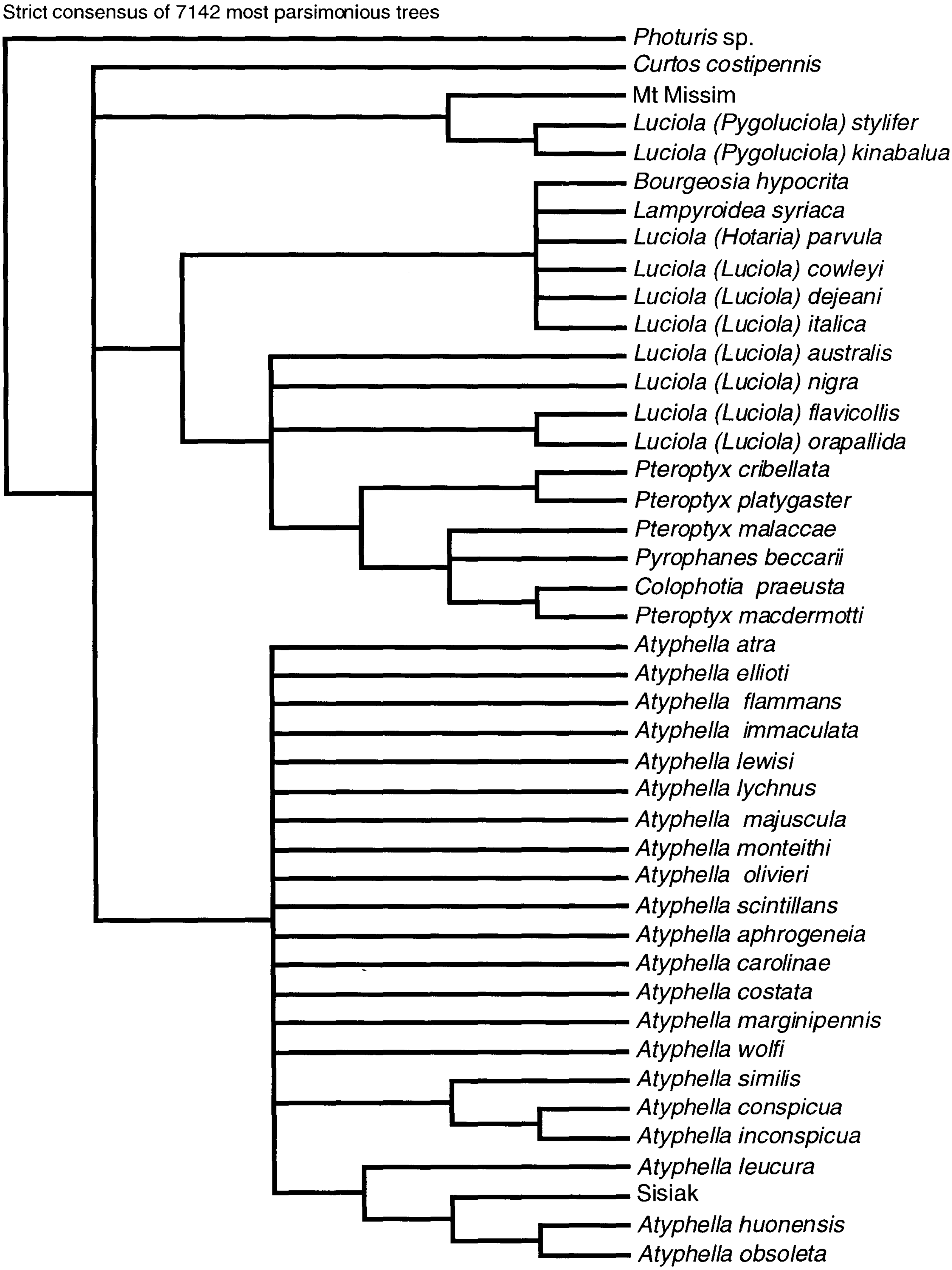


Fig. 20. Strict and semistrict consensus of 7142 most parsimonious trees for 104 characters, including polymorphisms, of 43 taxa.

now known from two males (Ballantyne, 1992), but is as yet undescribed and its taxonomic position undetermined.

The previous attempt to determine the correct position for the *Pygoluciola* subgenus was hampered because scoring was based on published descriptions only and many characters were scored as '?' (Ballantyne & Lambkin, 2000). It has been possible using specimens of *Luciola* (*Pygoluciola*) *kinabalua* sp. nov. to assign states to all but seven larval characters. As the other species in the subgenus are lacking either females or larvae, they have not been included here.

Two near taxonomic equivalent taxa (Wilkinson, 1995) (*Atyphella brevis* and *A. flammulans*) with many missing characters were removed to allow the analysis to complete (Ballantyne & Lambkin, 2000). These two species were removed from this analysis because, while missing all female and larval characters, they differ from other taxa by only a single homoplasious, but informative, character. Relationships were therefore inferred from 42 taxa (Figs. 20-21) in four genera of the Luciolinae.

Cladistic analysis

Where possible characters are given numbers and states to correspond to those used in Ballantyne & Lambkin 2000; e.g. 'head moderately exposed 4 (1)' = character 4, state 1 (Table 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.

Certain autapomorphic characters (modifications of female abdomen correlated with a possible copulation clamp, the narrow anterior prolongation of the aedeagal sheath sternite, the narrow apex of the median lobe and hooks on the lateral lobes of the aedeagus) were newly identified here and thus are not scored in Ballantyne & Lambkin's matrix. Additions necessary to the state descriptors of four of their characters to accommodate *L. (P.) kinabalua* are: character 6, additional state 2 = posterolateral corners of pronotum projecting beyond posterior margin but not delimited by a wide emargination (Fig. 1); character 22, additional state 3 = antennal sockets separated by greater than twice but not three times their width; character 68, additional state 3 = abdominal tergite eight longer than wide but not projecting considerably beyond ventrite seven; character 82, additional state 3 = fleshy lobes on aedeagal lateral lobes present as elongate flat hair bearing structures (Figs. 14, 15).

Cladistic analyses were performed with polymorphic characters interpreted as 'partial uncertainty'. PAUP chooses a state from the set of available states that allows minimisation of the tree length (Swofford, 1993).

We performed a parsimony-based phylogenetic analyses of the 104 characters for 43 taxa with heuristic searches of the data using 10 random step-wise addition sequences, tree-bisection-reconnection (TBR) branch swapping, MULPARS, and branches having maximum length zero collapsed to yield polytomies in effect, using PAUP 4.0b2 (Swofford, 1999) on a Power Macintosh 7100/66 with 15 MB memory assigned to PAUP.

Successive approximations character weighting (successive weighting) (Farris, 1969), an iterative character weighting procedure in which weights are assigned based on their observed level of homoplasy, was used on the large number of most parsimonious trees found during the initial analysis. Weights are derived from the most parsimonious tree/s under equal weighting, and subsequent heuristic searches completed based on the rescaled consistency index (Farris, 1989). The procedure is repeated until the weights (and trees) remain stable over iterations. Successive weighting of the most parsimonious trees was computed using PAUP* with a base weight of 1000.

Strict and semistrict consensus (Bremer, 1990) of the most parsimonious trees were computed using PAUP. Figures 20, and 21, both strict consensus trees, were prepared using PAUP*.

Results of cladistic analysis. – Analysis of the 104 characters for the 43 taxa, with 10 random additions, generated 7,142 most parsimonious trees of tree length 347, consistency index 0.53, consistency index excluding uninformative characters 0.49, retention index 0.70 and rescaled consistency index 0.37. The strict and semistrict consensus of the 7,142 most parsimonious trees were identical (Fig. 20), surprisingly well resolved, and indicated the presence of three clades, two of which were found in the previous analyses (Ballantyne & Lambkin, 2000). In all most parsimonious trees *Luciola (P.) stylifer* and *L. (P.) kinabalua* group together with the undescribed species, 'Mt Missim', but the relationships between this monophyletic group and the two other main clades are unclear. The position of *Curtos costipennis* remains problematical.

By decreasing the weight of the homoplasious characters, successive weighting can lead to changes in topology and resolution. Successive weighting recovered 18 trees. This decrease in the number of cladograms consequently increases resolution of the consensus of those cladograms. The identical strict (Fig. 21) and semistrict consensus of these 18 successively weighted trees show the same three clades within the Luciolinae that were found in earlier analyses (Ballantyne & Lambkin, 2000). *Luciola (P.) stylifer* and *L. (P.) kinabalua* continue to group together with the undescribed species, Mt Missim, but are joined by *Curtos costipennis to* form a medial clade between the *Atyphella* and the *Luciola* groups in all successively weighted trees. Three monophyletic clades are recognised in the Luciolinae. Basally the *Luciola/Pteroptyx* clade includes *Luciola (Luciola) australis, L. L. cowleyi, L. L. dejeani, L. L. flavicollis, L. L. italica, L. L. nigra, L. L. orapallida, Luciola (Hotaria) parvula, Pteroptyx cribellata, Pter. macdermotti, Pter. malaccae, Pter. platygaster, Bourgeosia hypocrita, Lampyroidea syriaca, Colophotia praeusta,* and *Pyrophanes beccarii.* Medially the *Curtos* clade is comprised of Mt Missim, *Curtos costipennis, L. (Pygoluciola) stylifer* and the new species *L. (Pygoluciola) kinabalua*. The terminal

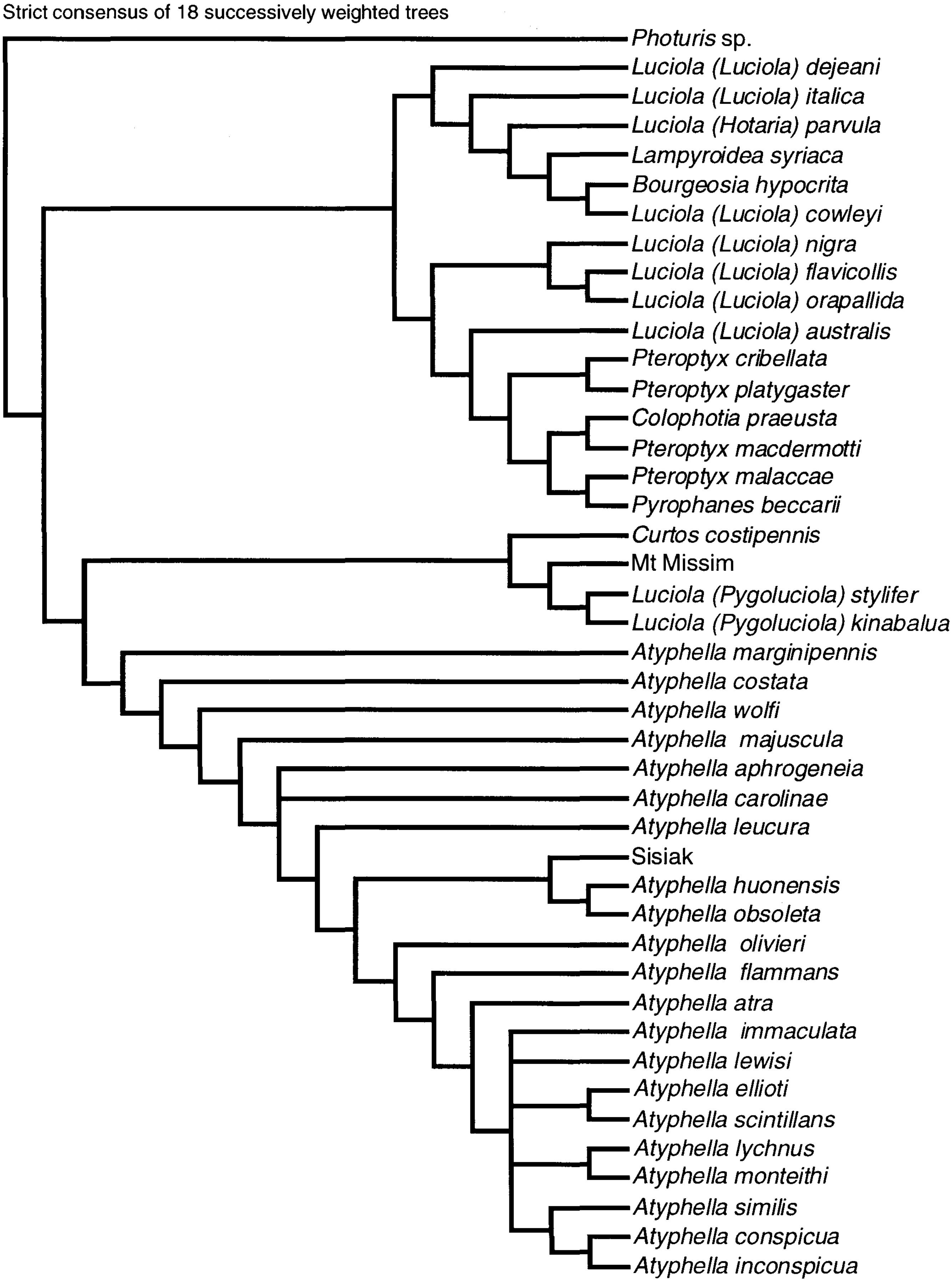


Fig. 21. Strict and semistrict consensus of 18 successively weighted trees from the 7142 most parsimonious trees for 104 characters, including polymorphisms, of 43 taxa.

Atyphella clade includes *Atyphella aphrogeneia, A. atra, A. brevis, A. carolinae, A. conspicua, A. costata, A. ellioti*, new species, *A. flammans A. flammulans*, new species, *A. immaculata, A. inconspicua, A leucura, A. lewisi, A. lychnus, A. majuscula, A. marginipennis, A. monteithi, A. olivieri, A. scintillans, A. similis, A. wolfi, A. huonensis, A. obsoleta*, and Sisiak.

DISCUSSION

The Luciolinae

Parsimony analysis produced many most parimonious trees, the consensus of which lacks basal resolution. In all most parimonious trees *Luciola (P.) stylifer* and *L. (P.) kinabalua* group together with an undescribed New Guinean species ('Mt Missim'), but the relationships between this monophyletic group and the two other main clades are unclear. *Luciola (P.) stylifer* and *L. (P.) kinabalua* continue to group together with the undescribed species from Mt Missim, and are joined by *Curtos costipennis* to form a medial clade between the *Atyphella* and the *Luciola* groups in all successively weighted trees. The same three clades are found within the Luciolinae that were identified in earlier analyses (Ballantyne & Lambkin, 2000). In those earlier analyses *Luciola (Pygoluciola) stylifer* and 'Mt Missim' formed a well supported group in all analyses that include both species. The inclusion of *Curtos costipennis* in the clade was poorly supported, as was the clade comprising the three species. The uncertain placement of *Curtos costipennis* in the consensus of all most parsimonious trees indicates that the situation has not changed. While Mt Missim, *Luciola (P.) stylifer* and *L. (P.) kinabalua* continually form a monophyletic group, the inclusion of *Curtos costipennis* in the clade remains problematical and probably based on unreliable colour pattern characters.

While this cladistic analysis indicates that *Luciola (Pygoluciola)* should be elevated to the level of genus, we have elected at this point to continue to regard the group in the form devised by McDermott (1966). Only two cladistic analyses have been performed on the Luciolinae; both lacked important data about females and larvae for many species and this generated a large number of most parsimonious trees (Ballantyne & Lambkin, 2000). The genus *Luciola* is not monophyletic, and a *Luciola/Pteroptyx* clade contained two well supported clades in all analyses Ballantyne & Lambkin, 2000 ran. However as they indicated these clades represent confused subgeneric and generic relationships which need further investigation. We believe, as we have already stated (Ballantyne & Lambkin, 2000), that a definitive change in taxonomic status within the genus *Luciola* at this point is premature, and more species need to be included, with details of female and larval morphology for as many species as possible.

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