

# *HYPTIOGASTRITES ELECTRINUS* COCKERELL, 1917, FROM MYANMAR (BURMESE) AMBER: REDESCRIPTION AND ITS PLACEMENT WITHIN THE EVANIOIDEA (INSECTA: HYMENOPTERA)

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**SYNOPSIS** The wasp *Hyptiogastrites electrinus* Cockerell, 1917, from the Lower Cretaceous (Upper Albian) Myanmar (Burmese) amber is redescribed from the well-preserved holotype and its relationship with extant Aulacidae and Gasteruptionidae (Hymenoptera: Evanioidea) evaluated. Although the wing venation is identical to the majority of extant Hyptiogastrinae (Gasteruptionidae), phylogenetic analysis places *H. electrinus* as sister taxon to the Aulacidae *s.str.*, (i.e. *Aulacus* + *Pristaulacus*). Thus, Hyptiogastrinae is confirmed as having a restricted Southern Hemisphere distribution (i.e. Australasia and South America). Consistent with this result, *H. electrinus* is included within a slightly more broadly defined Aulacidae rather than being placed in a new monotypic family. Characters that align this species with the Aulacidae include: having small circular eyes, percurrent Y-shaped notauli, pyramidal shape of the propodeum and the presence of a groove or ovipositor guide on the hind coxae.

**KEY WORDS** *Hyptiogastrites electrinus*, Hymenoptera, amber, Myanmar

## INTRODUCTION

Cockerell (1917) described a number of wasps from Burmese amber, including *Hyptiogastrites electrinus* Cockerell (Fig. 1), a member of the hymenopteran superfamily Evanioidea. The amber containing these inclusions is probably Lower Cretaceous (Upper Albian) in origin (Cruikshank & Ko 2003).

Extant Evanioidea have been divided into three families, the Aulacidae, Gasteruptionidae and Evaniidae since Hedicke (1930), and this classification has remained unchanged, although some authors, for example Townes (1950), have treated Aulacidae as a subfamily of Gasteruptionidae. Furthermore, the grouping of the Evaniidae with the Aulacidae and Gasteruptionidae has been questioned by numerous authors (e.g. Townes 1950; Crosskey 1951, 1962; Carlson 1979; Naumann 1991; Gauld & Bolton 1996). The Evaniidae may have acquired the high insertion of the metasomal independently, a character that is characteristic of the superfamily. More recently, Dowton & Austin (2001) found that

the monophyly of the Evanioidea is largely supported by molecular analysis, albeit on a restricted dataset. A close relationship between the Aulacidae and Gasteruptionidae is less problematic and is, at least putatively, supported by several morphological characters. Gasteruptionidae and Aulacidae have a similar, rigid abutment of the pronotum and mesepisternum and a similar fusion or partial fusion of the first and second metasomal segments (Naumann 1991). Quicke *et al.* (1994) found some similarities between the ovipositor in the Aulacidae and Gasteruptionidae, but not the Evaniidae. Both aulacids and gasteruptionids have a medial thickening of the ventral wall of the upper valve, but the latter has a mid-dorsal longitudinal ridge that is absent in aulacids. Evaniidae also differ in that their metasoma is usually laterally compressed and with a distinct tubular petiolate first tergite. Apart from the high point of insertion of the metasoma, the only other putative synapomorphy for the three families is the loss of functional spiracles from all segments of the metasoma except the eighth (Gauld & Bolton 1996). Aulacids are readily distinguished from evaniids and gasteruptionids



**Figure 1** *Hyptiogastrites electrinus*. Holotype, ln. 19098. Scale bar = 0.2 mm.

by the presence of fore-wing vein 2m-cu (Gauld & Bolton 1996).

The Gasteruptiidae are further divided into two subfamilies, Gasteruptioninae, comprising the single genus *Gasteruption*, and Hyptiogastrinae, comprising two genera, *Hyptiogaster* and *Pseudofoenus* (Jennings & Austin 2002). *Gasteruption* is worldwide in its distribution, whereas *Hyptiogaster* is restricted to Australia, and *Pseudofoenus* to Australasia (Australia, Fiji, New Caledonia, New Guinea, New Zealand and Vanuatu) and South America (Jennings & Austin 2002).

The biology of the three evanioid families is also quite different. Aulacids are endoparasitoids of wood-boring wasps (Xiphydriidae) and beetles (Cerambycidae and Buprestidae: e.g. Carlson 1979; Gauld & Bolton 1996; Smith 2001), gasteruptionids are predator-inquilines of various solitary bees and wasps (Jennings & Austin 2002) and evaniids are endoparasitoids of cockroach oothecae (e.g. Naumann 1991).

Since 1917, many additional evanioid fossil taxa have been described. Andreneliidae, based on a single specimen from the mid-Early Cretaceous of Spain, is apparently intermediate between basal Gasteruptionidae *s.l.* and Evaniidae *s.l.* (Rasnitsyn & Martínez-Delclòs 2000).

Bassinae is apparently the most basal subfamily of the Gasteruptionidae *s.l.* and is both abundant and diverse in the mid-Early Cretaceous of Eurasia. Currently it comprises some 30 described species (see Basibuyuk *et al.* 2002). Furthermore, Kotujellitinae, with two monotypic genera from the Late Cretaceous of North Siberia and mid-Early Cretaceous of Mongolia, is also placed within the Gasteruptionidae *s.l.* (Basibuyuk *et al.* 2002). Alternatively, both Bassinae and Kotujellitinae may be considered as separate families. For the purposes of this paper, both Bassinae and Kotujellitinae are considered as unplaced within the Evanioidea.

The Evaniidae *s.str.* includes six extinct genera from the mid-Early and Late Cretaceous of England, Siberia, Mongolia and China (Rasnitsyn *et al.* 1998; Zhang & Zhang 2000). There are also three extinct taxa from Upper Eocene Baltic amber included within the otherwise extant *Parevania* (Brues 1933).

Praeaulacidae, the putative stem group of the superfamily Evanioidea, is widely distributed in the Jurassic and

Lower Cretaceous of Kazakhstan, East Siberia, Mongolia and Australia (Rasnitsyn 1972). It comprises three subfamilies; Anomopterellinae, comprising one genus, *Anomopterella* (Rasnitsyn 1975), Praeaulacinae, comprising eight genera, and Cretocleistogastrinae, a subfamily widely distributed in the Lower Cretaceous of East Siberia, Mongolia and Australia (Rasnitsyn 1990). Given the current knowledge of extant Evanioidea, it is clear that few of the fossil evanioids show affinities with Aulacidae *s.str.* Of particular interest is *H. electrinus*, which superficially most resembles extant Aulacidae and which, at various times, has been included in both the Gasteruptionidae and the Aulacidae (see below under Phylogenetic Relationships). In order to confirm the position of *H. electrinus* in relation to the current hypothesis of hyptiogastrine biogeography (Jennings & Austin 2002), this paper redescribes *H. electrinus* on the basis of the well-preserved holotype and, after assessment of various characters and a preliminary phylogenetic analysis, places this species within the Aulacidae as a putative sister taxon to extant members of the family.

## MATERIALS AND METHODS

The specimen was examined and photographed under a dissecting microscope with digital camera attached. The phylogenetic analysis of Jennings & Austin (2000), which examined the higher level relationships among extant Aulacidae and Gasteruptionidae, was repeated, but with the addition of *H. electrinus*. As in the original analysis, *Schlettererius cinctipes* (Cresson) (Stephanidae) was used as the outgroup taxon. A heuristic search of 100 random replicates was undertaken using PAUP 4.0.0d (Swofford 1997) with random addition sequence, tree-bisection-reconnection branch swapping, steepest descent and MULPARS options. All character states were unordered, i.e. there was no *a priori* assumption made regarding character evolution. Six exemplar species of Aulacidae from Australia (3 each from *Aulacus* and *Pristaulacus*), four Australian and one unidentified South American species of *Gasteruption*, and 42 hyptiogastrines (5 *Hyptiogaster* and 37 *Pseudofoenus*) were included. A total of 57 characters (see Appendix) were employed, but with character 50 of Jennings & Austin (2000) excluded. Characters 2, 10, 19–23, 53 and 55 were uninformative but were retained in the analysis. Female-based characters were used unless otherwise specified. Primary absence of a character was given a character state number of '0' and '?' was used where the character state could not be determined (of the 57 characters used in the analysis, 28 could be coded for the holotype of *H. electrinus* – see Appendix).

## SYSTEMATIC PALAENTOLOGY

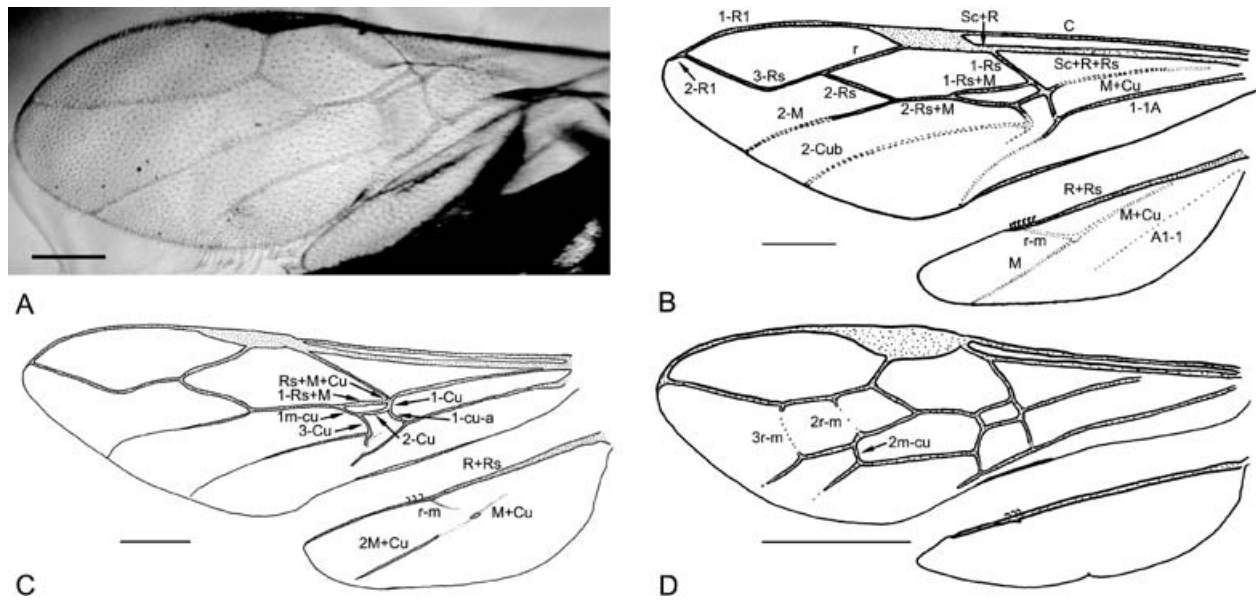
### Family AULACIDAE Hedicke, 1939

(For a complete taxonomic history of the Aulacidae, see Smith (2001)).

#### *Hyptiogastrites electrinus* Cockerell, 1917 (Figs 1 & 2A)

1917 *Hyptiogastrites electrinus* Cockerell: 19–20, fig. 2.

1920 *Hyptiogastrites electrinus* Fletcher: 986, pl. 164, fig. 5.



**Figure 2** Left wings of **A**, *Hyptiogastrites electrinus*; **B**, *Hyptiogaster arenicola* Turner; **C**, undescribed *Gasteruption* species from Australia; **D**, undescribed *Aulacus* species from Australia. Scale bars: **A** = 0.1 mm; **B–D** = 1 mm.

- 1933 *Hyptiogastrites electrinus* Brues: 157.  
 1962 *Hyptiogastrites electrinus* Crosskey: 393.  
 1978 *Hyptiogastrites electrinus* Zherikhin: 114.  
 1982 *Hyptiogastrites electrinus* Keilbach: 263.  
 1987 *Hyptiogastrites electrinus* Spahr: 16, 99.  
 1992 *Hyptiogastrites electrinus* Carpenter: 474.  
 2000 *Hyptiogastrites electrinus* Rasnitsyn & Ross: 23.  
 2000 *Hyptiogastrites electrinus* Ross & York: 14.

**TYPES.** Holotype: In. 19098, housed in The Natural History Museum, London.

**OCCURRENCE.** Cockerell (1917) indicates locality only as Burma. Lower Cretaceous (Upper Albian) Burmese amber (Burmite) in origin (Cruikshank & Ko 2003).

**DESCRIPTION.** The specimen appears to be female because of the presence of the hind coxal ovipositor grooves and an (damaged) ovipositor. Length 2.4 mm, excluding ovipositor. Colour dark brown or black, abdomen slightly lighter in colour than body. Head 0.5 mm wide when viewed dorso-posteriorly, height 0.6 mm. Occipital carina present. Eye  $0.5 \times$  height of head. Malar space not able to be measured, but greater than  $0.15 \times$  height of eye. Antennal insertions apparently low on face (not visible). Scape and pedicel not visible, 11 antennal flagellomeres clearly visible but scape, pedicel and possibly a short first flagellomere are obscured. Propleuron not elongate. Mesosoma 0.9 mm long. Mesoscutum in lateral view angular antero-dorsally, coarsely strigate (Fig. 1). Notauli percurrent, Y-shaped (Fig. 1). Hind coxa with groove to guide ovipositor present. Hind trochanter with dorso-lateral groove. Prefemur (trochantellus) present. Hind femur  $1.2 \times$  length hind tibia. Hind tarsal segment one  $2.3 \times$  length segment two; segment two  $1.4 \times$  length segment three; segment three  $1.3 \times$  length segment four; segment four  $0.75 \times$  length segment five. Hind tarsal segments not shortened and lack lateral projections. Hind tarsal claw  $0.5 \times$  length segment five. Claws not pectinate. Fore-wing

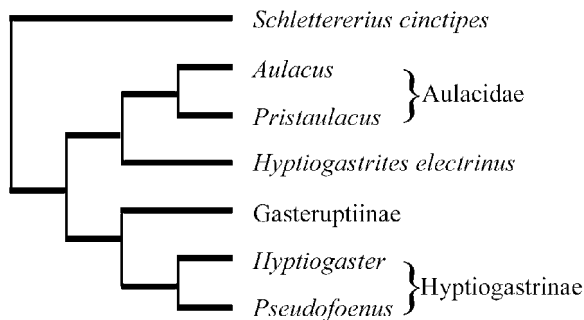
1.8 mm long, 0.7 mm wide; hind-wing 1.1 mm long, 0.2 mm wide (Figs 1 & 2A). Fore-wing veins 2m-cu, 2r-m and 3r-m absent (Fig. 2A). Hind-wing with 3 hamuli. Propodeum pyramidal. Metasoma sub-clavate, 1.4 mm long,  $1.6 \times$  length of mesosoma (Fig. 1). First metasomal tergite  $3.0 \times$  length tergite two, the two being fused dorsally; first tergite largely smooth except for prominent dorsal longitudinal medial ridge in anterior third. Penultimate metasomal tergite with a broad, inverted U-shaped notch in the medial dorsal-posterior margin. Male unknown.

**REMARKS.** Cockerell (1917) described the specimen as male, but given the occurrence of an ovipositor (which is apparently broken off near to the distal metasoma) and the ovipositor guides on the inner surface of the hind coxae, the specimen is clearly female.

The number of flagellomeres for extant Aulacidae and Gasteruptionidae males and females is 11 and 12, respectively (rarely 12 in some male Gasteruptionidae). Having 11 visible segments may be what prompted Cockerell (1917) to describe the specimen as male. However, the length of the first flagellomere varies considerably in extant aulacid and gasteruptionid genera ranging from short ( $0.3 \times$  length of second flagellomere) in many *Gasteruption* (Gasteruptionidae) and *Aulacus* to long (nearly twice the length of second flagellomere) for most *Pseudofoenus* (Hyptiogastriinae) (Jennings & Austin 2002). However, the first flagellomere is more commonly found to be approximately equal in length to flagellomere two. The orientation of the head of *H. electrinus* could easily obscure a short first flagellomere. Therefore, the precise number of flagellomeres for *H. electrinus* cannot be accurately determined.

## PHYLOGENETIC RELATIONSHIPS

*Hyptiogastrites electrinus* was originally accommodated by Cockerell (1917) in the Evaniidae, but his description



**Figure 3** Strict consensus tree of 95 072 equally most parsimonious trees each of 144 steps generated from a heuristic analysis of the data set described in Jennings & Austin (2000) and the Appendix. Consistency Index = 0.59. The tree has been collapsed to show only the generic and subfamilial relationships.

pre-dates the division of the Evaniidae into three families by Hedicke (1930). Cockerell (1917) speculated that it was related to *Hyptiogaster* but was 'more primitive'. Extant *Hyptiogaster* are placed within the Hyptiogastrinae (Gasteruptiidae), are confined to Australia (Jennings & Austin 1997, 2002) and have a number of character states that differ from extant Aulacidae. In particular they lack the fore-wing veins 2m-cu, 2r-m and 3r-m.

The placement of *H. electrinus* has been somewhat problematic given the lack of a clear definition of the family limits of Aulacidae and Gasteruptiidae. Fletcher (1920) placed it within the Evaniidae *s.l.*, as did Brues (1933), Zherikhin (1978) and Keilbach (1982). *Hyptiogastrites electrinus* is clearly not an evaniid, which, among other characters, have a hatchet-shaped metasoma (e.g. Naumann 1991). Crosskey (1962), however, placed it within the Hyptiogastrinae *s.str.* (Gasteruptiidae), but did not present any justification for this change. Spahr (1987) and Carpenter (1992) listed it in the Aulacidae *s.l.*, and Ross & York (2000) listed it within the Gasteruptiidae *s.l.*

Phylogenetic analysis, with *H. electrinus* coded using the same characters as those employed by Jennings & Austin (2000), produced 95,072 equally parsimonious trees, each 144 steps in length. The strict consensus tree (Fig. 3) had a Consistency Index (CI) of 0.59 indicating a high level of homoplasy. The analysis resolves *H. electrinus* as the sister taxon to the Aulacidae, i.e. *Aulacus* + *Pristaulacus* (Fig. 3), a relationship which is supported by four unequivocal character states; small, circular eyes (character 7), the presence of percurrent Y-shaped notauli (25), the pyramidal shape of the propodeum (33) and the presence of a groove or ovipositor guide on the hind coxae (41). It should be noted that, although some Aulacidae lack the ovipositor guide on the hind coxae, particularly those species with short ovipositors, no Gasteruptiidae possess one. Interestingly, these four character states were among those used by Crosskey (1962) to distinguish the Aulacidae from the Gasteruptiidae.

Although on phylogenetic grounds *H. electrinus* is clearly aligned with Aulacidae, intriguingly it has characters in common with both extant Gasteruptiidae and Aulacidae. For example, *H. electrinus* and extant Gasteruptiidae lack the fore-wing veins 2m-cu, 2r-m and 3r-m (Figs 2A–C), whereas these veins are present in extant Aulacidae (Fig. 2D). Furthermore, the fore-wing venational pattern, particularly the

juxtaposition of veins around the subdiscal cell, is identical to the majority of extant Hyptiogastrinae (c.f. Figs 2A & B), but not Gasteruptiidae (Fig. 2C). The presence of a complete occipital carina (Fig. 1) is also a character state shared with Gasteruptiidae, while Aulacidae either lack an occipital carina or it is incomplete and only weakly present laterally.

Although not coded for in the analysis, the mesoscutum of *H. electrinus* in lateral view is coarsely strigate, a characteristic of many Aulacidae, whereas in Gasteruptiidae the mesoscutum is not coarsely strigate. In addition, *H. electrinus* has a prefemur (trochantellus), a character state found in both Aulacidae and *Gasteruptia*, but not in Hyptiogastrinae. *Hyptiogastrites electrinus* also lacks pectinate hind tarsal claws, a character state shared with Gasteruptiidae (e.g. Jennings & Austin 1997, 2002) and also extant *Aulacus* but not *Pristaulacus*. Extant *Pristaulacus* are separated from *Aulacus* primarily on the basis of having pectinate hind claws. Although various authors use additional characters to separate *Aulacus* and *Pristaulacus*, these characters are variable among species of both genera (J. D. Jennings & A. D. Austin, unpublished results).

Where *H. electrinus* might occur in the phylogeny of Basibuyuk *et al.* (2002), where Gasteruptiidae + Kotujellitinae + Aulacidae + Baissinae form a monophyletic clade, has not been explored due to incompatibility between the datasets and also because the aim of the current analysis was to determine whether *H. electrinus* belonged to the Hyptiogastrinae. To avoid erecting a new monotypic family at this stage, we take a more pragmatic approach consistent with the results of the cladistic analysis and include *H. electrinus* within the Aulacidae. A ramification of this outcome is that the definition of Aulacidae must be broadened to include taxa that lack the fore-wing veins 2m-cu, 2r-m and 3r-m and have a complete occipital carina. We hope that this work will foster more detailed studies of other fossil evanioid wasps and their inclusion within current phylogenetic hypotheses for aulacid and gasteruptiid relationships will help to develop a better understanding of the evolution of this poorly studied group of parasitic Hymenoptera.

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## APPENDIX

Characters and character states from Jennings & Austin (2000) and the coding for *Hyptiogastrites electrinus* used in the phylogenetic analysis. Characters that could not be coded for *H. electrinus*, are indicated by a ‘?’.

1. Antennal insertion relative to eye: well below eyes (0); level with base of eyes (1); approximately half-way up eyes (2). Whilst it is probable that the antennal insertions are well below the eyes, this was not visible in *H. electrinus* and was coded (?).
2. Antennal segment number, female: multi-segmented (0); 14 (1). Whilst it is probable that there are 14 segments in *H. electrinus*, this character was coded (?).
3. Antennal segment number, male: multi-segmented (0); 13 (1); 14 (2). Not known for *H. electrinus* (?).
4. Width between antennal sockets: wide apart (0); close (1). The latter state is found in aulacids (Crosskey 1962). *H. electrinus* (?).
5. Clypeal margin: sinuate (0); truncate lobe (1). *H. electrinus* (?).
6. Clypeal ridge medially: absent (0); present (1). *H. electrinus* (?).
7. Eye size and shape: large and elliptical (0); small and circular/sub-circular (1). *H. electrinus* (1).
8. Flagellomere 1 length relative to flagellomere 2: first flagellomere greater in length than second (0); first flagellomere less than or equal to length of second (1). *H. electrinus* (?).
9. Frontal carina: absent (0); present (1). *H. electrinus* (?).
10. Head width: length when viewed dorsally: quadrate to lateral (0); elongate (i.e. longer than wide) (1). *H. electrinus* (0).
11. Lateral epistomal suture: absent (0); present (1). *H. electrinus* (?).
12. Malar space width: height eye:  $\leq 0.15$  (0);  $> 0.15$  (1). *H. electrinus* (1).

13. Mandibles broadly overlap: no (0); yes (1). *H. electrinus* (?).
14. Mandibular median teeth number: one tooth (0); two teeth (1); three teeth (2). *H. electrinus* (?).
15. Mouthparts extendible: fixed (0); extendible (1). *H. electrinus* (?).
16. Occipital carina: absent (0); incomplete (absent medially) (1); complete (2). *H. electrinus* (2).
17. Occipital carina sculpturing: sculptured (0); smooth (1). *H. electrinus* (?).
18. Scape in lateral view: convex (0); parallel-sided (1). *H. electrinus* (?).
19. Scape width relative to pedicel: scape much wider than pedicel (0); scape slightly wider than pedicel (1). *H. electrinus* (?).
20. Subantennal groove: absent (0); present (1). *H. electrinus* (?).
21. Dorsal tentorial pits on head: absent (0); present (1). *H. electrinus* (?).
22. Functional abdominal spiracles: other than 1 and 8 (0); 1 and 8 (1). *H. electrinus* (?).
23. Median sulcus of mesoscutum: absent (0); present (1). *H. electrinus* (?).
24. Mesothorax anterior face in lateral view: truncate (0); not so (1). *H. electrinus* (0).
25. Notauli percurrent: not percurrent (0); percurrent, not Y-shaped (1); percurrent, Y-shaped (2). *H. electrinus* (2).
26. Prepectus: absent (0); present (1). *H. electrinus* (?).
27. Antero-dorsal pronotal processes: absent (0); present (1). *H. electrinus* (0).
28. Dorso-lateral pronotal processes: absent (0); present (1). *H. electrinus* (0).
29. Propleural carina: absent (0); ventro-lateral (1). *H. electrinus* (?).
30. Propleuron shape: elongate (0); not elongate (1). *H. electrinus* (1).
31. Propodeal carina: absent (0); present (1). *H. electrinus* (?).
32. Propodeal spiracle: glabrous or almost so (0); fringed with setae (1). *H. electrinus* (?).
33. Shape of propodeum: not pyramidal (0); pyramidal (1). *H. electrinus* (1).
34. Fore-wing discal cell number: 2 cells (0); 1 cell (1). *H. electrinus* (0).
35. Fore-wing plication at rest: no (0); yes (1). *H. electrinus* (?).
36. Fore-wing vein 'r-m': absent (0); present (1). *H. electrinus* (1).
37. Fore-wing vein 1-Rs + M: joins at M + Cu, 1-R (0); joins 1-M and 1-Rs (1); fused – forms Rs + M + Cu(b) (2). *H. electrinus* (1).
38. Fore-wing vein 2-M colour: even (0); pale apically (1); pale basally (2). *H. electrinus* (?).
39. Hind-wing vein 1-Cu: absent (0); present (1). *H. electrinus* (?).
40. Submarginal cell number in fore-wing: 2 or 3 cells (0); 1 cell (1). *H. electrinus* (1).
41. Groove on hind coxa: absent (0); present (1). *H. electrinus* (1).
42. Groove on hind trochanter: absent (0); present (1). *H. electrinus* (1).
43. Hind claw: simple (0); pectinate (1). The claws of *H. electrinus* are apparently simple and although the presence or absence of the basal tooth could not be determined, this character was coded as state 0.
44. Hind tarsal segment 1: without projection, symmetrical (0); with lateral projection, highly asymmetrical (1). *H. electrinus* (0).
45. Lateral projections on hind tarsal segments 2–4: absent (0); present (1). *H. electrinus* (0).
46. Length of hind tarsal segments: normal (0); shortened (1). *H. electrinus* (0).
47. Hind tibia with ventro-apical pecten of stout spines: absent (0); present (1). *H. electrinus* (?).
48. Mid tibial notch: absent (0); present (1). *H. electrinus* (0).
49. Prefemur on hind leg: absent (0); present (1). *H. electrinus* (1).
50. Trochantellus absent or present has been excluded from this analysis as it is essentially the same character as 49, a fact overlooked by Jennings & Austin (2000).
51. Apical sternum: incised (0); not incised (1). *H. electrinus* (?).
52. Digitus length compared with length of basiparameres (male): digitus length < basiparameres (0); digitus length  $\geq$  basiparameres (1). The male of *H. electrinus* is unknown.
53. Metasomal insertion on propodeum: low (0); high (1). *H. electrinus* (1).
54. Metasomal shape: not sub-clavate (0); sub-clavate (1). *H. electrinus* (1).
55. Metasomal T1 and T2: not fused (0); fused (1). *H. electrinus* (1).
56. Metasomal T1 longitudinal medial ridge or line: absent (0); present (1). *H. electrinus* (1).
57. Ovipositor exertion: exerted (0); not exerted (1). *H. electrinus* (0).
58. Ovipositor sheath margin: smooth (0); undulate or serrate (1). *H. electrinus* (0).