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**Redescription of *Calohelcon* Turner
(Insecta: Hymenoptera: Braconidae),
Description of a New Species, and a
Reappraisal of the Significance of
Certain Character States in the Helconinae**

D.L.J. QUICKE¹* & G.A. HOLLOWAY²

¹ Department of Animal Biology, University of Sheffield,
Sheffield, England, S10 2TN

* Australian Museum Visiting Fellow

² Division of Invertebrate Zoology, Australian Museum,
6-8 College Street, Sydney, NSW 2000, Australia

ABSTRACT. *Calohelcon obscuripennis* Turner is redescribed and illustrated for the first time. *Calohelcon roddi* n.sp. from New South Wales is described, illustrated and differentiated from *C. obscuripennis*. The hindwing of *C. roddi* possesses a distinct transverse vein m-cu, a feature unknown in any other Helconinae but present in many members of the 'cyclostome' subfamilies Doryctinae and Rogadinae, and in the apparently related Alysiinae, Betylobraconinae, Gnampodontinae, Histeromerinae, Opiinae and Telengaiinae. The presence of hindwing vein m-cu is interpreted as a plesiomorphous character state in the 'cyclostome' assemblage, but it is suggested that the presence of m-cu in some *Calohelcon*, represents a re-expression of genetic information, the expression of which had been previously suppressed. The phylogenetic significance of a number of other features of *Calohelcon*, and of Helconinae in general, are discussed.

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Recently major advances have been made in our understanding of the phylogenetic relationships between the subfamilies of Braconidae (Capek, 1970; van Acterberg, 1984; Sharkey, personal communication),

although there is as yet no clear consensus of opinion, and several subfamilies are problematical. Application of Hennigian cladistics (Hennig, 1966) has proved invaluable in that by consistently differentiating between

synapomorphies and symplesiomorphies, a robust classification can be achieved and where necessary, the limits of subfamilies redefined (van Achterberg, 1976, 1979a-c, 1983b; Quicke, 1987). As a result of this work, a considerable effort has been put into finding new phylogenetically significant characters, and one that has been highlighted recently as being of considerable potential importance is the presence or absence of the transverse hindwing vein m-cu (Sharkey, 1988, personal communication). Hindwing vein m-cu occurs in the Doryctinae and Rogadinae, and in the apparently related subfamilies Alysiniinae, Betylobraconinae, Gnampodontinae, Histeromerinae, Opiinae and Telengaiinae. Importantly, its loss appears to be absolute in other braconid lineages with the single exception of the helconine genus *Calohelcon* Turner that is redescribed below. The significance of this and other character states displayed by *Calohelcon* are discussed.

The Australian genus *Calohelcon* has not been published on since its original description by Turner (1918), apart from its inclusion in subsequent catalogues, and it has never been illustrated. *Calohelcon* belongs to the tribe Helconini (see van Achterberg, 1976a, 1984) having forewing vein 1r-m present, having forewing vein 2-SR+M longitudinal (i.e. vein m-cu is inserted into the first rather than the second submarginal cell), and having both forewing veins 1A and 2A. However, *Calohelcon* is aberrant in several features, largely associated with a reduction of body sculpture, viz. the propodeum is smooth and not differentiated from the posterior part of the metapleuron, the first metasomal tergite lacks both dorsal and dorsolateral carinae and the precoxal suture is absent. The discovery of additional material of *Calohelcon* in both the Australian Museum and in the Australian National Insect Collection and the inadequacy of its original description in failing to mention many of its unique features, prompted us fully to redescribe and illustrate this interesting and uncommon Australian braconid genus.

Terminology follows that of van Achterberg (1979c). Figures are shaded as if illuminated from the upper right. Collections are abbreviated as follows: AM – Australian Museum; ANIC – Australian National Insect Collection; BMNH – British Museum (Natural History).

Redescription

Calohelcon Turner

Calohelcon Turner, 1918: 163, 165.

Type species. *Calohelcon obscuripennis* Turner, 1918 (monobasic).

Additional species. *Calohelcon roddi* n.sp.

Diagnosis. Moderately large braconid wasps with

wingspans greater than 2 cm. Maxillary and labial palps with 6 and 4 segments respectively. Antennal sockets with protruding lateral margin. Malar suture absent. Malar space large. Frons with a well-developed midlongitudinal carina. Eyes glabrous, not emarginate. Hypostomal and occipital carinae complete and lamelliform or the occipital carina largely reduced. Mesosoma smooth and shiny. Pronotum with a crenulate groove anteriorly. Propleuron with a lateral carina. Median lobe of mesoscutum not depressed relative to lateral lobes. Precoxal suture absent. Mesopleural suture crenulate. Propodeum without carinae, largely glabrous; not differentiated from the metapleuron. Propodeal spiracle small and elliptical. Metapleuron with a well-developed flange. Forewing with costal cell distinct for more than half length from tegula to pterostigma. Forewing with veins 1r-m, 2A and 3-1A. Hindwing with veins C and 2A well-developed; vein m-cu represented by a least a spur arising from 2-M; without veins r and r-m. Claws simple with small, rounded, non-pectinate basal lobes. Hind trochanter not slender. Hind femur smooth ventrally, without rugae. Metasoma smooth and shiny. First metasomal tergite large; without dorsal or dorsal-lateral carinae; strongly bulbously produced on each side anterodorsally. Ovipositor approximately as long as the body; with a preapical dorsal, circular notch in lateral aspect. Venom gland reservoir thin walled and weakly muscularised (Type II of Edson & Vinson, 1979).

Description. Terminal flagellomere pointed but not acuminate. All flagellomeres longer than wide. Lower margin of clypeus carinate, forming a narrow transverse 'hypoclypeal depression'. Clypeus distinctly differentiated from the face by a groove. Face broadly setose medially; with a midlongitudinal raised area. Antennal sockets margined by a flange laterally. Frons depressed, with a well-developed midlongitudinal carina.

Pronotum with a small pronope formed by the submedial pair of carinae. Notauli moderately well developed, not crenulate. Median lobe of mesoscutum distinctly protruding over the pronotum. Anterior scutellar sulcus broad and crenulate. Scutellum with a submarginal, posterior row of pits. Epicnemial area smoothly impressed, without sculpture. Episternal scrobe absent. Median area of metanotum with a medial and a pair of lateral anteriorly diverging carinae. Propodeum not differentiated from metapleuron.

Forewing. Costal cell narrow but distinct for at least the apical half of vein C. Second submarginal cell short. Vein r-m moderately curved, with one posterior bulla. Vein 1-SR+M sigmoid, with or without a short posteriorly directed spur. Vein 2-SR+M longitudinal. Vein cu-a postfurcal. Vein 1A reclivous.

Hindwing. Vein C well developed, without especially thickened bristles apically (see Quicke, 1982). Costal cell distinctly though weakly sclerotised posteriorly. Vein 2-SC+R longitudinal, without distinct large, erect bristle(s). Anterior margin of wing reaching vein SC+R1 considerably before the hamuli proper (= distal hamuli).

Vein R1 with 8 to 10 hamuli, the basal 3 being somewhat larger than the remainder. Vein M+CU much longer than 1-M. Vein m-cu sometimes represented by a short spur or a distinct short vein arising from near the base of vein 2-M. Vein cu-a approximately perpendicular to 1-M. Plical cell moderately large. Vein 2-A well developed. Setosity of wing membrane considerably less dense basally than apically.

Claws with a small rounded basal lobe, without pectination. Legs moderately slender. Tarsi without an obvious midventral, longitudinal row of setae.

Metasoma smooth and shiny, largely glabrous; inserted above hind coxae. First tergite large, without dorsal or dorsolateral carinae, strongly bulbously swollen on either side, anterodorsally; with a distinct laterope. First spiracle small. Laterotergites of all tergites well developed.

Spiracles of tergites behind the first, in the laterotergites. Sternites largely sclerotised though less strongly so medially and posteriorly. Hypopygium small. Ovipositor approximately as long as the body, distinctly curved dorsally except for the apex; with a weak preapical dorsal notch or a small, almost circular (in lateral aspect) dorsal hollow with apicoventral serrations.

Biology. Helconines are usually koinobiont endoparasitoids of concealed coleopterous larvae (Gauld & Bolton, 1988). However, one specimen of *C. obscuripennis* bears a label that it was "probing tree trunks with cossid larvae", and although this is hardly a confirmed record it does suggest that *Calohelcon* species may actually be parasitoids of Lepidoptera rather than Coleoptera larvae.

Key to the Species of *Calohelcon*
(females only)

- 1. First metasomal tergite constricted submedially in dorsal aspect (Fig.1a); mesoscutum and metasomal tergites 5-9 black; wings yellowish on basal half, grey-brown apically.....*C. obscuripennis*
- First metasomal tergite not constricted submedially in dorsal aspect (Fig.3f); mesoscutum and metasomal tergites 5-9 orange; wings more or less evenly light brown.....*C. roddi* n.sp.

***Calohelcon obscuripennis* Turner**

Fig.1

Calohelcon obscuripennis Turner, 1918: 165.

Material examined. HOLOTYPE female (BMNH, 3c 901): "Australia. R.E. Turner. 1909 - 220.", "*Calohelcon obscuripennis* Type Turn. ". "B.M. TYPE HYM. 3.c. 901" & "Type H.T.". PARATYPE male (BMNH): "c7.2.01 Victoria", "Australia R.E. Turner 1909 - 220" & "*Calohelcon obscuripennis* cotype Turn."

1 female (ANIC): "Bonville NSW 23 Aug. 1977 R.S. McInnes & J Green. Probing tree trunks with cossid larvae"; 1 female (BMNH) - no data.

Description. *Females.* Length of body 14.0-14.5 mm, of forewing 14.0-15.0 mm, of ovipositor (part extended beyond the metasomal tergites) 16.5-19.0 mm and aof antenna (broken in holotype) 16.0 mm.

Antenna with 47 flagellomeres, slightly longer than the forewing. Terminal flagellomere partially fused to the penultimate flagellomere. Median flagellomere parallelogram-shaped in profile; 1.35 x longer laterally than wide. First flagellomere 1.2 x longer than both the 2nd and 3rd separately, the latter being 2.2 x longer than maximally wide. Ratios of height of clypeus:

intertentorial distance: tentorio-ocular distance = 17:26:30. Malar space 0.61 x height of eye. Ratio of height of eye: width of face: width of head = 41:69:112. Facial ridge densely punctate, bordered laterally by grooves. Antennal sockets with crenulate margins anteriorly and laterally. Frons largely without carinae except anteriorly. Ratios of distance between posterior ocelli: transverse diameter of posterior ocellus: shortest distance between posterior ocellus and eye = 12:8:27.

Mesosoma 1.6-1.68 x longer than high. Scutellar sulcus with 5-6 transverse crenulae. Scutellum sometimes with a short midlongitudinal row of fine pits.

Forewing. Ratios of length of veins r:3-SR: SR1 = 23:28:135. Ratios of lengths of 2-SR: 3-SR : r-m = 34:28:29. Vein m-cu 1.57 x longer than shortest distance between 1st discal cell and 2nd submarginal cell. Vein 3-CU1 very weakly expanded posteriorly.

Hindwing. Vein M+CU 2.73 x longer than 1-M. Vein R1 with 9 hamules.

Ratios of lengths of fore femur: tibia: tarsus = 21:25:25. Fore basitarsus 5.7 x longer than maximally deep. Ratios of lengths of hind femur: tibia: tarsus = 29:52:14. Hind basitarsus 5.4 x longer than deep. Hind femur 4.5 x longer than deep. Inner hind tibial spur 0.28 x length of basitarsus.

First metasomal tergite approximately as long as maximally wide; distinctly narrowing behind the

basodorsal lobes. Second tergite 3.0 wider than long.

Largely black; the head largely yellow except for a mark on the stemmaticum and the centre of the frons; posterior third of propodeum, posterior half of metapleuron, first tergite except for a medial mark subposteriorly, ivory white. Basal half of both wings yellowish becoming gradually grey-brown apically; venation brownish (paler basally); pterostigma brown

except for a small yellowish mark basally.

Calohelcon roddi n.sp.

Type material. Female HOLOTYPE and PARATYPE in the Australian Museum collected by Norman Rodd from Lane

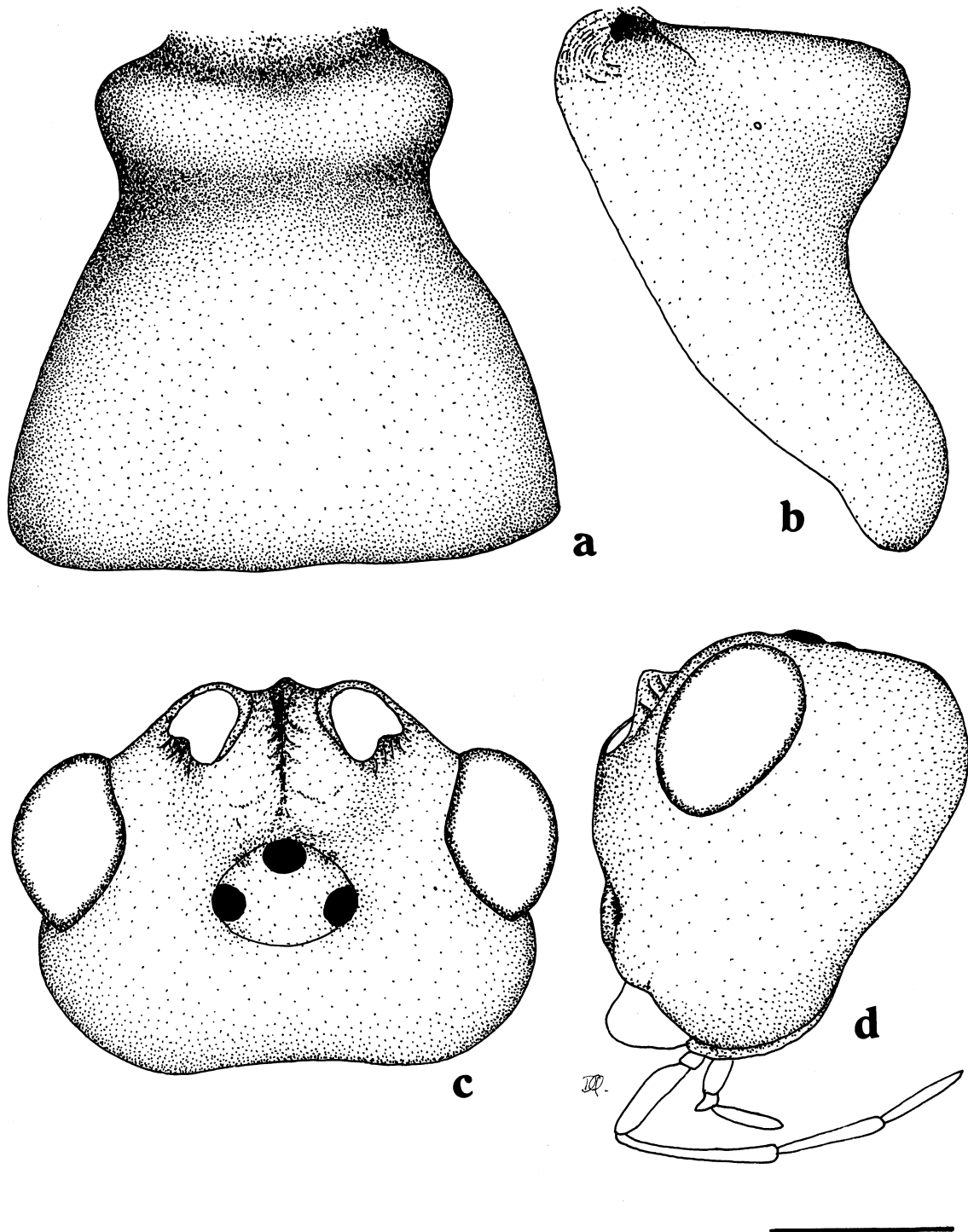


Fig.1. *Calohelcon obscuripennis* Turner, female: a, first metasomal tergite, dorsal aspect; b, first metasomal tergite, lateral aspect; c, head, dorsal aspect; d, head, lateral aspect.

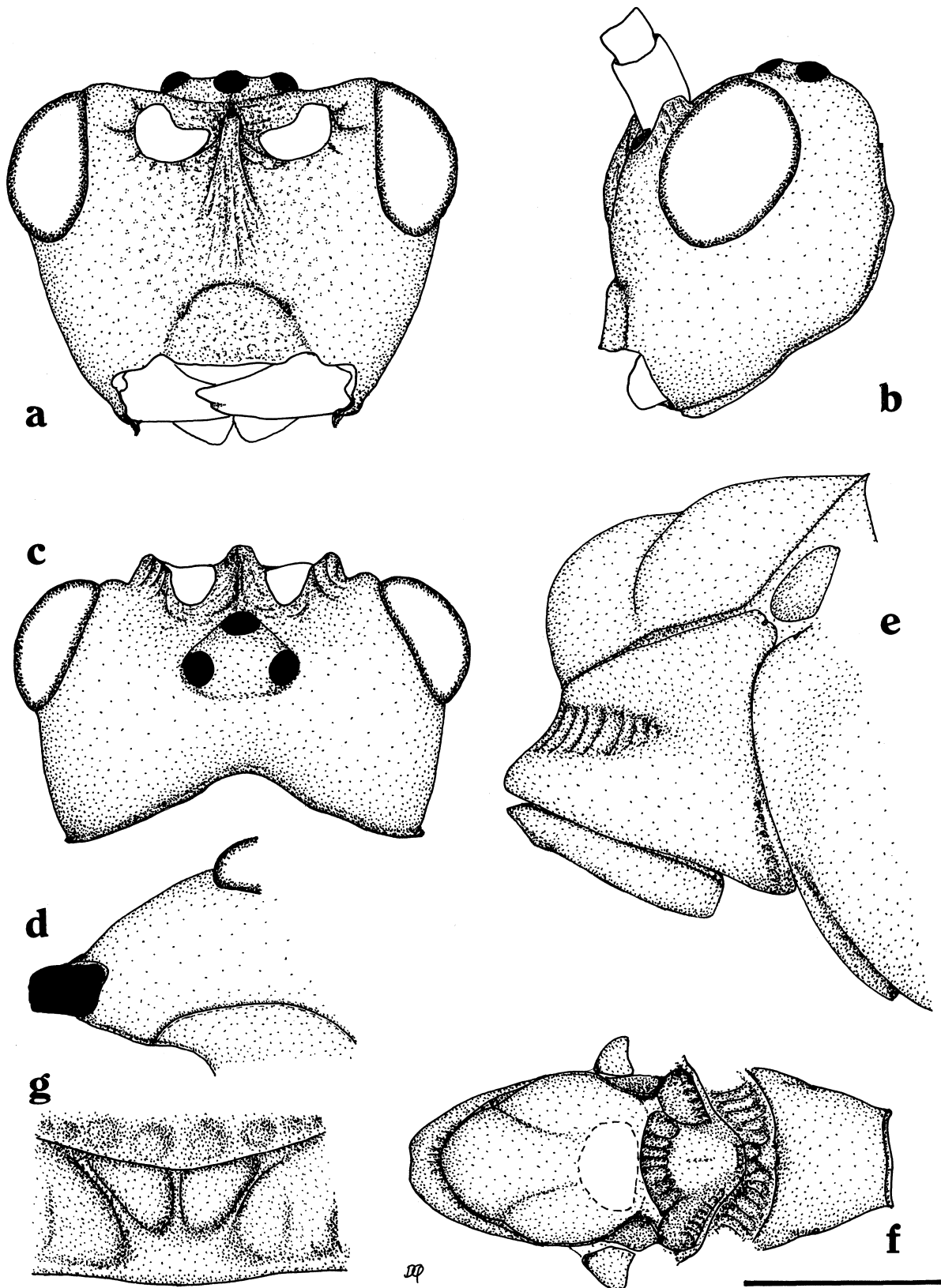


Fig.2. *Calohelcon roddi* n.sp., female: a, head, frontal aspect; b, head, lateral aspect; c, head, dorsal aspect; d, head, oblique aspect of posterior, lower left part (mandible black); e, anterior of mesosoma, lateral aspect; f, mesosoma, dorsal aspect; g, median area of metanotum and posterior of scutellum, dorsal aspect. Scale line a,b,c,d,e = 1 mm; f = 2.0 mm; g = 0.5 mm.

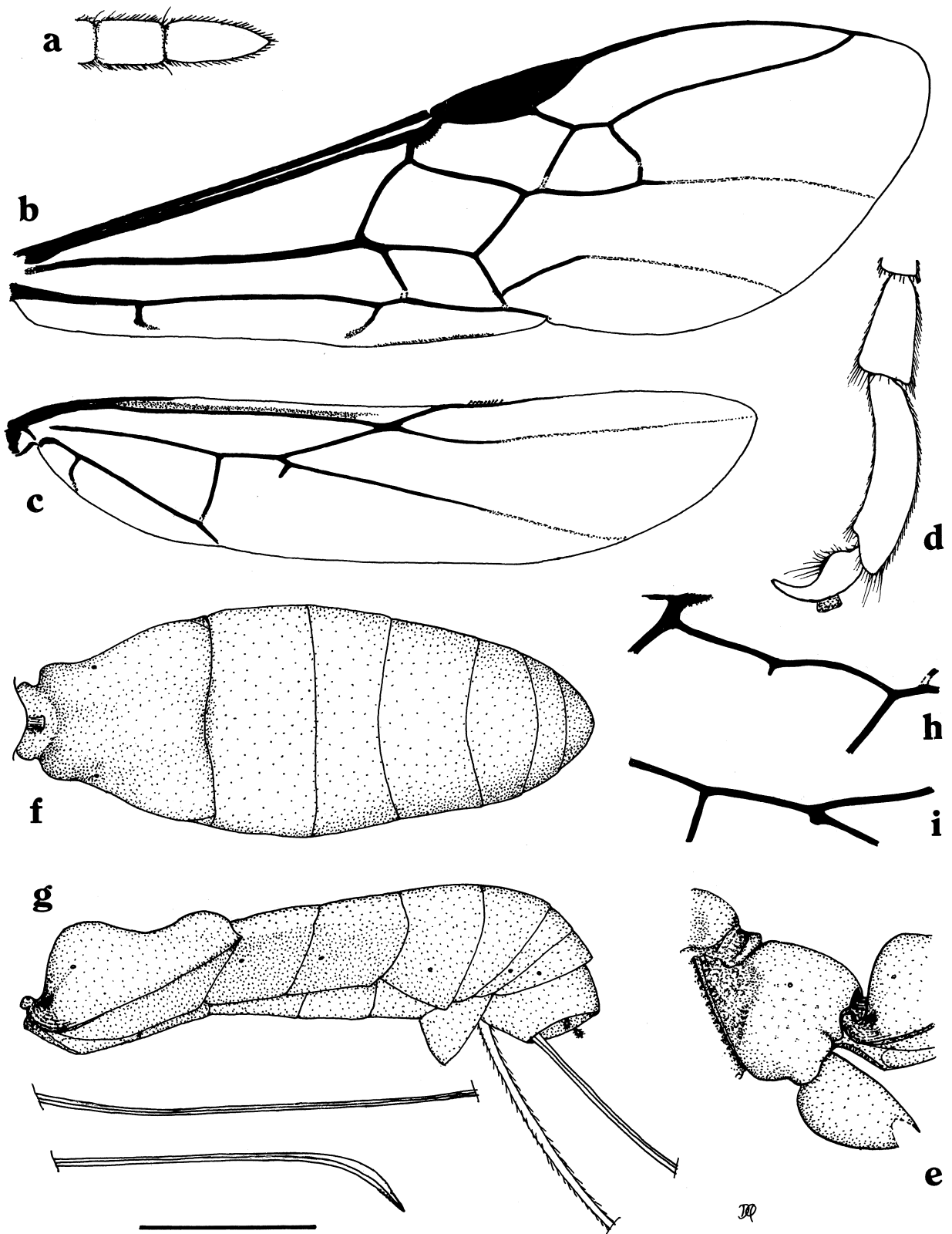


Fig.3. *Calohelcon roddi* n.sp., female: a, terminal 2 flagellomeres; b, right forewing; c, right hindwing; d, apex of hind tarsus, lateral aspect; e, posterior of mesosoma and anterior of metasoma, lateral aspect; f, metasoma, dorsal aspect; g, metasoma and ovipositor, lateral aspect; h, vein 1-SR+M of right forewing; i, vein 1-M of right hindwing. Scale line: a = 0.25 mm; b,c,e,f,g = 2.0 mm; d = 0.5 mm; h,i = 0.1 mm.

Cove, Sydney, NSW; holotype collected 17 July 1943; paratype collected on 11 Aug. 1946.

Description. *Females.* Length of body 13.3-13.5 mm, of forewing 11.3-12.5 mm, of ovipositor (part exerted beyond metasomal tergites) 14.5-16.0 mm and of antenna 12.5 mm.

Antenna with 44-45 flagellomeres; approximately as long as the forewing. Terminal flagellomere 2.4 x longer than maximally wide. Penultimate flagellomere 1.6 x longer than wide. Median flagellomeres parallelogram-shaped in profile; 1.7 x longer laterally than wide. First flagellomere 1.17 x and 1.37 x longer than the 2nd and 3rd respectively, the latter being 1.7 x longer than wide. Ratios of height of clypeus : intertentorial distance : tentorio-ocular distance = 16 : 19 : 25. Malar space 0.76 x height of eye. Ratios of height of eye : width of face : width of head = 33 : 57 : 91. Facial ridge with fine longitudinal carinae. Antennal sockets with crenulate margins anteriorly and laterally. Frons with fine curved carinate sculpture. Ratios of distance between posterior ocelli : transverse diameter of posterior ocellus : shortest distance between posterior ocellus and eye = 3 : 2 : 6.

Mesosoma 1.64 x longer than high. Scutellar sulcus with 6 or 7 transverse crenulae. Scutellum sometimes with a short midlongitudinal row of fine pits.

Forewing. Ratios of lengths of veins $r : 3-SR : SR1 = 4 : 3 : 24$. Ratios of lengths of $2-SR : 3 - SR : r-m = 6 : 3 : 5$. Vein m-cu 2.5 x longer than shortest distance between 1st discal cell and 2nd submarginal cell. Vein 3-CU1 very weakly expanded posteriorly.

Hindwing. Vein M+CU 2.9 x longer than 1-M.

Ratios of lengths of fore femur : tibia : tarsus = 79 : 88 : 105. Fore basitarsus 8.4 x longer than maximally deep. Ratios of lengths of hind femur : tibia : tarsus = 50 : 86 : 68. Hind basitarsus 7.7 x longer than deep. Hind femur 9.5 x longer than deep. Inner hind tibial spur 0.16x length of hind basitarsus.

First metasomal tergite 1.1 x longer than maximally wide, not narrowing behind the basodorsal lobes. Second tergite 2.35 x wider than long.

Antennae, apical 3 segments of both pairs of palps, stemmaticum, tegulae, scutellum, mesopleuron, mesosternum, metanotum, anterior half of propodeum and metapleuron, forelegs (except for coxae), ventral side of femur, mid- and hindlegs, metasomal tergites 2-4, metasomal sternites (except for hypopygium) and ovipositor sheaths, black. Posterior halves of propodeum and metapleuron, first metasomal tergite except for a small dark mark medioposteriorly, ivory white. Remainder of head and body, orange-red. Wing venation piceous brown, wing membrane more or less evenly light brown.

Discussion

Members of the Helconinae possess many plesiomorphous character states, and the subfamily as

whole is difficult to characterise on the basis of apomorphic character states and tends to fall out at the end of keys to braconid subfamilies (van Achterberg, 1976). The presence of a distinct forewing costal cell (Fig.2b), forewing veins 1A and 2A, hindwing vein 2A, complete occipital, hypostomal (Fig.1d) and prepectal carinae (Fig.1e) and having metasoma inserted above the hind coxae collectively indicate an early origin from the remainder of the family. Nevertheless, the Helconinae appears to be clearly associated with the majority of non-cyclostome, braconid subfamilies on the basis of their endoparasitism, of the presence in young larvae of an evaginated rectum (both apparently apomorphic character states) and by the possession of a weakly muscularised, thin walled venom gland reservoir (type II of Edson & Vinson, 1979) (a plesiomorphous character state).

Further, in all of van Achterberg's (1984) groups III (excluding the Betylobraconinae which belong elsewhere) and IV comprising the subfamilies Helconinae (except for *Calohelcon*), Meteorideinae, Blacinae, Euphorinae, Cercobarconinae, Trachypetinae, Xiphozelinae, Homolobinae, Sigalphinae, Cenocoeliinae, Agathidinae, Macrocentrinae, Amicrocentrinae, Orgilinae, Cheloninae, Neoneurinae, Cardiochilinae, Khoikhoiinae and Microgastrinae, hindwing vein m-cu is absent. In contrast, m-cu is present, albeit with a rather reticulate distribution in the Alysiinae, Betylobraconinae, Doryctinae, Gnampodontinae, Histeromerinae, Opiinae, Rogadinae and Telegaiinae. Clearly, m-cu has been repeatedly lost within the Doryctinae and Rogadinae but it is represented in many distantly related genera in both of these subfamilies. It is never present in the Braconinae although a possible remnant may be present at the base of the poorly developed distal abscissa of the cubital vein (?3-CU) present in some *Calcaribracon* Quicke. It is also absent from the Mesostoinae which show a marked reduction in venation (van Achterberg, 1975).

The presence of a trace of m-cu in *Calohelcon* firstly reinforces the notion that the Helconinae is a group that has diverged relatively little from the ancestral braconid groundplan. Secondly, it raises the problem of whether its presence in *Calohelcon* should be regarded as plesiomorphous or apomorphic. If plesiomorphous, then the assumption is made implicitly that it has been retained in all the ancestors of the taxon under consideration. Thus, considering what we know of the relationship of the Helconinae and the relationships within the Braconidae in general, would appear to be less parsimonious than assuming a re-expression of a gene or genes for vein m-cu is also absent in the Ichneumonidae. Riegel (1948) and Tobias & Belokobylsky (1983) similarly use the occurrence of aberrant wing venation features in the Braconidae as a means of interpreting phylogeny. Forewing vein 2m-cu is a good example. It is present in the vast majority of Ichneumonidae (it is only absent in a few species) but has also been found as an aberrant condition in *Histeromerus* Wesmael (Histeromerinae) and *Orgilus*

Haliday (Orgilinae) and is 're-fixed' in *Apozyx* Mason (a member of the cyclostome group of Braconidae; Sharkey, personal communication). A similar interpretation seems to be appropriate for the presence of hindwing vein m-cu in *Calohelcon* and indeed in the other braconids which possess it. Nevertheless, we do not want to suggest that the reappearance of such 'plesiomorphous' character states is independent of phylogenetic position or of evolutionary distance. Such re-expressions critically depend on the retention within the organism's genome of ancient genetic information (unless one assumes an evolutionary predisposition to re-evolve given 'genes' *de novo*). It is not surprising therefore that hindwing vein m-cu is present in a helconine given that members of this subfamily appear to possess many other plesiomorphous character states.

We should like to point out, however, that current computer programs for finding the most parsimonious cladogram for a group of taxa fail to treat such characters adequately, and care should be taken when considering the significance of phylogenetic decisions based on probable character re-expressions as opposed to truly plesiomorphous states for which there has been a complete evolutionary continuity from the ancestral (root) taxon. The placement of *Apozyx* in a separate family (the Apozygidae Mason, 1978) is a case in point, the presence of a forewing vein 2m-cu having been taken to outweigh all the other characters indicating that *Apozyx* should be regarded as an aberrant cyclostome braconid (Mason, 1978; Sharkey, personal communication).

In addition to the presence of hindwing vein m-cu, several other characters occurring in *Calohelcon* and other Helconinae warrant further discussion and are considered below.

Lateral carina of mesoscutum. Van Achterberg (1979a) states that the absence of a lateral mesoscutal carina in his new subfamily, the Amicrocentrinae, should be considered as plesiomorphous. However, a well-developed carina is present in most, if not all Helconinae, and therefore, since this subfamily undoubtedly had an ancient origin, it seems reasonable to consider that the presence of a lateral mesoscutal carina is a plesiomorphous character state for the Braconidae, otherwise it has to be assumed to have arisen independently. Further, it should be noted that many Ichneumonidae have a well-developed (even if somewhat obscured) lateral mesoscutal carinae (e.g. many Pimplinae, Tryphoninae).

Forewing with an open costal cell. An open forewing costal cell (Fig.2b) is known to occur in only a few subfamilies of Braconidae, it is best developed in the Amicrocentrinae (van Achterberg 1979a, 1983a) but a partly open cell is also found in some Helconinae and Trachypetinae. It is unknown among the Ichneumonidae. An open costal cell is undoubtedly the plesiomorphous condition for the Hymenoptera as it represents a more complex venational state as seen in the Symphyta and also in the extinct Praeichneumonidae (Rasnitsyn, 1983). Closure of the costal cell is usually considered a

synapomorphy for the Braconidae + Ichneumonidae and it should be pointed out that it is highly unlikely that the somewhat open costal cell found in these three braconid subfamilies represents a continuity in evolution from the Symphyta all the way through to the Braconidae; if that were the case then one requires multiple independent closures of the costal cell at least in three lineages of braconid subfamilies and also in the Ichneumonidae. It seems to us more likely that, as argued for hindwing vein m-cu above, an open costal cell represents the re-expression of genes which have previously been suppressed. Thus, strictly speaking, such character re-expressions should be regarded as apomorphous rather than plesiomorphous character states, albeit that they may be more likely to be re-expressed in groups showing a large proportion of other, truly plesiomorphous character states such as in the Helconinae.

Position of spiracles of second metasomal tergite. Van Achterberg (1984) regards the plesiomorphous character state for the Braconidae to be with the spiracles located in the tergum as is the case in its sister group, the Ichneumonidae rather than in the latero-tergite (= epipleuron). Care has to be taken when examining this character in some Braconidae, because the lateral crease of the second metasomal tergite does not necessarily coincide with the border between the tergum and the laterotergite (e.g. in the Histeromerinae). However, in *Calohelcon*, KOH treatment of the metasoma reveals a distinct zone of reduced sclerotisation corresponding with the lateral crease of the second metasomal tergite and corresponding zones in the less distinctly creased or uncreased posterior tergites. Thus, in this genus there can be no doubt that the spiracles are located in the true laterotergites (Fig.3g). Given this and the overall assemblage of plesiomorphous character states displayed by the Helconinae, the possibility that the Helconinae display the plesiomorphous character state for the Braconidae should also be considered. The alternative is that migration of the spiracle into the laterotergite has occurred independently in the Braconidae in at least four lineages (van Achterberg, 1984), viz. in the Alysiniinae, in the Aphidiinae, in the Ypsistocerinae + Mesostoinae, and in van Achterberg's proposed lineage III + IV which includes the Helconinae and the majority of non 'cyclostome' subfamilies. Since there appears to have been no such trend in the Ichneumonidae and because the second metasomal spiracle is also situated laterally in the Stephaniidae, it would be more parsimonious to consider this to be the plesiomorphous condition. This view was proposed by Mason (1981) who additionally cites the fact that the second and subsequent metasomal spiracles are situated in the laterotergites in the Symphyta, and that in the primitive subfamilies, Xyelidae and Pamphiliidae, the first metasomal spiracle is also in the laterotergite. Assuming that Mason was correct in his polarity decision, then we see that the majority of cyclostome and related subfamilies of

Braconidae are united by an apomorphic migration of the spiracle to the tergum (subfamilies Braconinae, Vaepellinae (nearly - see Quicke, 1987), Telengaiinae, Doryctinae, Rogadinae, Opiinae, Gnamptodontinae, Histeromerinae (the statement in van Achterberg, 1984 is incorrect) and Betylobraconinae (the placement of this subfamily in van Achterberg's, 1984 cladogram is considered erroneous; Tobias, 1979; Sharkey, personal communication). The placement of the remaining subfamily with a notal spiracle van Achterberg's (1984) Dirrhopinae needs further consideration but it appears to be close to the Microgastrinae (Sharkey, personal communication). With this arrangement three reversals only have to be cited; for Alysiinae which has the second spiracle in the epipleuron, in the Dirrhopinae and in the peculiar subfamilies Ypsistocerinae and Mesostoinae. The Ypsistocerinae are associated with termites and may be derived from the Doryctinae. The Mesostoinae are very small wasps and too poorly known for further comment.

Number of hamules. The plesiomorphous number of hamules on vein R1 of the hindwing of Braconidae is approximately ten as indicated by outgroups comparison with the Ichneumonidae (Townes, 1969) and other equivalent sized Hymenoptera. However, in the majority of Braconidae, the number is usually reduced to three or sometimes up to six. Few braconids other than *Calohelcon* have eight to ten. Among these are members of the endemic Australian subfamilies, the Cercobarconinae and the Trachypetinae, and it may be significant that *Trachypetus* is one of the few braconids with a partially opening forewing costal cell. Thus, the number of hamules indicates another possibly atavistic character state in *Calohelcon* and in the Trachypetinae.

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References

- Achterberg, C. van, 1975. A new genus, *Mesostoa* gen. nov., from W. Australia, belonging to a new subfamily (Hymenoptera, Braconidae). *Entomologische Berichten* 35: 158-160.
- Achterberg, C. van, 1976a. A revision of the tribus Blacini (Hymenoptera, Braconidae, Helconinae). *Tijdschrift voor Entomologie* 118: 159-322.
- Achterberg, C. van, 1976b. A preliminary key to the subfamilies of the Braconidae (Hymenoptera). *Tijdschrift voor Entomologie* 119: 33-78.
- Achterberg, C. van, 1979a. A revision of the species of Amicrocentrinae, a new subfamily (Hymenoptera, Braconidae), with a description of the final larval instar of *Amicrocentrum curvinervis* by J.R.T. Short. *Tijdschrift voor Entomologie* 122: 1-28.
- Achterberg, C. van, 1979b. A revision of the new subfamily Xiphozelinae (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* 122: 29-46.
- Achterberg, C. van, 1979c. A revision of the subfamily Zelinae auct. (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* 122: 241-479.
- Achterberg, C. van, 1983a. A revision of the new tribe Brulleiini (Hymenoptera, Braconidae). *Contributions of the American Entomological Institute* 20: 281-306.
- Achterberg, C. van, 1983b. Revisionary notes on the subfamily Gnaptodontinae, with description of eleven new species (Hymenoptera, Braconidae). *Tijdschrift voor Entomologie* 126: 25-57.
- Achterberg, C. van, 1984. Essay on the phylogeny of Braconidae (Hymenoptera, Ichneumonoidea). *Entomologisk Tidskrift* 105: 41-58.
- Brothers, D.J., 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *University of Kansas Science Bulletin* 50: 483-648.
- Tobias, V.I., 1975. Two new and one little known subfamilies of Braconidae (Hymenoptera) from Australia. *Entomologicheskoe Obozrenie* 58: 1-37 [In Russian].
- Tobias, V.I. & S.A. Belokobylsky, 1983. Aberrant wing venation in Braconidae (Hymenoptera) and its significance in the study of phylogeny of the family. *Entomologicheskoe Obozrenie* 62: 341-347 [In Russian].
- Townes, H., 1969. The genera of Ichneumonidae, Part 1. *Memoirs of the American Entomological Society* 11: 1-300.
- Turner, R.E., 1918. Notes on the Braconidae in the British Museum. IV. On new Helconinae, mostly Australian. *Annals of the Museum of Natural History* 9(22): 163-173.