The cladistics and biology of the *Callajoppa* genus-group (Hymenoptera: Ichneumonidae, Ichneumoninae)

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A cladistic analysis is presented for the genera of the former ichneumonine tribe Trogini. The tribe Heresiarchini is paraphyletic with respect to the Trogini, and so maintaining Trogini as a separate tribe is unsatisfactory. Within Heresiarchini, the following changes are made: (a) the subtribes Apatetorina and Heresiarchina are referred to as the *Apatetor* and *Heresiarches* genus-groups, (b) the genera of the paraphyletic subtribe Protichneumonina are treated as *incerta sedis* within Heresiarchini, and (c) the Trogini are referred to as the *Callajoppa* genus-group, with the former subtribe Trogina referred to as the *Trogus* subgroup. Thirty-five genera are recognized as valid within the *Callajoppa* genus-group. *Catadelphops*, *Catadelphus*, *Cobunus*, and *Facydes* are transferred to this group; *Holojoppa* is removed and is *incertae sedis* within Heresiarchini. Three new synonyms are proposed: *Araeoscelis* and *Cryptopyge* are junior synonyms of *Macrojoppa*, and *Neamblyjoppa* is a junior synonym of *Catadelphops*. *Trogus latipennis* Cresson is transferred to *Pedinopelte* from *Macrojoppa*, and *Trogus mactator* Tosquinet and its related species (*T. bicolor* Radoszkowski, *T. heinrichi* Uchida, and *T. tricephalus* Uchida) are transferred to *Holcojoppa*. *Tricyphus* is redefined and a neotype is designated for *Tricyphus cuspidiger* Kriechbaumer, the type-species of the genus. Thirteen new genera are described (authorship of all is Wahl & Sime): ***Charmedia*** (type-species: *Charmedia chavarriai* Wahl & Sime, sp. n.)**,** ***Daggoo*** (type-species: *Daggoo philoctetes* Wahl & Sime, sp. n.), ***Dothenia*** (type-species: *Dothenia hansoni* Wahl & Sime, sp. n.), ***Humbert*** (type-species: *Humbert humberti* Wahl & Sime, sp. n.), ***Laderrica*** (type-species: *Laderrica feenyi* Wahl & Sime, sp. n.), ***Mokajoppa*** (type-species: *Tricyphus respinozai* Ward & Gauld), ***Metallichneumon*** (type-species: *Metallichneumon neurospastarchus* Wahl & Sime, sp. n.), ***Myocious*** (type-species: *Myocious orientalis* Wahl & Sime, sp. n.), ***Quandrus*** (type-species: *Trogus pepsoides* Smith, transferred from *Callajoppa*), ***Queequeg*** (type-species: *Gathetus flavibasalis* Uchida, transferred from *Neofacydes*), ***Saranaca*** (type-species: *Trogus elegans* Cresson; includes *Trogus apicalis* Cresson, *Tricyphyus ater* Hopper, and *Tricyphus floridanus* Heinrich), ***Tashtego*** (type-species: *Tashtego janzeni* Wahl & Sime, sp. n.), and ***Xanthosomnium*** (type-species: *Xanthosomnium froesei* Wahl & Sime, sp. n.). A key to the genera of the *Callajoppa* genus-group is provided. The evolution of biological traits within the *Callajoppa* genus-group is discussed with reference to the elucidated phylogeny. The groundplan biology is parasitism of Sphingidae, with oviposition into a host pupa/prepupa. There have been two transitions to butterfly parasitism within the *Trogus* subgroup: one a transition to Papilionidae (followed by a switch to Nymphalidae at *Psilomastax*) and the other to Nymphalidae (followed by a switch to Papilionidae within *Macrojoppa*). ©2002 The Linnean Society of London. *Zoological Journal of the Linnean Society*, **134**, 1–56.

ADDITIONAL KEY WORDS: cladistics – evolutionary patterns of host utilization – Nymphalidae – Papilionidae – parasitoid – Sphingidae.

INTRODUCTION

The species of the ichneumonid subfamily Ichneumoninae are all internal parasitoids of Lepidoptera. Although pupation is always within the host's pupal remains, some directly oviposit into pupae whereas others oviposit into the larvae and delay development until host pupation. Specialization upon host taxa is relatively common in ichneumonines, and the relationships between clades of wasps and hosts can be extremely specific (Heinrich, 1960). The restriction of this large subfamily (consisting of approximately 370 genera) to Lepidoptera is one example, with others

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being Listrodromini on Lycaenidae, Platylabini on Geometridae, *Hoplismenus* Gravenhorst on Nymphalidae, and *Thyrateles* Perkins and the related *gracilicornis* species-group of *Ichneumon* Linnaeus on butterflies, mainly Nymphalidae (Heinrich, 1960).

The tribe Trogini is another ichneumonine group that exhibits remarkable host fidelity. Prior to this study, it consisted of 18 genera and 115 described species (Yu & Horstmann, 1997); its distribution is almost entirely Holarctic, Oriental, and Neotropical, with only four species in Africa and one in Australia. Trogines are of particular interest because they are parasitoids of Sphingidae, Papilionidae, and Nymphalidae, insects sufficiently well known to have variously served as model systems in chemical ecology, population and community biology, genetics, and conservation biology (Janzen, 1984; Vane-Wright & Ackery, 1984; Pittaway, 1993; Scriber *et al.,* 1995). In addition, the food plants, natural history, and distributions of the hosts are very well known. Because the caterpillars are frequently collected and reared by amateur and professional lepidopterists, there are abundant sources for reliable host records, permitting in many cases the identification of host range with some certainty.

Heinrich (1962) proposed an evolutionary sequence of host shifts for the Trogini from an ancestral, relatively generalist, association with various heterocerous Lepidoptera, to specialization on Sphingidae and thence to specialization on butterflies. One of the goals of this research was the testing of Heinrich's hypothesis against a cladistic analysis of trogine relationships, thereby establishing a framework for evaluating hypotheses about trogine ecology and the evolution of host associations.

MATERIAL, METHODS, AND TERMINOLOGY

The specimens examined in this study were borrowed from or deposited in the following collections and we are indebted to the curators listed below:

AEIC: American Entomological Institute: Gainesville, Florida.

AMNH: American Museum of Natural History: New York, New York (J. Carpenter).

ANSP: Academy of Natural Sciences: Philadelphia, Pennsylvania (D. Azuma).

CCPC: Charles C. Porter collection: Gainesville, Florida.

CNCI: Canadian National Collections: Ottawa, Canada (J. Huber).

CUIC: Cornell University: Ithaca, New York (E.R. Hoebeke).

DNHC: Denver Museum of Natural History: Denver, Colourado (R.S. Peigler).

EIHU: Entomological Institute, Hokkaido University: Sapporo, Japan (M. Ohara).

HMNS: Houston Museum of Natural Science: Houston, Texas (C. Stuart).

HMOX: Hope Entomological Collections: Oxford, United Kingdom (C. O'Toole).

JHIC: D.H. Janzen and W. Hallwachs collection: Philadelphia, Pennsylvania.

KRSC: Karen R. Sime collection: Ithaca, New York.

HNHM: Hungarian Natural History Museum: Budapest, Hungary (J. Papp).

IMLA: Fundacion e Instituto Miguel Lillo: Tucumán, Argentina (C.B. de Fernández).

ITLJ: National Institute of Agro-environmental Sciences: Tsukuba, Japan (K. Konishi).

NHMW: Naturhistorisches Museum Wien: Vienna, Austria.

NHML: The Natural History Museum: London, United Kingdom (L. Tarel & S. Lewis).

NMNH: National Museum of Natural History: Washington, D.C. (D. Furth).

STRI: Smithsonian Tropical Research Station: Balboa, Panama (A. Aiello).

UCDC: University of California, Davis: Davis, California (S. Heydon).

UGCA: University of Georgia: Athens, Georgia (J. McHugh).

ZMHB: Museum für Naturkunde der Humboldt Universität der Berlin: Berlin, Germany (F. Koch).

ZMPA: Institute of Zoology, Polish Academy of Science: Warsaw, Poland (T. Huflejt).

ZSMC: Zoologische Staatssammlung: Munich, Germany (E. Diller).

The deficiencies and pitfalls of rearing records are summarized by Shaw (1990: 453–455). Rather than relying upon catalogue listings, original references were sought. The most reliable records are considered to be those based upon extensive field studies or established by associated wasp and host remains. Next are literature records that are: (1) traceable to tangible evidence in collections (2) substantiated by some natural history observations, or (3) repeatedly and independently corroborated. Isolated reports that could not be traced to specimens are simply noted. New records for genera without previously reported host data are referred to reared voucher specimens.

The morphological terminology is mostly that of Townes (1969). *Anterior transverse carina* and *posterior transverse carina* are used (respectively) for 'basal transverse carina' and 'apical transverse carina', *epicnemial carina* for 'prepectal carina', *gena* for 'temple', *gonoforceps* for 'clasper', *hypopygium* for 'female subgenital plate', *laterotergite* for 'epipleurum', *occiput* for 'postocciput', *malar space* for 'cheek', *supra-antennal*

area for 'frons', and *supraclypeal area* for 'face'. *O.D.* is an abbreviation for 'ocellar diameter'. The 'ocellar diameter' refers to the greatest transverse measurement of either of the lateral ocelli. The *posterior section of the vertex* is the section extending from the lateral ocelli to the occipital carina. The nomenclature of wing veins and cells is based upon Ross (1936) and Mason (1986); abcissae are numbered so that '*2/Cu*' refers to the second abcissa of vein *Cu*. *Mesosoma* and *metasoma* are used to refer to the apparent thorax and abdomen, respectively. *MS1* is used for the first metasomal segment (second true abdominal segment). *T1*, *T2*, etc., are used for the first metasomal and subsequent tergites. When the lengths of the body and wing are given, the values in parentheses are those of the holotype. Reference to metasomal colour in the descriptions applies only to the tergites and first sternite unless otherwise indicated.

The terminology of the cephalic sclerites of the mature larva is that of Finlayson (1975) and Short (1978), with modifications by Wahl (1990). Methods of larval preparation are those of Wahl (1989). Wahl's notation for larval preparations follows the museum acronym. It consists of his initials, the day, month, year, and a letter designating the individual preparation.

CLASSIFICATORY HISTORY

Förster (1869) erected Trogoidae for *Trogus* Gravenhorst, *Dinotomus* Förster, and *Automalus* Wesmael, based upon an elevated convex or conical scutellum. Ashmead (1895) recognized it without comment as a tribe of Ichneumoninae. Although Kriechbaumer (1898) was dissatisfied with the elevated scutellum character, he nevertheless used it in his treatment of the group, which was notable for (1) elevating the group to a subfamily, Joppinae, based upon the oldest included genus, and (2) omitting Förster's genera. Ashmead (1900a) treated the genera *Psilomastix*(!) Tischbein, *Trogus*, *Automalus*, and *Trogomorpha* Ashmead as a tribe, Joppini. In the same year, Ashmead (1900a) published a classification of Ichneumonoidea which again recognized Joppini, this time including Kriechbaumer's genera together with Förster's. Its definition was based upon (1) the elevated scutellum (2) the deep depression between the propodeum and postscutellum, and (3) the tendency for the areola to be either reduced to a tubercle or to be confluent with the petiolar area. Ashmead (1900b) is 'hastily contrived and full of errors. based largely upon the generic keys of Foerster' (Carlson, 1979) and it should be no surprise that many of the included genera do not conform to the tribal definition.

Heinrich (1934) radically revised the tribal classification of Ichneumoninae. Trogini was separated from

Joppini and restored as a tribe, defined by (1) reduction of the areola to a small polished area, and (2) compression of the propodeum so that it is steeply sloping both anteriorly and posteriorly. While Heinrich did note that the scutellum was almost always strongly convex to conical (with rare exceptions), his emphasis was on the propodeal characters. The regional nature of the monograph precluded a comprehensive tribal treatment but the following genera were placed into Trogini: *Callajoppa* Cameron, *Dimaetha* Cameron, *Facydes* Cameron, *Gathetus* Cameron, *Stirojoppa* Cameron, and *Trogus*. Within the tribe, Heinrich (*ibid.*) recognized the *Trogus* Group and the *Callajoppa* Group, defined by morphology and biology. Species of the *Trogus* Group are parasitoids of Rhopalocera and have the tergites strongly convex and conspicuously set-off from one another. In contrast, the species of the *Callajoppa* Group are parasitoids of Sphingidae and have unspecialized tergites. Heinrich provided a phylogeny of the major lineages of ichneumonines (his table 1). One of the lineages consisted of the Ichneumonini, Heresiarchini (Protichneumonini of Heinrich; Wahl & Mason, 1995), and Trogini. A morphocline of propodeal structures linked these tribes, ranging from that of Ichneumonini with its distinct dorsal-posterior planes, to the more abbreviated and evenly convex propodeum of the Heresiarchini, and culminating in the steeply sloping propodeum of the Trogini.

The Nearctic Trogini were revised by Hopper (1939), using Heinrich's more restrictive definition of the group. The following genera were placed in the tribe: *Callajoppa*, *Catadelphus* Wesmael, *Conocalama* Hopper, *Gnamptopelta* Hopper, *Macrojoppa* Kriechbaumer, *Tricyphus* Kriechbaumer, and *Trogus*.

Heinrich (1962) provided a more thorough treatment of the Nearctic trogines and provided an extensive discussion of the tribe's systematics. He pointed out that the shape of the fore wing cell 1 + 2Rs ('areolet' of authors) provided an additional defining character. Not only is it often petiolate in trogines but it is irregularly quadrangular, in contrast to the regularly pentagonal shape of heresiarchines and other ichneumonines. The *Callajoppa* Group and the *Trogus* Group were raised to the level of subtribes, Callajoppina and Trogina, respectively. The Callajoppina consisted of *Callajoppa*, *Catadelphus*, *Conocalama*, *Dimaetha* (treated as *Erythrojoppa* Cameron by Heinrich), *Gnamptopelta*, *Tmetogaster* Hopper, and *Tricyphus*; the earlier inclusion (Heinrich, 1934) of *Gathetus*, *Facydes*, and *Stirojoppa* was reversed without comment. The Trogina was composed of *Araeoscelis* Schulz, *Cryptopyge* Kriechbaumer, *Holcojoppa* Cameron, *Macrojoppa*, *Neofacydes* Heinrich, *Pedinopelte* Kriechbaumer, *Psilomastax* Tischbein, and *Trogus*. Heinrich noted that *Neofacydes*, although

morphologically a member of Trogina, had been reared from a sphingid. In conjunction with certain other morphological features, he stated that this 'hints at the correctness of my morphological hypothesis, that the Rhopalocera-feeding Trogina may have ascended from the slightly less specialized sphingid-feeding Callajoppina, and that both groups can be united in one tribe.In contrast to Heinrich's placement of *Callajoppa* and *Trogus* in the same tribe, Townes (in Townes *et al.,* 1961) placed the *Callajoppa* Group in the Heresiarchini, restricting Trogini to the *Trogus* Group. He believed that the areola in the two groups was formed in fundamentally different ways, so that one could not be derived from the other (Townes, pers. comm. to DBW). As summarized in Townes *et al.* (1961: 459), the small polished areola in the *Callajoppa* Group is formed of the entire areola, while the areola in the *Trogus* Group has been lost due to the absence of the median section of the posterior transverse carina. Heinrich did not agree with Townes and apparently believed that the areola of the *Callajoppa* Group was the precursor to the condition found in the *Trogus* group, summarizing the difference between the two classifications as whether or not to 'cut the chain of forms "above" the *Callajoppa* group instead of 'below' as done until now . . .' (1962: 808).

Relatively little was added to the literature after Heinrich (1962). The 'clear and constant *tendency*' (emphasis added) of cell 1 + 2Rs 'to be petiolate and obliquely trapezoidal by prolongation of the second intercubitus and abbreviation of the second abcissa of cubitus' was emphasized by Heinrich (1967) as being as important to the definition of the Trogini as propodeal structure. Using this criterion, *Catadelphus* was later transferred from the Trogini to the Heresiarchini (Heinrich, 1971). Gillespie & Finlayson (1983) discussed the distribution of larval characters in separating the subtribes. In the Callajoppina, *Pepsijoppa* Heinrich (Heinrich, 1967) and *Yeppoona* Gauld (Gauld, 1984) were described as new; *Afrotrogus* Heinrich was elevated from a synonym of *Dimaetha* (Heinrich, 1967), and *Holojoppa* Szépligeti and *Stirojoppa* were transferred to the subtribe from Heresiarchini (Ward & Gauld, 1987).

RELATIONSHIPS AND CHOICES OF OUTGROUPS

Although the monophyly of the Ichneumoninae has not been formally established, its placement in the Ichneumoniformes (Wahl 1993), a clade consisting of the Brachycyrtinae, Cryptinae, and Ichneumoninae, leads to the identification of a number of putative autapomorphies for the subfamily: these include adult (presence of gastrocoeli), larval (losses of the hypostomal spur, labral sclerite, labial sclerite, mandibu-

lar denticles, and central papillus of the antenna), and biological (endoparasitoids of Lepidoptera with pupation within the host pupa) characters.

The relationships of the currently recognized 15 tribes (Wahl & Mason, 1995) have not been subjected to cladistic analysis. Traditionally, the subfamily has been divided into the Ichneumoninae Cyclopneusticae (the Alomyini) and the Ichneumoninae Stenopneusticae (all other tribes), reflecting the circular vs. elongate shape of the propodeal spiracle. The two groups are monophyletic and represent the basal clades of the subfamily (Wahl, unpublished research).

For the Ichneumoninae Stenopneusticae, Heinrich (1934) provided a phylogeny of the major lineages that was supported by characters given in the text. Of special interest is Heinrich's transformation series of propodeal structures: the propodeum of Ichneumonini with its distinct dorsal-posterior faces gives rise to the abbreviated and evenly convex propodeum of Heresiarchini, which in turn changes into the steeply sloping propodeum of Trogini. His phylogeny implies that Ichneumonini are paraphyletic to other tribes in his scheme, and in particular that Heresiarchini are paraphyletic with respect to the Trogini.

Hilpert (1992: 40) published a cladogram for the subtribes of Ichneumonini, using the phylogeny of Heinrich (1934) as a starting point. It included the novel treatment of the Heresiarchini (Protichneumonini of Hilpert) as a subtribe of Ichneumonini. A detailed critique of this cladogram is beyond the scope of this paper but a few points are mentioned in order to justify rejection of this phylogeny. A cursory inspection of the cladogram's synapomorphies reveals most of them to be trends (e.g. tendency to form a scopa, tendency toward a rectangular areola, reduction of propodeal carinae), biological characters for which data are lacking for most species (overwintering of adults), or errors of interpretation (presence of a median tooth on the propodeal anterior margin as a ground plan of Ichneumonini). For these reasons, his characters are not used as guides to heresiarchine outgroups nor is the Heresiarchini treated as a subtribe. Although Hilpert apparently accepted Heinrich's belief in a close relationship between Heresiarchini and Trogini (ibid., p. 38), he did not mention Trogini when he discussed heresiarchine placement.

Heinrich (1970) ultimately recognized three subtribes of Heresiarchini: Apatetorina, Heresiarchina, Protichneumonina. His definitions of Apatetorina and Heresiarchina are vague. Apatetorina (ibid.) is based upon (1) fusion of the basal area and areola to form a region larger than the petiolar area, and (2) a reduction of the metapostnotum so that the propodeum and metanotum are more or less contiguous. Heresiarchina (Heinrich, 1967) shares that metapostnotal reduction and has the lower mandibular tooth

turned under. Protichneumonina lack these characters. Examination of the constituent genera of Apatetorina and Heresiarchina reveals Heinrich's propodeal characters to be *trends*, and not shared by all genera. There is a core of related genera in each subtribe; two representative genera were chosen from each subtribe, since the aim was finding representative outgroups and not the resolution of heresiarchine internal relationships. *Apatetor* Saussure and *Pseudocillimus* Roman were chosen from the Apatetorina, and *Heresiarches* Wesmael and *Legnatia* Cameron from Heresiarchina. Heinrich's propodeal characters were used with some modifications (see comments for characters 22 and 24, below). In the Protichneumonina, the following genera were chosen to represent morphological and biological diversity: *Amblyjoppa* Cameron, *Atanyjoppa* Cameron, *Catadelphops* Heinrich, *Catadelphus*, *Cobunus* Uchida, *Coelichneumon* Thomson, *Facydes*, *Gathetus*, *Hedyjoppa* Cameron, *Lymantrichneumon* Heinrich, *Neamblyjoppa* Heinrich, and *Protichneumon* Thomson. *Ichneumon* was used as an example of a non-heresiarchine.

TAXA

Eighteen species were selected from the Heresiarchini and Ichneumonini to serve as outgroups (see above). In the Trogini, 51 species were selected to represent diversity in the 19 described genera. In addition, 20 problematical species that did not fit existing genera were entered; they are described below as the new genera *Charmedia*, *Daggoo*, *Dothenia*, *Humbert*, *Laderrica*, *Lagavula*, *Metallichneumon*, *Mokajoppa*, *Myocious*, *Queequeg*, *Tashtego*, and *Xanthosomnium*. The species are listed in Table 1.

As the focus of this revision is on generic relationships, species determinations by recognized authorities (such as Townes and Heinrich) have been accepted at face value. These largely tropical genera are poorly known at the species level, however, and current determinations are likely to be changed. In order to ensure that the species used in this revision can be recognized in the future, voucher tags have been placed on exemplar specimens of each species. The tags are yellow and read: 'VOUCHER/[species name]/Sime & Wahl 2000'.

CHARACTERS

The following informative characters were used, with the presumed plesiomorphic state denoted by a '0' and derived states by integers. Comments are included where relevant. The data matrix for character distributions is given in Table 1.

1. Flagellum of female: (0) lanceolate (subapical region ventrally flattened and widened; (1) bristle-shaped (subapical region not flattened and widened).
2. Flagellomere 3 of female: (0) 1.1–2.6× as long as wide; (1) 3.0–4.0× as long as wide.
3. Flagellomeres of male: (0) with tyloids; (1) without tyloids.
4. Apical margin of clypeus: (0) straight; (1) concave.
5. Apical margin of clypeus: (0) simple; (1) medially produced as tooth of varying sharpness.
6. Clypeus: (0) uniformly thick; (1) tapering toward apex, so that apical 0.3 is noticeably thinner than base.
7. Clypeus: (0) uniformly thick; (1) centrally concave, tapering toward apex so that apical 0.2 is semitranslucent.
8. Clypeus: (0) apicolateral margin forming an angle of approximately 40° (Figs 17–19); (1) apicolateral margin forming an angle of approximately 90° (Figs 20–22).
9. Clypeus: (0) uniformly flat, lateral margin weakly angled (Fig. 40); (1) basally convex and with median concavity just above apical margin, lateral margin sharply angled (Fig. 69). (The uniformly flattened and weakly angled clypeus is the groundplan condition for Stenopneusticae, although many exceptions are found throughout the clade.)
10. Clypeal punctures: (0) evenly distributed; (1) sparse (separated by ≥2× their diameter) and irregularly distributed, or absent.
11. Mandible: (0) elongate, 1.8–2.0× as long as basal width; (1) short, 1.3–1.6× as long as basal width. [The derived state is one of the defining characters of the *Trogus* subgroup. Although many genera outside the *Callajoppa* genus-group have short and stout mandibles, the teeth are large and equal; genera of the *Trogus* subgroup have the teeth small and the ventral tooth decidedly smaller (Fig. 43).]
12. Ventral mandibular tooth: (0) in same plane as dorsal tooth; (1) turned under; (2) absent.
13. Supra-antennal area medially: (0) simple; (1) with two low vertical ridges (Fig. 41) (2) with two denticles (Fig. 42).
14. Vertex with posterior section: (0) 1.0–1.3 times as long as ocellar triangle, gently sloping to occipital carina (Fig. 39); (1) 1.0–1.3× as long as ocellar triangle, strongly convex (Fig. 38); (2) about 1.5× as long as ocellar triangle, steeply sloping to occipital carina (Fig. 37).
15. Genae: (0) convex, evenly receding behind eye in dorsal view (Figs 10, 26); (1) swollen, bulging out behind eye in dorsal view (Figs 27, 45); (2) flat and sharply receding in dorsal view (Figs 9, 11, 12); (3)

Table 1. Data matrix for the *Callajoppa* genus-group. '?' denotes missing data; '$' is used for a subset polymorphism (in the sole case, the included values are 1 and 2)

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                                1111111111222222222233333333334444444444555555555566
                                1234567890123456789012345678901234567890123456789012345678901
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Ichneumon caliginosus	0000000000000000000000000000000000010010000000000000000000
Amblyjoppa fuscipennis	0000000000002000000000000000000000010011000000000000000100
Atanyjoppa violaceipennis	0000000000002001000010100000000001000000021201000000?????
Catadelphops buccatus	001001010002001001010100001000041010211100000100001000311????
Catadelphus arrogator	0010010100000010010100000100000000011110000000001000111?1??
Catadelphus atrox	0010010100000010010100000100001000111100000201001000111?1??
Cobunus pallidiolus	01?0001001000010000000000000040002100000022000000000000????
Coelichneumon brunneri	0001000010000000103000000000001001000000001000000000000000
Facydes purpureomaculatus	01000010010000010012110010000010400021010000020000000000????
Gathetus melanocerus	00?000000000020110300001010010000020000000210020000000????
Hedyjoppa sp.	00?0100100000020000300000000000010100000200000000????
Lymantrichneumon disparis	00?00000000000200000101000000010000000020000000000?0???
Neamblyjoppa nasuta	001001010002000010001000110014101011210000211001000211????
Protichneumon pisorius	0000100000000000030000100000040000110100000200000000000100
Apatetor blandus	00001000010000000010010100000000011110000021200000050????
Pseudocillmus rubrithorax	0000000000000201001000000000000010010000010000000000?0??
Heresiarches secundus	0100000010100020000000010000000400011000000020000000000????
Legnatia sp. 8	0100000010100020001001000000000011000000200000000????
Afrotrogus rufipedalis	0000000000000100101001010000400002011000002120000000????
Callajoppa cirrogaster	00001001000000010100001010000400012111000001020010001110110
Callajoppa caspica	000010010000000101000010100004000211100000100001000111????
Callajoppa exaltatoria	000010010000000102000010100004000211100000101001000311?11?
Callajoppa pepsoides	000001010000000010200001010004000221$110000201001000311?1??
Charmedia chaverriai	000000000000000010000101000041000212100002010010030110110
Conocalama bolteri	0000110100000001000010100101000000002121000022010010030110110
Conocalama brullei	0000110100000001000010100101001001000212100002201001000311????
Conocalama occidentalis	0000110100000001000010100101001000002121000022010010030110110
Conocalama violipennis	00001101000000010000101001010010000021210000220100100311????
Dimaetha sp. 1	0000000010010200001000101000040002011000000000000000????
Dimaetha sp. 2	0000000010010200001000101000040002011000000000000000????
Dothenia hansoni	0?101101000001000010100101000100122121100012010010003???1??
Dothenia sp. 2	001011010000001000010100101000010002212110000201001000411????
Dothenia sp. 3	00?011010000001000010100101000010002212110000201001000411????
Dothenia sp. 7	00101101000000100001010010100010012212110000201001000411????
Dothenia sp. 8	00?01101000001000100010100003101211210000201001000311????
Gnamptopelta obsidianator	000100000000000020000101000000000212100001010010001110110
Holojoppa grandis	00?0000000100300001010000000204000100110000201001000000????
Humbert humberti	00?001010000010000101001010010400021210000212001000411????
Laderrica feenyi	00?00000000000201001011000410002121110002010000000301????
Lagavula gauldi	??10000000002010100100100000004012021211000021200000003???1??
Lagavula sp. 3	??0000000000201000010010010214112021211000021200000003?????
Lagavula sp. 4	00?0000000002010000100100102141021212110000212000000401????
Mokajoppa sp. 1	0011000000001000000001011021410202121000020000000003110110
Myocious orientalis	??00110100000000110001001010000400102?1100002010010003?????
Pepsijoppa gryps	00000010000000010100000000000001110000101001000311????
Stirojoppa thoracica	000000001001000000110001010000401002011000002020000000100????
Stirojoppa sp. 1	00?000001001000000110001010000401002011000002020000000100????
Tmetogaster nublipennis	00101010000001001010000101000040001212100002201001000311?1??
Tricyphus cuspidiger	00?000000000200001000101100041000212112100201000000301????
Tricyphus elegans	00000000000000100010100004000212111000201001000311?1??
Tricyphus floridana	00000000000000100010100004000212111000201001000311????
Tricyphus nigriventris	00?0000000000200001000010110014000212112100201000000301????

Table 1 (cont.)

Tricyphus respinozai	0011100000000010000000001011011400102121100002000000003110110
Xanthosomnium froesei	00?0010000010010000001001111020400002121100002100000000301?1??
Yeppoona sp. 1	0?10000000000000010100101000040000 2?010000021100000003??????
Yeppoona sp. 2	0?100000000000000101001000000400002?010000021100000003??????
Yeppoona sp. 5	0?100000000000000101001010000400002?010000021100000003??????
Araeoscelis pulcherrima	10110000111020211222011010211214010021211003021012021052 11210
Araeoscelis rufa	1111000011102021122201101021121401002121100302101202105211210
Cryptopyge picta	0111000011101021022001101021121401002122000201001201105311310
Cryptopyge sp. 2	0111000011101021022001101021121401002122000201001201105311310
Cryptopyge sp. 4	01?1000011101021022001101021121401002122000201001201105311310
Daggoo philoctetes	11?00000101000210232010010201214000021211000021002011000112001
Daggoo sp.	??1000001010002102320100102012140000212110000210020110 0??1201
Holcojoppa orientalis	1010000010101121021200001020020300002111000000000202125211202
Holcojoppa sp. 1	1010000010101121021200001020020300002111000000000202125 21????
Holcojoppa sp. 2	??1000001010112102130000102002020100 2?11000000000202125??1201
Macrojoppa blandita	0110000111010210202010010201214010021210001010012011 05101310
Macrojoppa bogatensis	0110000111010210201010010201214010021110001010012011 0510????
Macrojoppa latipennis	10110000101000210232010010200214000021210000110001021031 11200
Macrojoppa polysticta	0110000111010210201010010201214010021210001010012011 0510????
Macrojoppa sp. 8	???000001110102102020100102012140100212100010100120110 5101310
Metallichneumon neurospastarchus	00?00001010002102020000102002040000212110000100110110000????
Neofacydes flavibasalis	00?0000010102220022000010200204000021210000020002021 3020????
Neofacydes marlisae	0110000101000200202000010200204000021110000000002011 0010????
Neofacydes sinensis	0110000101000200202000010200204000021110000000002011 00101??
Neofacydes sp. 2	0?10000101000200202000010200204000021110000010002011 00?????
Neofacydes sp. 3	0110000101000200202000010200204000021110000000002011 0010????
Pedinopelte gravenstii	1011000010100021023301001021021411202111000011000101103 11????
Pedinopelte sp. 2	1011000010100021023301001021021411202121000011000101103111201
Pedinopelte sp. 3	10?1000010100021023201001020021000002121100011000101103 11?2??
Psilomastax pyrimidalis	1010000010102021022000010200202000021110000000001011 05111300
Queequeg sp. 1	01?0000010100221021200001020021400002111000002000202 13020????
Queequeg sp. 2	01?0000010100221022000010200214000021110000020002021 3020????
Tashtego janzeni	0111000011100021022101001021021401002100000010020202 11000????
Trogus bicolor	1010000010101121021200001020020300002111000000000202125 21????
Trogus lapidator	1010000010102021020200001020020300002111000000000202123211202
Trogus mactator	1010000010101121021200001020020300002111000000000202123211202
Trogus pennator	1010000010102021020200001020020300002111000000000202123211202

flat and parallel to median axis of head in dorsal view (Fig. 46).

16. Juncture of hypostomal and occipital carinae: (0) separated from mandibular base by about 0.5× basal mandibular width; (1) separated from mandibular base by 0.7–1.0× basal mandibular width; (2) meeting at mandibular base.

17. Occipital carina: (0) dorsal and ventral regions with same height; (1) with ventral region above mandible produced as low flange (section just above mandible about 0.6× as wide as 5th maxillary palpomere).

18. Pronotal flange: (0) high and with posterior face concave; (1) low and with posterior face convex; (2) high and with posterior face flat. (The anterior margin of the pronotal collar is produced as a distinct elevation (Fig. 70), which is here called the *pronotal flange*.)

19. Epicnemial carina: (0) complete, extending to mesopleural dorsal margin or turned anteriorly to touch (or almost touch) anterior mesopleural margin; (1) dorsally incomplete or obsolete; (2) present only on mesothoracic venter; (3) absent.

20. Scutellum: (0) weakly to moderately convex (Fig. 47); (1) strongly convex, shelf-like (surfaces intersecting at about 90° in lateral view) (Figs 48–50), or sometimes with definite planar surfaces and forming a more or less acute angle in lateral view; (2) conical (radially symmetrical); (3) flat. (The range of shapes in state 1 can intergrade such that a sharp division is impossible. Examples can be found in several genera, of which *Stirojoppa* is an excellent example.)

21. Scutellum: (0) lateral carinae absent or extending to at most 0.2–0.3× scutellar length; (1) lateral carinae extending to at least 0.5× scutellar length.

22. Juxtacoxal carina: (0) present or obsolescent; (1) absent.

23. Metanotum: (0) central convexity narrow and with large flanking lateral foveae (Fig. 51); (1) central convexity broad and lateral foveae correspondingly reduced (Fig. 52).

24. Metapostnotum: (0) present as normal groove; (1) propodeum contacting metanotum and more or less obliterating groove, at least laterally.

25. Anterior margin of propodeum: (0) forming normal groove with metapostnotum; (1) steeply and abruptly sloping downward from areola (Figs 29, 47).

26. Basal area and areola: (0) separated by anterior transverse carina; (1) anterior transverse carina absent or obsolete.

27. Areola: (0) large and well-defined by carinae (Figs 53, 54); (1) reduced, ranging from partially to completely filled-in, often appearing as a polished boss (Figs 55, 56); (2) posterior transverse carina medially incomplete and areola not distinguishable (Fig. 57). (Character 29 should not be confused with state 1: the swollen median section of the anterior transverse carina is anteriad the anterior transverse carina, while the reduced, boss-like areola is posteriad the anterior transverse carina. It should be noted that both *Protichneumon* and *Amblyjoppa* have the areola filled in and higher than the adjacent region.)

28. Anterior transverse carina: (0) complete (at least medially); (1) absent.

29. Anterior transverse carina: (0) of same width as other propodeal carinae; (1) with median section swollen (Fig. 58).

30. Posterior transverse carina: (0) complete; (1) medially incomplete; (2) absent.

31. Lateral longitudinal carinae: (0) more or less complete (anterior sections can be absent); (1) absent.

32. Median longitudinal carinae anteriad anterior transverse carina: (0) present; (1) close together and on raised area; (2) present and with median carina; (3) absent, only median carina present; (4) absent.

33. Median longitudinal carinae posteriad anterior transverse carina: (0) present; (1) absent.

34. Punctures of first lateral area: (0) uniformly distributed; (1) scattered or absent.

35. First and second lateral areas: (0) first punctate, second rugosopunctate (1) both finely and contiguously punctate; (2) first with punctures ranging from uniformly distributed to scattered or absent, second with punctures ranging from large and uniformly spaced to scattered or absent.

36. Metapleural sculpture: (0) varying from rugosopunctate (rugae irregular in size and orientation) to punctate; (1) rugosopunctate, rugae long and transverse; (2) punctures small, contiguous/confluent, rugae absent.

37. Propodeal lateral profile: (0) with distinguishable dorsal and postero-dorsal faces which meet at an angle (Fig. 59); (1) evenly convex (Figs 15, 28, 60); (2) steeply sloping (Figs 16, 29, 61).

38. Scopa of hind coxa: (0) present; (1) absent.

39. Cell 1 + 2Rs (areolet) of fore wing: (0) anteriorly truncate; (1) anteriorly pointed; (2) petiolate.

40. Cell 1 + 2Rs (areolet) of fore wing: (0) veins 2/Rs and 3r-m of equal length; (1) vein 2/Rs < vein 3r-m; (2) vein 2/Rs > 3r-m.

41. Cell 1 + 2Rs (areolet) of fore wing: (0) vein 2m-cu interception at or near midpoint of posterior margin (vein 2/M about as long as vein 3/M); (1) vein 2m-cu interception apicad midpoint of posterior margin (vein 2/M $1.6–5.8\times$ as long as vein 3/M).

42. MS1 in lateral view: (0) petiole flattened, postpetiole convex (Figs 59–61); (1) evenly curved with highest point at middle (Fig. 24), petiole strongly laterally compressed and with strong angled margins; (2) evenly curved with highest point at middle (Fig. 23), petiole basally cylindrical or weakly compressed with gently rounded margins.

43. S1: (0) sclerotized anterior portion $0.9–1.5\times$ as long as distance from posterior margin of anterior portion to apex of T1; (1) sclerotized anterior portion $0.5–0.6\times$ as long as distance from posterior margin of anterior portion to apex of T1.

44. Petiole of MS1 basally: (0) without projections; (1) with dorsal bulge (Fig. 31); (2) with dorsal and lateral bulges; (3) with lateral bulge only (Fig. 30).

45. Postpetiole of MS1: (0) base simple; (1) with basal convexity (Fig. 62); (2) with basal conical projection (Fig. 14).

46. Median longitudinal carinae of T1: (0) complete and extending to apex; (1) apically incomplete (present only on base of postpetiole); (2) absent on postpetiole.

47. Postpetiole of T1: (0) with distinct median field; (1) without distinct median field.

48. Postpetiole of T1 (at least laterally): (0) rugosopunctate or with punctures distorted and large; (1) with fine and dense punctures, no trace of rugae (Fig. 71); (3) punctures scattered or absent, rugae absent.

49. Ventral margin of T2: (0) simple; (1) denticulate (Fig. 32).

50. T2-4: (0) with longitudinal rugae restricted to basal 0.1–0.2 (usually with rugae present only on T2, weak or absent on other tergites); (1) with weak longitudinal rugae restricted to midline of each tergite; (2) with weak to strong longitudinal rugae over entire surface of each tergite.

51. T2-4 punctation: (0) punctures medium to coarse (greater than or equal to $57\,\mu m$); (1) punctures fine (less than or equal to 38 micrometers).

52. T2-4: (0) evenly convex in profile (Fig. 63); (1) laterally weakly flattened (Fig. 64); (2) laterally strongly flattened (Fig. 65).

53. T2-5: (0) not basally constricted (Fig. 7); (1) basally constricted (Fig. 8).

54. T2-5: (0) without dorsolateral ridges; (1) T2-4 with dorsolateral ridges; (2) T2-5 with dorsolateral ridges; (3) T3-4 ridges with some degree of posterior development.

55. S2-5: (0) S2-4 divided, S5 entire; (1) S2-3 divided, S4-5 entire; (2) S2 divided, S3 partly divided, S4-5 entire; (3) S2 divided, S3-5 entire; (4) S2-5 entire; (5) S2-5 divided. ('Divided' means that the sternite consists of two sections separated by a membranous or weakly sclerotized longitudinal area. A median plica is usually present. The plica of S2 may be absent, however, with *Saranaca* being an example. Careful examination will reveal colour differences between the two lateral sections and the median area. While the state recognized here is apparently plesiomorphic for the Stenopneusticae, it should be noted that state 5 is the plesiomorphic state for the Alomyini and Cryptinae.)

56. Apex of female metasoma: (0) with T7-8 projecting well beyond apex of T6; (1) with T7-8 barely projecting beyond apex of T6; (2) with T6-8 barely projecting beyond apex of T5; (3) with T6-8 retracted below T5 and not visible.

57. Hypopygium of female: (0) short, exposing most of ovipositor (oxypygous); (1) elongate, exposing only apex of ovipositor (amblypygous).

58. Position of emergence hole in host pupa: (0) anterior (formed by cutting of host pupa's anterior 0.1); (1) lateral (site of host pupa's wing pads). (The apomorphic state is restricted to the *Trogus* subgroup.)

59. Hosts: (0) Heterocera; (1) Sphingidae; (2) Papilionidae; (3) Nymphalidae.

60. Larva: interior of spiracular atrium: (0) without spines; (1) with large spines.

61. Larva: posterior end of hypostoma: (0) normal length, straight (Fig. 66); (1) elongate, straight (Fig. 67); (2) elongate and upcurved (Fig. 68).

CLADISTIC ANALYSIS

The taxa and characters summarized in Table 1 were analysed using Nixon's Ratchet (or the 'parsimony ratchet') (Nixon, 2000) as implemented under Dada (version 1.2.7; Nixon, 1998b) and executed by NONA (version 1.8; Goloboff, 1997). Nixon's Ratchet relies on sampling (at random) a small subset of characters in the original matrix to generate an initial topology, then the full matrix is considered as a search begins from that starting point. The procedure is repeated many times and the results are compared to discard all suboptimal solutions. Because only 10–20% of the original data are used to generate the starting point, it is unlikely that the searches will become trapped on the same suboptimal islands each time. Nine searches of 200 replications each were performed, with three searches using a sampling of 10% (6) of the characters, three using 15% (9), and three using 20% (12). All multistate characters were treated as nonadditive. The resulting trees were then subjected to branch swapping using tree bisection-reconnection (**max***). This gave 9 cladograms with a length of 363 steps, a consistency index of 0.27, and a retention index of 0.79. NONA's successive weighting routine (**swt.run**) produced three cladograms with a length of 370 steps. It should be noted that NONA uses the consistency index in the successive weighting calculations, unlike HENNIG86 (Farris 1988) which instead uses the unit rescaled consistency index.

The cladograms resulting from the successive weighting analyses are shown in Figs 1–6: one cladogram with its supporting characters (Figs 1–4) and the variant sections of the other two (Figs 5, 6). All character states have been shown for all branches, necessitating the presentation of a considerable number of figures. We deem this essential, as no statistical tests were used to estimate character support for the cladograms. Such tests are misleading, as phylogenies are 'historically unique and have no associated probabilities; the use of statistics to test their distribution is, consequently, nonsense' (Grandcolas, 1998; see also Carpenter, 1992; Wenzel & Carpenter, 1994). This particularly true for morphology-based trees, where portrayal of character-state changes along branches, and whether or not they are homoplasious, is more important than statistical tests that ignore information on the **kind** of character support. Statistical measures are generally offered for molecular studies, where interpreting the relative strength of character changes is problematical. For morphological studies, however, the basis of interpreting character support is on firmer ground (T. Shultz and J. Wenzel, pers. comm.). It should be noted in passing that there is a regrettable tendency in many recent works to show naked cladograms; this obscures evidence, making the evaluation and testing of hypotheses of relationship by others unnecessarily difficult.

TAXONOMY

The three NONA cladograms differ in (1) the positions of *Callajoppa*, *Charmedia* + *Saranaca*, *Gnamptopelta*, and *Pepsijoppa*, and (2) the composition of *Callajoppa*.

This has led to different combinations of defining autapomorphies for *Callajoppa*, *Gnamptopelta*, *Myocious*, *Pepsijoppa*, and *Quandrus* (discussed in detail in the following treatments of those genera).

Heinrich was correct in implying that the tribe Heresiarchini was paraphyletic with respect to the Trogini (although he did not use cladistic terminology), and so maintaining Trogini as a separate tribe is unsatisfactory. Conversely, placing it as a subtribe of Heresiarchini also poses problems. The Protichneumonina are paraphyletic with respect to Apatetorina, Heresiarchina, and Trogini. Certain genera (*Amblyjoppa* and *Protichneumon*) are more closely related to Trogini than to other Protichneumonina; *Holojoppa* falls between *Amblyjoppa* and *Protichneumon*. As noted above (Relationships and choices of outgroups), Apatetorina and Heresiarchina have problems with their defining characters. The best solution for now is a system of informal genus-groups [examples are Gauld (1984) for Ophioninae and Wahl (1993) for Campopleginae]. Within Heresiarchini, the following suprageneric changes are made:

a) The subtribes Apatetorina and Heresiarchina are referred to as the *Apatetor* and *Heresiarches* genus-groups.

b) The subtribe Protichneumonina is unsupported by characters and does not merit recognition: we treat the genera as *incertae sedis* within Heresiarchini.

c) Heinrich defined the tribe Trogini on the basis of the steeply sloping propodeum and a suite of venational characters in cell 1 + 2Rs. Concerning the latter, Heinrich conceded that these were based upon trends (Heinrich 1967: 233). These characters (#s 39–40) show excessive variation and are not useful for defining groups. In contrast, the steeply sloping propodeum (#37–2) defines Heinrich's Trogini (although reversed in certain genera). As it is useful to maintain this group as a named entity in light of its biological and historical interest, the tribe Trogini is henceforth referred to as the *Callajoppa* genus-group. This genus-group is not synonymous with Callajoppina: the latter is paraphyletic with respect to Trogina and thus not a valid taxon. *Catadelphops*, *Catadelphus*, and *Neamblyjoppa* are firmly placed within the *Callajoppa* genus-group despite Heinrich's transfer of *Catadelphus* from his Trogini to Heresiarchini (Heinrich 1971) and his placement of *Catadelphops* and *Neamblyjoppa* in Heresiarchini at the time of description (Heinrich 1962). *Cobunus* and *Facydes* also belong to this genus-group, a relationship not previously suspected. *Holojoppa*, in contrast, is not a member of the *Callajoppa* Group.

d) The subtribe Trogina is strongly supported and as it includes biologically interesting character

changes, it merits informal recognition as the *Trogus* subgroup. One consequence of using informal genus-groups is that it bypasses the problems associated with the family group name Trogini. Based upon Trogoidae Förster (1869); the ichneumonid name is a junior homonym of Trogoidae MacLeay (1819); based upon the coleopterous genus *Trox* Fabricius (Wahl & Mason 1995). Carlson (1979) attempted to solve the problem by emending Trogini to Trogusina, an illegal action under Article 55(b) of the *International Code of Zoological Nomenclature* (International Commission for Zoological Nomenclature, 1985). Yu & Horstmann's (1997) use of Callajoppini in place of Trogini is unsatisfactory given the problem with the status of the other tribes in Heresiarchini.

The following generic changes are made:

a) *Gathetus flavibasalis* Uchida does not belong in *Neofacydes* and is placed in the new genus *Queequeg*.

b) *Macrojoppa* is paraphyletic with respect to *Araeoscelis* and *Cryptojoppa*. In order to maintain monophyletic taxa, *Araeoscelis* and *Cryptojoppa* are treated as junior synonyms of *Macrojoppa* (**syn. n.**).

c) *Macrojoppa latipennis* is not related to the other species of *Macrojoppa* and is placed in an expanded *Pedinopelte*.

d) *Trogus* is paraphyletic with respect to *Holcojoppa*, as *T. mactator* Tosquinet and its related species (*T. bicolor* Radoszkowski, *T. heinrichi* Uchida, and *T. tricephalus* Uchida) comprise the sister group to *Holcojoppa*. These species are transferred to *Holcojoppa*, leaving a monophyletic *Trogus*.

e) Three groups of undescribed species within the *Trogus* subgroup are placed in the new genera *Daggoo*, *Metallichneumon*, and *Tashtego*.

f) *Tricyphus* as recognized by Townes & Townes (1966), Heinrich (1977), and Ward & Gauld (1987) is polyphyletic. In addition to the eight described species, an additional 12 Neotropical species were discovered that key to *Tricyphus* as defined by Townes & Townes (1966). *Tricyphus* is now restricted to *apicalis* Kriechbaumer, *cuspidiger* Kriechbaumer, and *nigriventris* Kriechbaumer. *T. respinozai* Ward & Gauld is the type-species of the new genus *Mokajoppa*, and the remaining described species (*apicalis* Cresson, *ater* Hopper, *elegans* Cresson, and *floridanus* Heinrich) are placed in the new genus *Saranaca*. The undescribed species are placed in the new genera *Charmedia*, *Dothenia*, and *Humbert*.

g) The composition of *Callajoppa* varies amongst the three cladograms. *Callajoppa pepsoides* is never closely associated with the other species. Of the

three remaining species, all form a monophyletic group in only one cladogram (Fig. 4): *exaltatoria* (Panzer). A conservative treatment of this genus is taken in which *C. pepsoides* is transferred to the new genus *Quandrus*, and the other species are retained in *Callajoppa* pending an examination of the species not included in the analysis (*flavinerva* (Cameron), *pictoptera* Heinrich, and *taiwana* Uchida).

h) The genera *Catadelphops* and *Neamblyjoppa* are monotypic genera from the south-western United States that have a sister-group relationship. *Neamblyjoppa* is treated as a junior synonym of *Catadelphops* (**syn. n.**), based upon the synapomorphy of a turned-under ventral mandibular tooth (12–2).

i) Some authors (Heinrich, 1962; Carlson, 1979) recognize *Tmetogaster* as a genus while others (Townes & Townes, 1951) treat it as a subgenus of *Conocalama*. In this study, the relationship of *Tmetogaster* to *Conocalama* s.s. has swung between being the sister group to being separated by one or two internodes. It is maintained as a genus in light of the fact that changes to the data matrix could easily change the sister-group relationship.

j) Three undescribed species are placed in the new genera *Laderrica*, *Myocious*, and *Xanthosomnium*.

Table 2 summarizes the generic situation within the *Callajoppa* genus-group.

Several character systems used by past authors are of interest in light of the analysis. Gillespie & Finlayson (1983) separated Callajoppina and Trogina on the basis of larval characters: the Trogina have a hypostoma that is sharply upcurved and lacking spines in the spiracular atrium, while the Callajoppina have straight hypostoma and spines in the spiracular atrium. Evidence from additional genera of the *Trogus* subgroup reveals the upcurved hypostoma (#61–2) to be a synapomorphy of *Trogus* + *Holcojoppa*, not shared with other genera. The spines of the spiracular atrium (#60–1) are found in the *Trogus* subgroup as an autapomorphy of *Macrojoppa*.

A character of special interest in the *Callajoppa* genus-group is the areola and its modifications, as Townes considered this to be evidence that the *Trogus* subgroup was not related to *Callajoppa* and its relatives (see above, Classificatory history). Townes was indeed correct that the *Trogus* subgroup had lost the central section of the posterior transverse carina with the result that the areola is not distinguishable (#27–2), and that this was not derived from the reduced and filled-in areola (#27–1) of the traditional Callajoppina. His contention that the groups are not related is, however, incorrect.

Table 2. Genera of the *Callajoppa* genus-group

Callajoppa genus-group
Afrotrogus Heinrich, 1938
Callajoppa Cameron, 1903
Catadelphops Heinrich, 1962
 Neamblyjoppa Heinrich, 1962 syn. n.
Catadelphus Wesmael, 1854
***Charmedia* Wahl & Sime, 2001 gen. n.**
Cobunus Uchida, 1926
Conocalama Hopper, 1939
Dimaetha Cameron, 1901
 Erythrojoppa Cameron, 1902
Dothenia Wahl & Sime, 2001
Facydes Cameron, 1901
Gnamptopelta Hopper, 1939
Humbert Wahl & Sime, 2001
***Laderrica* Wahl & Sime, 2001 gen. n.**
***Lagavula* Wahl & Sime, 2001 gen. n.**
***Mokajoppa* Wahl & Sime, 2001 gen. n.**
***Myocious* Wahl & Sime, 2001 gen. n.**
Pepsijoppa Heinrich, 1936
***Quandrus* Wahl & Sime, 2001 gen. n.**
***Saranaca* Wahl & Sime, 2001 gen. n.**
Stirojoppa Cameron, 1911
 Camarota Kriechbaumer, 1898; preocc. by Meigen, 1836
 Camarotella Morley, 1917
 Hymenocamarota Cushman, 1922
 Camarotana Strand, (1926)1928
Tmetogaster Hopper, 1939
Tricyphus Kriechbaumer, 1898
***Xanthosomnium* Wahl & Sime, 2001 gen. n.**
Yeppoona Gauld, 1984

(*Trogus* subgroup)
***Daggoo* Wahl & Sime, 2001 gen. n.**
Holcojoppa Cameron, 1902
 Pedinojoppa Heinrich, 1960
Macrojoppa Kriechbaumer, 1898
 ***Cryptopyge* Kriechbaumer, 1898 syn. n.**
 ***Ischnopus* Kriechbaumer, 1898 syn. n.**
 Cryptopyga Schulz, 1906; emendation of *Cryptopyge*
 ***Araeoscelis* Schulz, 1911 syn. n.**
 Areoscelis of authors. *Lapsus*
 Aglaojoppidea Viereck, 1913
***Metallichneumon* Wahl & Sime, 2001 gen. n.**
Neofacydes Heinrich, 1960
Pedinopelte Kriechbaumer, 1898
Psilomastax Tischbein, 1868
 Cercodinotomus Uchida, 1940
***Queequeg* Wahl & Sime, 2001 gen. n.**
***Tashtego* Wahl & Sime, 2001 gen. n.**
Trogus Panzer, 1806
 Dinotomus Förster, 1869

BIOLOGY OF THE *CALLAJOPPA* GENUS-GROUP

Heinrich (1962) recognized that host associations in the *Callajoppa* group could be useful in determining generic relationships. He suggested, for example, that biological as well as morphological evidence supported his placement of *Neofacydes* as the most basal of the *Trogus* subgroup, and that host data would help establish the position of *Macrojoppa*. He also proposed a sequence of biological transitions that supported his concepts of the Trogini and subtribes therein (1960, 1962). Heinrich's Trogini were distinguished by host specificity, a condition he thought derived from the relatively generalist host associations of the Heresiarchini; his Callajoppina were defined by specialization on Sphingidae, with the butterfly specialization exhibited by the Trogina (our *Trogus* subgroup) representing the ultimate expression of this trend. These ideas were tested in our analysis by including host association as a single character (#59) with four nonadditive states (see Deleporte 1993; Luckow & Bruneau 1997; for justifications of this approach).

In general, Heinrich's (1960, 1962) ideas about host associations in the *Callajoppa* group are supported by our results. His contention that the Callajoppina are 'exclusively parasitoids of Sphingidae' has been borne out by critical review of host records; we found no verifiable reports for parasitism of other Lepidoptera. Sphingid parasitism, however, is not diagnostic for this group: it arose elsewhere in the Here-siarchini, for *Protichneumon* and *Amblyjoppa* specialize on Sphingidae as well. Heinrich suggested a possible distinction – association of *Protichneumon* with the Sphinginae and his Callajoppina with the Macroglossinae – but our host-range data indicate much overlap among sphingid subfamilies. He also proposed that sphingid parasitism might 'link' *Neofacydes* to the more primitive Callajoppina and placed this genus as the most basal of his Trogina, which he characterized otherwise as parasites of butterflies. In our results, sphingid parasitism is indeed the groundplan for the *Trogus* subgroup. Contrary to Heinrich's predictions, however, *Neofacydes* is nested within this clade and the distribution of character 59 predicts that several basal genera (their biologies currently unknown) are sphingid parasitoids as well. It should also be noted that the 'Rhopalocera'-feeding discussed by Heinrich is limited to the papilionid subfamily Papilioninae and to three clades of the Nymphalidae: Charaxinae, Apaturinae, and Nymphalinae (as defined by Miller, 1987a; Harvey, 1991).

As Heinrich (1962) indicated, butterfly parasitism is derived from sphingid parasitism. Although he knew that *Psilomastax* specializes on nymphalids, he was not aware of the extent of nymphalid parasitism in the *Trogus* subgroup and did not address the transitions between nymphalids and papilionids. Our discovery that several species of *Macrojoppa* attack nymphalids prompted us to consider this problem more closely. The analyses show a single origin of sphingid parasitism followed by two transitions to butterfly parasitism, one a transition to Papilionidae (followed by a switch to Nymphalidae at *Psilomastax*) and the other to Nymphalidae (followed by a switch to Papilionidae within *Macrojoppa*). The homoplasy evident in the relationships with butterflies could be a consequence of coding the host-association character at the family level. The separate origins of nymphalid parasitism are associated with different subfamilies of Nymphalidae (*Psilomastax* on Apaturinae and species of *Macrojoppa* on Charaxinae and Nymphalinae), and the two origins of papilionid parasitism are associated with different tribes of the Papilioninae (Troidini and Papilionini). These differences might indicate inaccuracies in the original homology assessments. However, the lack of host records for *Queequeg*, *Metallichneumon*, and most species of *Macrojoppa* precludes improvement of the coding at this time.

Our results, in summary, identify a conserved relationship with Sphingidae, from which a more plastic association with two butterfly families arises. Cladistic analyses of host-use patterns typically invoke association by descent as the null hypothesis of historical explanation (Mitter & Brooks, 1983; Miller, 1987b). Examination of accepted phylogenies for the Lepidoptera (Nielsen, 1989; Weller *et al.*, 1996), however, refutes any notion that parallel cladogenesis explains our results, as it would require the implausible scenario that the butterfly clades arise from the midst of the Sphingidae and that the Nymphalidae and Papilionidae be paraphyletic with respect to each other. Instead, various considerations indicate that colonization has dominated the evolution of host relationships. Basal wasp genera are not associated with basal host groups at any level. Although Africa and Australia have rich sphingid faunas (Pinhey, 1962; Moulds, 1996), the *Callajoppa* group is represented in each region by just a few species. The *Trogus* subgroup is entirely absent from these regions, although they contain many Papilionidae and Nymphalidae (Ackery *et al.,* 1995; Edwards, 1996a,b). In addition, while the greatest species diversity of the papilionid tribe Troidini occurs in south-east Asia (Weintraub, 1995), only a few Neotropical species are parasitized by these wasps. Such patterns indicate that diversification of host taxa occurred first, and some were later colonized. This finding does not exclude the possibility of stepwise or strict coevolution (*sensu* Jermy, 1984) within genera, which would not be detectable at this level of analysis. Similar scenarios of colonization have been described for other parasitoids for which cladis-
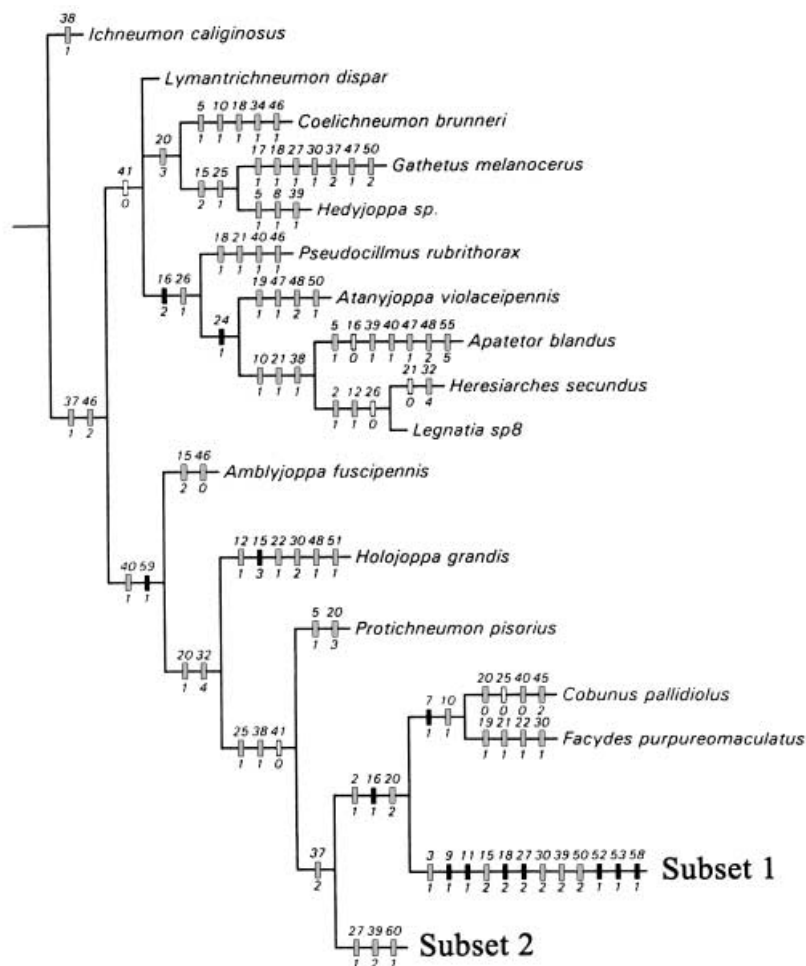
Figures 1. First of three cladograms for the *Callajoppa* Group. Subsets of this cladogram are shown in Figs 2–4. For this and following cladograms, black bar = apomorphy, grey bar = parallelism, white bar = reversal. All cladograms were made with the Clados program of Nixon (1998a).

tic tests are available (e.g. euphorine braconids (Shaw 1988)).

While the pattern of host shifts in the *Callajoppa* genus-group is inconsistent with the hypothesis of association by descent, phylogenetic constraints in the form of ecological factors have likely played a role in maintaining conservatism in host associations and determining the direction of transitions. Patterns of taxonomic fidelity and colonization are often ascribed to chemical similarities among hosts (Price, 1981; Barbosa, 1988; Gauld, 1988; Shaw, 1988). In the present study, consideration of chemistry is a particularly suitable approach, as the chemical milieu of the hosts is well known and distinctive. This was recognized by Mell & Heinrich (1931: 381), who suggested that the Ichneumoninae are the most 'chemically specialized' of the ichneumonoids, and that the high degree of host specificity of the *Callajoppa* group in particular is related to the dietary peculiarities of

their sphingid and butterfly hosts. We formulate Mell and Heinrich's observations as two hypotheses: (1) chemical similarities between Sphingidae, Nymphalidae, and Papilionidae facilitated the two transitions to these butterfly groups, and (2) the relative plasticity of associations with Papilionidae and Nymphalidae reflects the finer similarities (in chemical and other biological attributes) shared by the butterfly taxa. Support for these hypotheses is discussed below.

The initiation of a host shift requires, first, that an ovipositing female wasp find and accept the novel host; host-searching behaviour thus underlies the origin of host shifts (Brues, 1920; Shaw, 1988; Feeny, 1991). Because parasitoids typically rely on chemicals to locate hosts and host habitats (Vinson, 1984), the distribution of attractant chemicals among potential hosts and their food plants determines which host shifts are most likely to occur. Among the *Callajoppa*-group genera, the importance of plant and host chemi-
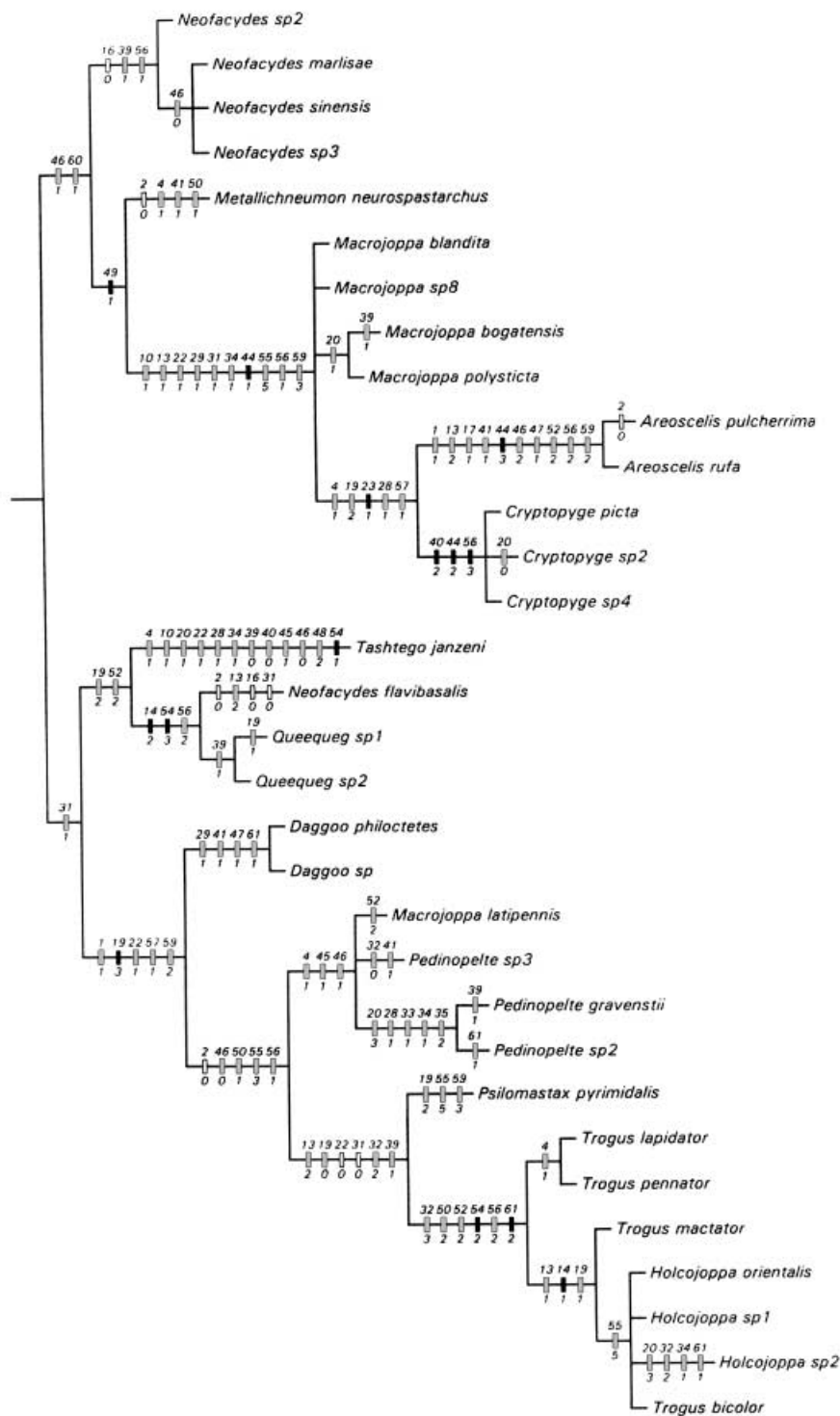
Figures 2. Subset of cladogram of Fig. 1.

cal attractants has been experimentally established for *Macrojoppa rufa* (A. Morais, pers. comm.) and *Trogus pennator* (Sime, in prep.). Mell & Heinrich (1931) proposed that the attraction of female wasps to the food plants of their hosts explained the narrow host range in the *Callajoppa* genus-group, particularly in the *Trogus* subgroup: the similarities in essential oils among the food plants of the Papilionidae (see also Dethier, 1941; Ehrlich & Raven, 1964) would tend to restrict the wasps to hosts on like-smelling plants.
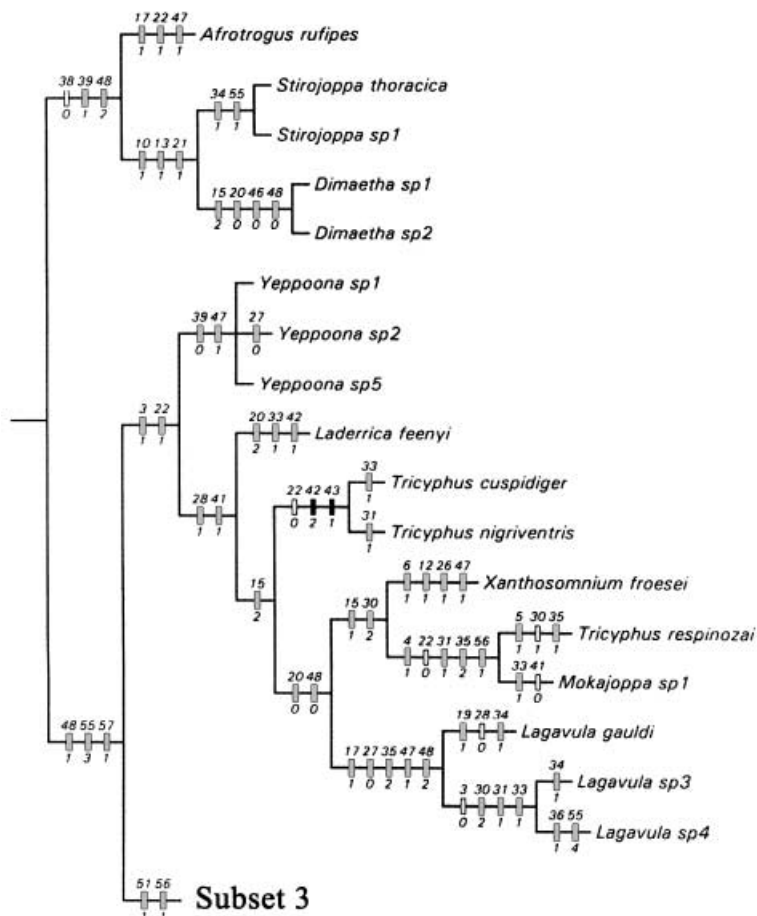
Figures 3. Subset of cladogram of Fig. 1.

Similarly, Feeny (1991) has suggested that the use of similar phytochemical cues in searching for oviposition sites might constrain both the Papilionidae to their select group of food plants and the *Trogus* subgroup to their select group of hosts. These explanations for host fidelity are incomplete, however, as they cannot explain why these extremely specialized wasps do not attack other large Lepidoptera feeding on some of the same plants. Many in the *Callajoppa* genus-group are associated with a greater diversity of plants than of hosts (e.g. species of *Callajoppa*, *Mokajoppa*, *Quandrus*), which indicates that responses to plant odours are more labile than are responses to host larvae (Vet & Dicke 1992). The host range is probably better explained by the distribution of compounds characteristic of host taxa and used in finding or recognizing host larvae. In a sense, such compounds are the true characters underlying the 'host taxon' character we used (see Miller 1987b; Miller & Wenzel 1995). Similarities in plant odour, while not determining the taxonomic borders of host range, would contribute to host specificity and make

certain host shifts less likely than others by limiting the variety of plants usually encountered in searching for hosts.

The success of a particular host shift also requires that the offspring can tolerate the novel physiological environment. Plant chemicals in host tissues can be detrimental to endoparasitoid larvae and may require specialized adaptations for tolerance (Duffey *et al.,* 1986; Gauld & Gaston, 1994). Sphingid and butterfly food plants are characterized by qualitative toxins (*sensu* Feeny, 1976), particularly alkaloids (Janzen, 1984; Feeny, 1991). Similarities in toxin content among food plants would have made the evolutionary transition from sphingid parasitism to papilionid or nymphalid parasitism much more likely than shifts to other large Lepidoptera. Tropical Saturniidae, for example, tend to use plants defended by classes of chemicals different from those in plants favoured by Sphingidae (Ehrlich & Raven, 1964; Janzen & Waterman, 1984; Janzen, 1984), though shifts from sphingids to saturniids have occurred in other ichneumonid lineages (Gauld & Janzen, 1994). Butterfly
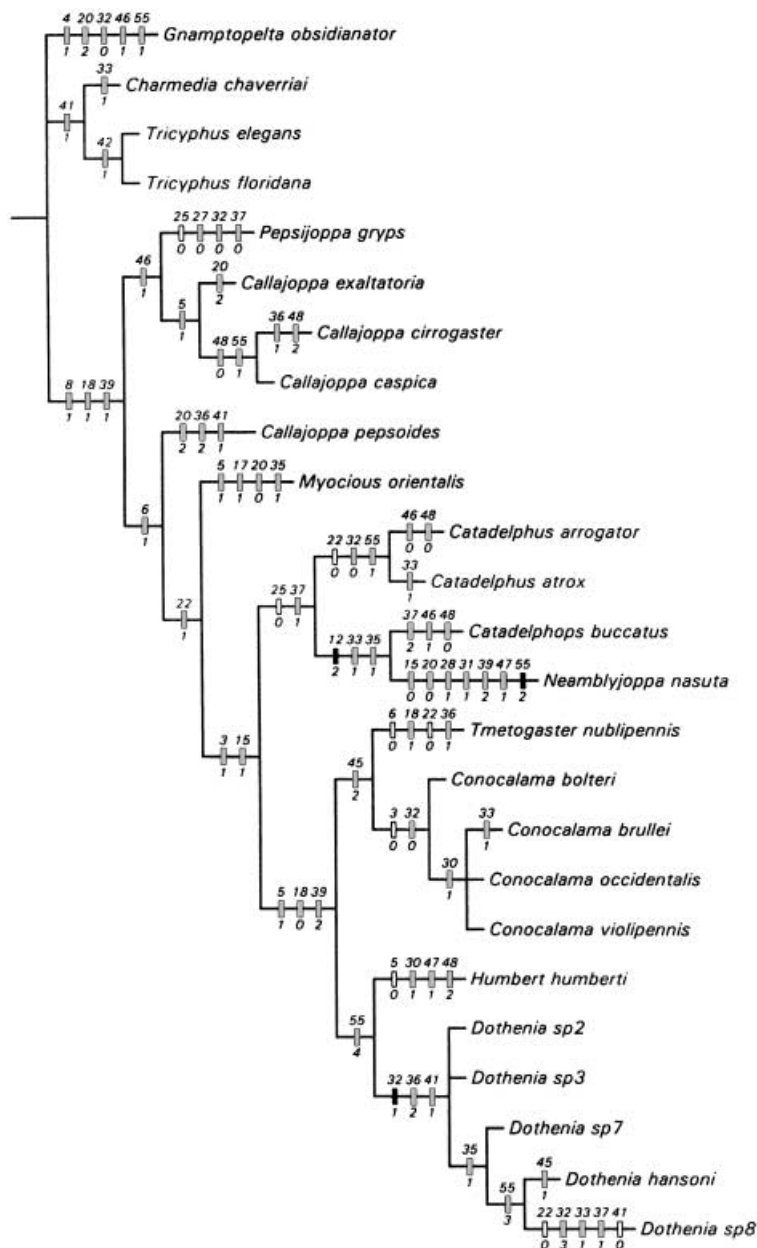
Figures 4. Subset of cladogram of Fig. 1.

parasitoids in the *Trogus* subgroup are associated with a distinct class of toxins: most food plants of the Papilionidae contain benzylisoquinoline alkaloids, which are unusually toxic to insects (Miller & Feeny, 1989). While the range of nymphalid hosts is less completely known, many of the food plants involved, such as those of the Charaxinae, also contain benzylisoquinoline alkaloids (Seigler, 1977; DeVries, 1987).

The relative toxicity of food plants used by their hosts helps explain the host specialization observed in the *Trogus* subgroup. Many are restricted to hosts on particular plant families. For example, most species of

Pedinopelte and *Holcojoppa* specialize on Rutaceae-feeding *Papilio*, and *Daggoo* and members of the *rufa* species-group of *Macrojoppa* specialize on *Aristolochia*-feeders. Interestingly, it is only in the few temperate species that considerable polyphagy is observed: *Trogus lapidator* attacks five *Papilio* species on three plant families, *T. pennator* attacks 10 species on nine plant families, and *Holcojoppa mactator* attacks five species on at least three plant families. These observations, along with the prevalence of plant families containing benzylisoquinoline alkaloids, are consistent with the 'nasty host hypothesis':

tropical herbivores are 'less available to parasitoids as on average they are more chemically defended' than temperate herbivores, and parasitoids contending with toxic hosts will tend to have relatively narrow host ranges (Gauld *et al.,* 1992; Gauld & Gaston, 1994).

Daggoo and the *rufa* species-group of *Macrojoppa* are particularly interesting because they specialize on the 'nastiest' of hosts. All species of the papilionid tribe Troidini feed on the Aristolochiaceae (Weintraub, 1995). Sequestration of aristolochic acids, a group of compounds affiliated with benzylisoquinoline alkaloids and unique to the Aristolochiaceae, has been demonstrated for many species and is considered to cause the unpalatability indicated by their roles as models for mimicry rings (Brower & Brower, 1964; Nishida, 1995). Aristolochic acids are apparently extremely toxic to most insects and very few groups other than papilionids can tolerate them (Brown *et al.* 1981; Miller & Feeny, 1989). *Battus polydamas* (L.), the host of the *rufa* clade, contains them (Urzúa & Priestap, 1985), as do species of *Parides*, the hosts of *Daggoo* (Klitzke & Brown, 2000). Although the effects of aristolochic acids on parasitoids have not been directly examined, it appears that the Troidini are relatively free of parasitoids; certainly no other ichneumonines have been reported, despite considerable study (Mell & Heinrich, 1931; Straatman & Nieuwenhuis, 1961; Straatman, 1969; Rausher, 1981; Sime, 2000; J. Weintraub, pers. comm.). It is thus remarkable that parasitism of the Troidini has arisen twice in the *Trogus* subgroup. The pattern suggests that the *Trogus*-subgroup genera have some means of tolerating benzylisoquinoline alkaloids that has preadapted them to cope with the biosynthetically related Aristolochiaceae toxins (cf. Miller, 1987b; Miller & Feeny, 1989). The observation that the *rufa* species-group specializes on *Battus* and *Daggoo* on *Parides* may be another consequence of the unusual toxicity: broad tolerance of aristolochic acids is unlikely (Brown *et al.,* 1981), and, even when feeding on the same plants, *Parides* and *Battus* larvae can contain different mixtures of sequestrants as a result of selective uptake and metabolism (Urzúa *et al.,* 1987).

Chemical constraints are not sole determinants of host breadth. The transition from oviposition into pupae (the groundplan biology of the Ichneumoninae; Gauld, 1988) to oviposition into larvae is in several respects the critical innovation underlying the evolution of host associations in the *Callajoppa* group. Although the lack of biological data for basal genera of the *Callajoppa* group makes a precise estimate impossible, the transition to larval-pupal parasitism most likely occurred among heresiarchine sphingid parasitoids. In particular, the position of *Amblyjoppa*,

a larval parasitoid of Sphingidae (Pittaway, 1993), and our observation that all members of the *Callajoppa* group for which data are available attack larvae, indicate that larval-pupal parasitism most likely arose prior to the divergence of the *Callajoppa* group. As various physiological constraints (host immune and endocrine system, phenology, etc.) make larval parasitoids typically more specialized than pupal parasitoids (Askew & Shaw, 1986), this transition likely caused the high degree of host specialization characterizing the *Callajoppa* group compared to other heresiarchines. Plant chemistry is one of these constraints and presents a challenge for larval, but not pupal, parasitoids of Sphingidae: sphingids do not usually sequester allelochemicals and the pupae do not contain them if they are expelled with the pupal meconium (Janzen, 1984; Bowers, 1993; Gauld & Gaston, 1994). The evolution of larval-pupal parasitism would also have facilitated the shift from Sphingidae to butterflies, which have different pupation habits but similar feeding niches. Sphingidae pupate on or in the ground, whereas Papilionoidea usually pupate on plants or other above-ground structures (Pittaway, 1993; Tyler *et al.,* 1994). The larvae of both families, however, feed on leaves, and, as discussed above, often on the same, or chemically similar, plant taxa.

There is some debate as to whether morphological changes accompany the transition to larval-pupal parasitism. In the Ichneumoninae, the female metasomal apex is either oxypygous (a robust ovipositor exposed by a short S9) or amblypygous (a more delicate, often shorter ovipositor nearly covered by S9). It has been proposed that the oxypygous condition is associated with pupal parasitism, while the amblypygous condition is associated with attacking larvae (Heinrich, 1960; Hinz, 1983). However, Heinrich (1960) was skeptical that the correlation would hold for all ichneumonines, and our results (character #57), along with scattered biological observations, indicate that it is unlikely that ovipositor morphology and attack strategy are strictly related. As discussed above, our data suggest that larval-pupal parasitism arose among the Heresiarchini outside of the *Callajoppa* group. Our results show amblypygous ovipositors originating three times within the *Callajoppa* group. According to the one biological account available for oxypygous genera in the *Callajoppa* group (Mell & Heinrich, 1931), *Neofacydes sinensis* (Heinrich) attacks larvae. The functional correlation remains entirely speculative. Species of *Ichneumon*, *Cratichneumon*, and related genera prefer freshly molted, still-soft pupae, or even (occasionally) attack prepupae (Heinrich, 1960; Hinz, 1983), which implies that the oxypygous ovipositor has nothing to do with attacking hardened pupae. This observation also suggests that the transition to larval-pupal parasitism was not a direct shift
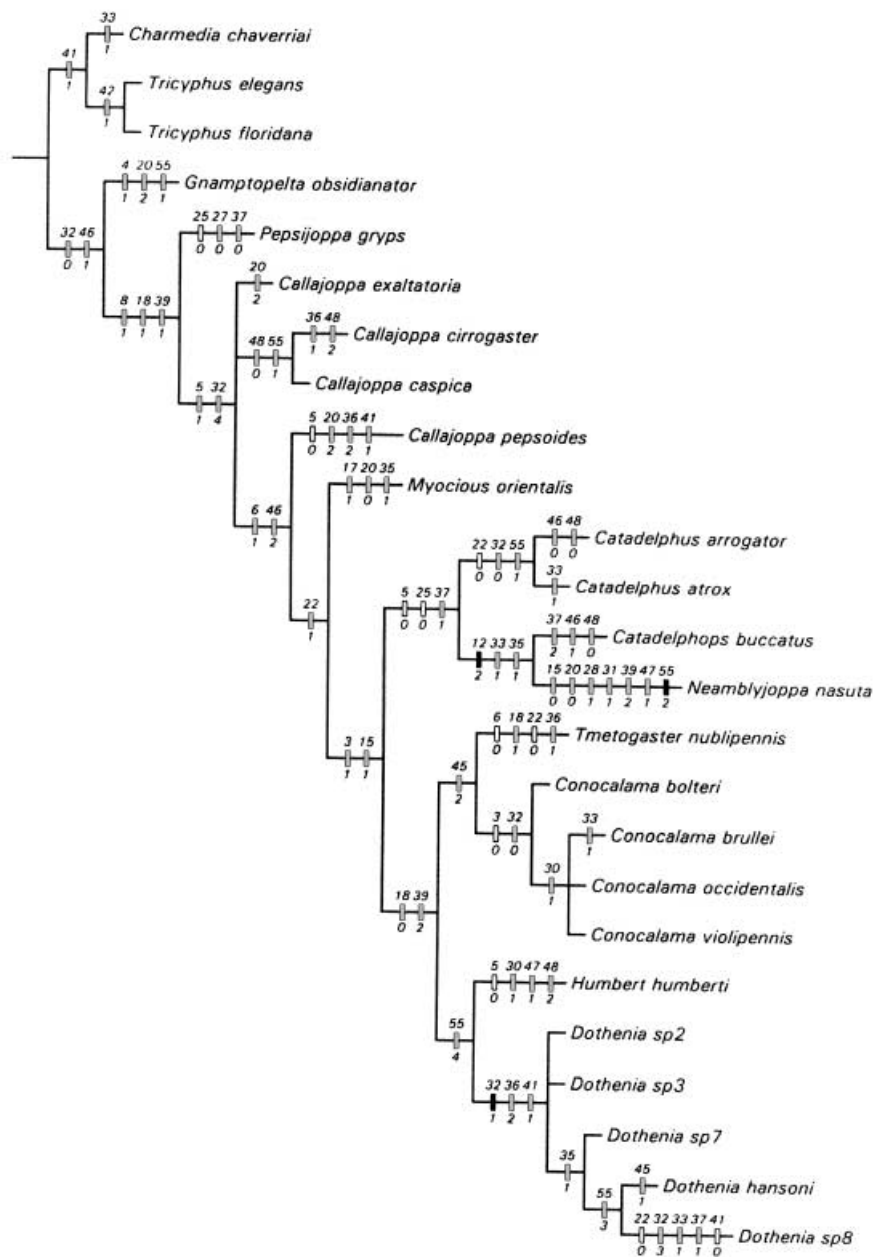
Figures 5. Second of three cladograms for *Callajoppa* Group: variant section.

from attacking hard pupae to attacking soft caterpillars, but instead involved a sequence of transitions, from hardened pupae to fresh pupae to prepupae to nearly mature larvae (cf. Gauld 1988: 369). The existence of intermediate behaviours is another argument against the likelihood of finding a strict correlation between parasitism modes and the two ovipositor morphologies.

Within the *Callajoppa* group, some genera have evidently made another transition, from attacking mature larvae to attacking younger larvae. Some species may prefer older hosts, although it is not always clear whether this preference is simply an artifact of the relative rarity of collections of small caterpillars. Mell & Heinrich (1931) state that *Quandrus pepsoides*, *Amblyjoppa sinensis* (Heinrich), and '*Trogus* sp.' tend to attack mature larvae within 2–3 days of pupation. Species of *Macrojoppa*, *Mokajoppa*, *Psilomastax*, *Gnamptopelta*, *Trogus*, and *Holcojoppa* attack and successfully parasitize younger larvae, with no evident preference for host age (see biological summaries under the individual generic treatments).

According to our results, then, the ability to attack young larvae is widespread in the *Callajoppa* group, which may reflect the advantages inherent in exploiting a more numerous and thus more easily discovered host stage (Gauld, 1988).

The transition from attacking pupae to attacking larvae implies a transition from an idiobiont to a koinobiont lifestyle, i.e. from a strategy of commencing feeding without delay to a strategy of permitting the host to continue its development (as from larva to pupa) after parasitoid oviposition (Askew & Shaw, 1986; Gauld, 1988). These terms subsume a suite of behavioural and physiological traits that are unlikely to change in concert; rather, the sequence of transitions described above is more consistent with gradual and offset changes in these traits than with a sudden switch from idiobiont to koinobiont per se. Although it has been proposed that the change from idiobiancy to koinobiancy in Ichneumoninae coincides with the shift from pupal to larval-pupal parasitism (Gauld, 1988), it seems that only in genera that attack young larvae would most traits associated with koinobiontism (changes or delays in developmental timing (cf. Omata, 1984; on *Holcojoppa mactator*), adaptations to living with the host for an extended period, etc.) occur. Parasitoids that attack prepupae, or even mature larvae, just a few hours before the pupal molt may be essentially idiobionts, with few or no developmental and physiological innovations required to survive the prepupal period.

Certain changes in the behaviour of the female wasp are associated with, and may be prerequisite to, the evolution of larval-pupal parasitism. Gauld (1988) proposed that, in the Ichneumoninae, the transition results from an emphasis on the use of host-derived cues at the expense of habitat-related cues. This hypothesis is consistent with Mell & Heinrich's (1931) suggestion that, since Sphingidae pupate at or under the surface of the ground, the transition to larval-pupal parasitism in the *Callajoppa* group implies a behavioural shift from searching the ground to searching plants. However, these behavioural changes could be minor—some sphingid larvae rest in the leaf litter (Janzen, 1984)—and would be facilitated by the presence of similar semiochemicals in both larvae and pupae. Hinz (1983) suggested that the tendency of some ichneumonines to attack freshly molted pupae indicates that they use the odour of the larvae to find their pupal hosts (see also Price (1970), on the related subfamily Cryptinae). The critical change would more likely be an enhancement of plasticity in preference for pupae vs. mature larvae.

In summary, the evolution of host range in the *Callajoppa* group represents a complex interaction between ecological and chemical constraints. Behavioural plasticity in habitat searching and host accep-tance permitted a transfer from pupal to larval-pupal parasitism, which facilitated in turn the transitions from Sphingidae to Papilionoidea. Behavioural and physiological responses to plant allelochemicals, including alkaloids and essential oils, apparently made the transition from Sphingidae to certain butterflies more likely than shifts to other large Lepidoptera. The relative plasticity of associations with nymphalid and papilionid hosts reflects more specific similarities in the chemistry, behaviour, and physiology shared by these two groups. Heinrich's (1960, 1962) ideas about host shifts in the *Callajoppa* group have been refined but largely confirmed by our results, as has his intuitive hypothesis that their patterns of host use reflect 'chemical specialization.'

GENERA OF THE *CALLAJOPPA* GENUS-GROUP

AFROTROGUS HEINRICH, 1938

Afrotrogus Heinrich, 1938: 26. Type-species: *Camarota madagascariensis* Szépligeti. Original designation.
Species and distribution. There are three described species from sub-Saharan Africa and Madagascar (Yu & Horstmann 1997).
Autapomorphies. Occipital carina with ventral region above mandible produced as low flange (#17–1); juxtacoxal carina absent (#22–1); postpetiole of T1 without distinct median field (#47–1).
Biology. Unknown.

CALLAJOPPA CAMERON, 1903

Callajoppa 1903: 236. Type-species: *Callajoppa bilineata* Cameron. Monotypic.
Species and distribution. After the removal of *pepsoides* Smith to *Quandrus*, there are six described species from the Palearctic region, southern China, and north-western India (Yu & Horstmann, 1997).
Autapomorphies. Apical margin of clypeus medially produced as blunt tooth (#5–1). Alternate combinations [in the absence of *C. exaltatoria* (Panzer)]: (1) postpetiole of T1 rugosopunctate (#48–0), S2-3 divided, S4-5 entire (#55–1), or (2) #s 5–1, 48–0, and 55–1.
Comments. As discussed above (Taxonomy), *Callajoppa* is maintained in the traditional sense after the removal of *pepsoides*.

Although Heinrich (1962) recorded *C. cirrogaster* (Schrank) from the Nearctic on the basis of two old specimens collected in Toronto, Canada (CNCI), Townes *et al.* (1965) believed them to be mislabelled. Their position is bolstered by the failure to find more specimens despite subsequent intensive collecting in southeastern Canada.
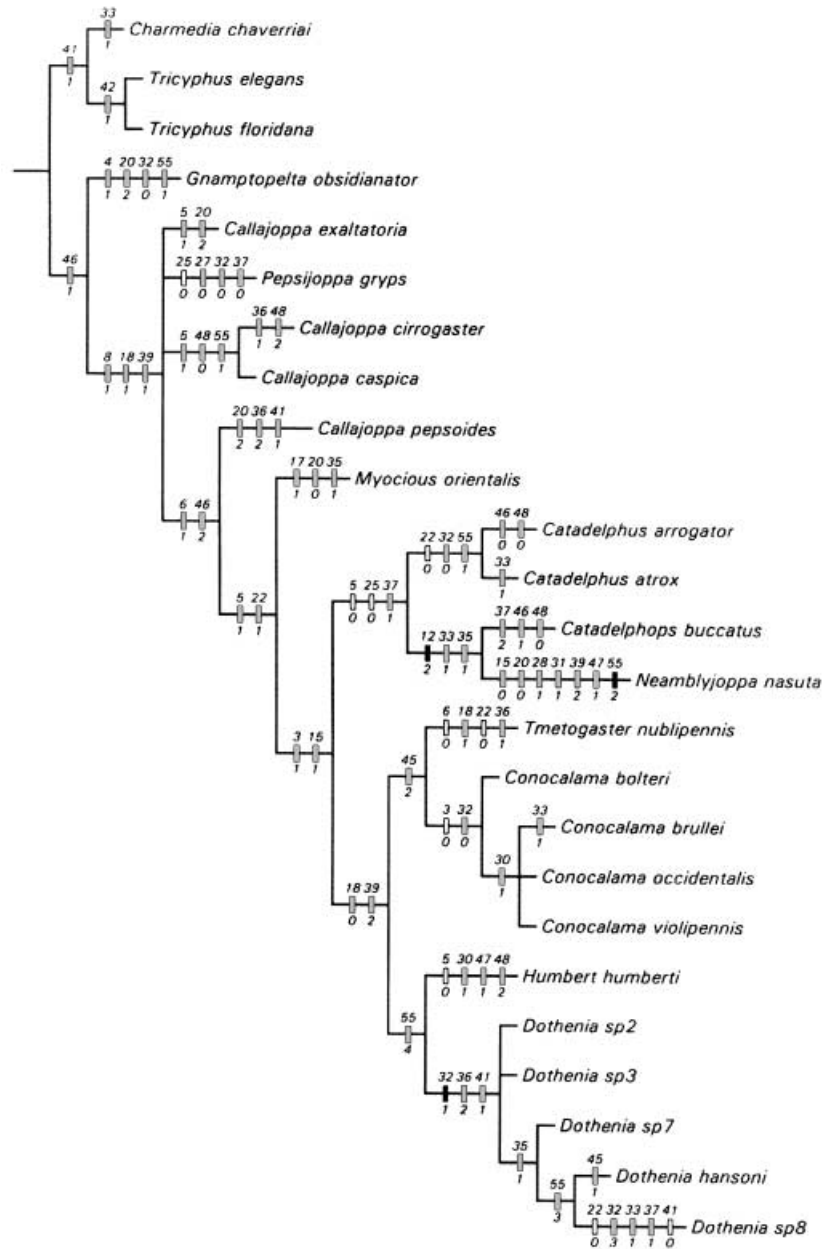
Figures 6. Third of three cladograms for *Callajoppa* Group: variant section.

Biology. Although dozens of records indicate that *Callajoppa* species are larval-pupal parasitoids of Sphingidae, almost all of them are poorly documented. Well supported records place *C. exaltatoria* (Panzer) on *Smerinthus planus* Walker (Uchida, 1926); Heinrich (1960) asserts without evidence that it is monophagous on *Sphinx ligustri* L. Hopper (1939), Kaltenbach (1874), Meyer (1933), Morley (1903, 1915), Pittaway (1993), Schmiedeknecht (1930), and Uchida (1924, 1926, 1930, 1932) together report another 14 sphingid host species (in seven genera) for *C. cirro-* *gaster* (Shrank) and eight (in six genera) for *C. exaltatoria*. However, the unreliability of these records (no voucher materials or supporting biological data) renders further discussion of host-association patterns within *Callajoppa* groundless, particularly as we have found that misidentifications of parasitoid and host materials for these species are not uncommon.

No corroborating evidence supports associations with hosts other than Sphingidae. Such reports include *C. exaltatoria* on *Dendrolimus pini* (L.) (Lasiocampidae) (Meyer, 1933); *C. quebecensis* (Provancher)

on *Eacles imperialis* (Drury) (Saturniidae) (Heinrich, 1962); and *C. cirrogaster* (Schrank) on *Lymantria dispar* (L.) (Lymantriidae) (Meyer, 1933), *Dendrolimus* sp. (Meyer, 1933), *Papilio machaon* L. and *P. hospiton* Géné (Papilionidae) (Schmiedeknecht, 1930; Meyer, 1933).

CATADELPHOPS HEINRICH, 1962

Catadelphops Heinrich, 1962: 863. Type-species: *Trogus buccatus* Cresson. Monotypic and original designation.

Neamblyjoppa Heinrich, 1962: 865. Type-species: *Neamblyjoppa nasuta* Heinrich. Monotypic and original designation. **Syn. n.**

Species and distribution. There are two described species from western North America (Yu & Horstmann 1997).

Autapomorphies. Ventral mandibular tooth absent (#12–2); median longitudinal carina of propodeum absent posteriad anterior transverse carina (#33–1); first and second lateral areas finely and contiguously punctate (#35–1).

Comments. When describing *Catadelphops (sensu stricto*: consisting of only *C. buccatus*), Heinrich argued that it should be placed in the Heresiarchini (Heinrich, 1962: 863): '[T]he carination of the propodeum is more complete and regular than in *Catadelphus*, the area superomedia being clearly defined, hexagonal. In this respect the type-species is still more closely related to *Amblyjoppa* Cameron than is *Catadelphus*.' The areola (Heinrich's 'area superomedia') may be regularly hexagonal, but it is small and the same size as typical for the *Callajoppa* genus-group. Furthermore, it is filled-in in more than half the specimens. Heinrich ignored the important propodeal characters of an abruptly sloping anterior margin (#25–1) and a steeply sloping lateral profile (#37–2). Needless to say, Heinrich's postulated relationship to *Amblyjoppa* was not confirmed. A similar line of reasoning led Heinrich to place *Neamblyjoppa* in the Heresiarchini (Heinrich, 1962).

Synonymization of *Neamblyjoppa* with *Catadelphops* seemed the best course, as these monotypic genera have a sister-group relationship and are found in the same geographical area.

Biology. Unknown.

CATADELPHUS WESMAEL, 1854

Catadelphus Wesmael, 1854: 134. Type-species: *Ichneumon arrogator* Fabricius. Monotypic.

Species and distribution. There are five described species: one from the western Palearctic and four from North America (Yu & Horstmann, 1997).

Autapomorphies. Juxtacoxal carina present (#22–0); propodeum with median longitudinal carina present anteriad anterior transverse carina (#32–0); S2-3 divided, S4-5 entire (#55–1).

Comments. Heinrich placed great importance on cell 1 + 2Rs of the fore wing as a primary defining character of Callajoppina, discussing it at length in Heinrich (1967) where he stated that the cell had '. . . a clear and constant tendency to be petiolate and obliquely trapezoidal by prolongation of the second intercubitus [vein 3r-m] and abbreviation of the second abcissa of cubitus [vein 2/Rs].' He later moved *Catadelphus* to the Heresiarchini (Heinrich, 1971: 967–968), on the grounds that the cell is not petiolate and that the constituent veins are of equal length (Heinrich, 1962: 810). Unfortunately, direct examination reveals that the veins are not equal (vein $2/R_s <$ vein 3r-m, #40–1). The present study shows the petiolate cell to be the result of a complex series of acquisition and loss in the *Callajoppa* genus-group, and it cannot be used as a defining character above the generic level.

Biology. No specimens are associated with host remains, but several independent reports indicate that *Catadelphus* species are parasitoids of Sphingidae, possibly specializing on Macroglossini. *Catadelphus atrox* (Cresson) is recorded from *Proserpinus juanita* (Strecker) (Hopper, 1939) and *C. arrogator* (Fabricius) from *P. proserpina* (Pallas) and *Hyles gallii* (Rottemburg) (Morley, 1915; Schmiedeknecht, 1930; Pittaway, 1993). These records are supported by Schmiedeknecht's (1930) observation that the adults of *C. arrogator* are associated with *Epilobium*, the usual food plant for all three of the hosts listed above. Biological similarities among the reported host species also support the notion of *Catadelphus* using all three: they feed principally on herbs in the Onagraceae and overwinter in loose cocoons in the leaf litter (Hodges, 1971; Pittaway, 1993).

CHARMEDIA WAHL & SIME, GEN. N.

Type-species. **Charmedia chavarriai sp. n.**

Description. Flagellum of female lanceolate, with flagellomere 3 about 2.0× as long as wide; flagellum of male with tyloids present. Clypeus flat and wide, apicolateral margin forming an angle of approximately 40°, punctures evenly distributed, apical 0.3 not thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without paired median ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena convex in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by

about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum strongly convex, shelf-like; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced and completely filled-in, appearing as polished boss. Anterior transverse carina complete, median section not swollen; posterior transverse carina weak but complete; lateral longitudinal carinae complete; median longitudinal carinae absent. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleuron rugosopunctate. Juxtacoxal carina present. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2 m-cu interception apicad midpoint of posterior margin (vein 2/M about 3.1× as long as vein 3/M).

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 about 1.1× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field absent, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 without longitudinal. T2-4 evenly convex, with fine contiguous punctures. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma with T7-8 barely projecting beyond apex of T6; amblypygous.

Autapomorphies. Median longitudinal carina of absent (#33–1).

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is feminine.

Species and distribution. There is one species, *Charmedia chavarriai*, found in Costa Rica.

Biology. A series of rearings establishes *C. chavarriai* as a larval–pupal parasitoid of Sphingidae, probably specializing on species of *Xylophanes* (D. Janzen, pers. comm.). The hosts, all collected as nearly mature larvae on Rubiaceae, include *Xylophanes chiron* (Drury) and *X. hannemanni* (Closs) on *Psychotria horizontalis* Swartz, *X. ceratomioides* (Grote & Robinson) on *Hamelia patens* Jacquin (3 specimens), *X. crotonis* (Walker) on *Psychotria panamensis* Standl and *Coussarea carliana* [Rubiaceae]., and *X. juanita* Rothschild & Jordan on *Psychotria pubescens* [Rubiaceae]. (Costa Rica: Area de Conservación Guanacaste; '95-SRNP-9318', '96-SRNP-183', '97-SRNP-1912', '97-SRNP-1913', '99-SRNP-650', '97-SRNP-1892', '99-SRNP-938', '99-SRNP-8735', respec-

tively [AEIC, JHIC]). Additional specimens (see paratype data, below) have been reared from *X. amadis* Stoll (Costa Rica: Monteverde [JHIC]) and from a pupa of *Xylophanes* (determination by D. Janzen) (Panama: Chiriquí, Aiello lot 93–32 [STRI]).

Detailed rearing records for all specimens reared by D. Janzen and W. Hallwachs ([JHIC] and other materials listed with 'SRNP' identification codes), including *Charmedia* and genera discussed below, can be found at the website http://www.janzen.sas.upenn.edu

CHARMEDIA CHAVARRIAI WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Callajoppa* genus-group by the characters given above in the generic description of *Charmedia*, and by the overall black colouration and patterned wings.

Female. Structure. As in generic description. *Colour.* Overall colour black with faint bluish overtones. Following areas yellowish-white: paraocular area, gena bordering posterior margin of eye, labrum, apical 0.5 of ventral surface of middle basitarsus, hind tarsus except for fuscous 0.2 of basitarsus and tarsomore 5. Fore and middle legs fuscous beyond trochantellus, with apex of fore femur and ventral surface of fore tibia somewhat lighter. Fore wing clear with two dark brown bands. Hind wing clear except for dark brown of cell C and apical 0.2 (Fig. 72). *Length.* 19.5–21.8 mm (21.8 mm); fore wing 18.3–19.0 mm (17.9 mm).

Male. Structure. As for female. *Colour.* Similar to female except that yellowish-white areas vary from that found in females to the following extreme: clypeus except for median fuscous marks at base and centre; supraclypeal area; paraocular area; gena bordering posterior margin of eye; malar space; ventral margin of propleuron; pronotal flange except for median 0.3; short strip on dorsal margin of posterior dorsal corner of pronotum; following areas of mesopleuron: area surrounding epicnemial carina, subalar ridge, anterior 0.5 of hypoepimeron, and ventral posterior corner; apical 0.7 of anterior surface of fore coxa; apical 0.5 of anterior face of middle coxa. *Length.* 19.1–21.0 mm; forewing 16.0–18.3 mm.

Type material. Holotype ♀, COSTA RICA: *Guanacaste*, Area de Conservación Guanacaste, Sector Cacao, Estación Cacao, Lambert coord. 330200–380200, 800–1600 m, 12–17.vii.1993, 'INBIO CRI001 954550' (*Garcia*) [INBC]. Condition of holotype: intact except right antenna broken beyond flagellomere 38 and left antenna broken beyond flagellomere 32. Paratypes: COSTA RICA: 1 ♂, *Alajuela*, Area de Conservación Guanacaste, Sector San Rámon, Lambert coord. 318100–381900, 620 m, 27. iv-23.vi.1994, 'INBIO CRI001899308' (*Araya*) [AEIC];

1 ♂, same data as holotype except 'INBIO CRI001824278' (*Carballo*) [INBC]; 1 ♂, *Guanacaste*, Area de Conservación Guanacaste, Sector Cacao, Gongora, Lambert coord. 318600–375150, 560 m, *ex Xylophanes chiron* (larva collected 6.ix.1995, wasp emerged from host pupa 14.x.1995), '95-SRNP-9318' [JHIC]; 1 ♀, same data as preceding except *ex Xylophanes hannemanni* (host larva collected 23.i.1996, wasp emerged from host pupa 26.iii.1996), '96-SRNP-183' [JHIC]; 1 ♂, *Guanacaste*, Area de Conservación Guanacaste, Sector Cacao, Sendero Nayo, Lambert coord. 322450–375250, 1000 m, *ex Xylophanes ceratomioides* (host larva collected 21.x.1997, wasp emerged from host pupa 6.xii.1997) '97-SRNP-1913' (*Moraga*) [JHIC]; 1 ♂, same data as preceding except wasp emerged 6.xii.1997 '97-SRNP-1912' [AEIC]; 1 ♂, same data as preceding except *ex Xylophanes crotonis* (host larva collected 10.x.1997, wasp emerged from host pupa 8.xii.1997) '97-SRNP-1892' [JHIC]; 1 ♀, same data as preceding except host larva collected 17.vi.1999 and wasp emerged from host pupa 22.viii.1999 '99-SRNP-938' (*Ramirez*) [AEIC]; 1 ♂, *Guanacaste*, Area de Conservación Guanacaste, Sector Cacao, Sendero Derrumbe, Lambert coord. 323300–376300, 1300 m, *ex Xylophanes* sp. (host larva collected 9.vi.1997, wasp emerged from host pupa 30.vii.1997) '97-SRNP-1251' [AEIC]; 1 ♀, same locality data as above, *ex Xylophanes ceratomioides* (host larva collected 17.v.1999, wasp emerged from host pupa 4.viii.1999) '99-SRNP-650' (*Pereira*) [AEIC]; 1 ♂, *Guanacaste*, Area de Conservación Guanacaste, Sector Orosi, Estación Martiza, Lambert coord. 326900–373000, 600 m, 1.viii-1.x.1992, 'INBIO CRI001931006' [INBC]; 1 ♂, *Guanacaste*, Area de Conservación Guanacaste, Sector Pitilla, Estación Pitilla, 9 km S Santa Cecillia, Lambert coord. 330200–380200, 700 m 1995, 'INBIO CRI002131397' (*Moraga*) [AEIC]; 2 ♀♀, same data as preceding except collected 19.v-3.vi.1993 'INBIO CRI001342234', 31.iii-15.iv.1992 'INBIO CRI000706600' [AEIC, INBC]; 1 ♂, same data as preceding except collected 27.ii-2.iii.1989 'INBIO CRI000603517' (*Miranda*) [INBC]; 1 ♂, *Guanacaste*, Area de Conservación Guanacaste, Sector Santa Rosa, Bosque Humido, Lambert coord. 314800–360500, 300 m, *ex Xylophanes juanita.* (host larva collected 7.vi.1999, wasp emerged from host pupa 26.vii.1999) '99-SRNP-8735' [DHIC]; 1 ♀, *Puntarenas*, Monteverde, San Luis, Lambert coord. 250850–449250, 1040 m 'INBIO CRI000 842771' (*Fuentes*) [AEIC]; 1 ♂, *Puntarenas*, Monteverde, 'Hoge's Lower Farm', *ex Xylophanes amadis* (host larva collected 2.xii.1978, wasp emerged from host pupa 16.ii.1979) (*Haber*) [JHIC]. PANAMA: 1 ♂, *Chiriquí*, Quebrada La Mina, near Hornito, 1400 m, *ex Xylophanes* (host larva collected 6.v.1993, wasp emerged from host pupa 26.v.1993), Aiello lot 93–32

[STRI]; 1 ♂, Canal Zone, Barro Colourado Island, 10.viii.1977 (*Kimsey & Kimsey*) [UCDC].

Etymology. Named after Sr. Luis Felipe Chavarría Días, in recognition of his outstanding contributions to the invention, development, and evolution of biodiversity prospecting at INBio and the Area de Conservación Guanacaste.

COBUNUS UCHIDA, 1926

Cobunus Uchida, 1926: 65. Type-species: *Cobunus pallidiolus* Matsumura. Original designation.

Species and distribution. There are five described species distributed from Japan to Sulawesi (Yu & Horstmann 1997).

Autapomorphies. Scutellum moderately convex (#20–0); anterior margin of propodeum forming narrow groove with metapostnotum (#25–0); cell 12Rs of fore wing with veins 2/Rs and 3rs-m of equal length (#40–0); postpetiole of MS1 with basal conical projection (#45–2).

Biology. Unknown.

CONOCALAMA HOPPER, 1939

Conocalama Hopper, 1939: 319. Type-species: *Trogus brullei* Cresson. Original designation.

Species and distribution. There are 14 described species distributed from Canada to southern Mexico (Guerrero) (Yu & Horstmann, 1997).

Autapomorphies. Flagellomeres of male with tyloids (#3–0); median longitudinal carinae present anteriad anterior transverse carina (#32–0).

Biology. Host data are available only for *C. brullei* (Cresson), which has been reared from the sphingid *Manduca sexta* (L.) (Heinrich 1962). Hopper (1939) lists three more sphingid hosts for this species – *Paonias astyalus* (Drury), *P. myops* (J.E. Smith), and *Dolba hylaeus* (Drury) – and mentions *P. myops* as a host of *C. copei* (Cresson), but these records are completely unsupported. Heinrich (1962) discusses a specimen of *C. quebecensis* (Provancher) that, according to the label, was reared from the saturniid moth *Eacles imperialis* Drury; host remains were not preserved, however, and Heinrich himself doubted the record [which is, incidentally, reiterated without comment in Carlson (1979)].

DIMAETHA CAMERON, 1901

Dimaetha Cameron, 1901: 277. Type-species: *Dimaetha tibialis* Cameron. Monotypic.

Erythrojoppa Cameron (1902a): 146. Type-species: *Erythrojoppa ferruginea* Cameron. Monotypic. Synonymized by Townes *et al.* (1961).

Species and distribution. There are two described species, distributed from north-eastern India to Sulawesi (Yu & Horstmann 1997).

Autapomorphies. Gena flat and sharply receding (#15–2); scutellum moderately convex (#20–0); median longitudinal carinae of T1 complete and extending to apex (#46–0); postpetiole of T1 rugosopunctate (#48–0).

Biology. Unknown.

DOTHENIA WAHL & SIME, GEN. N.

Type-species. **Dothenia hansoni sp. n.**

Description. Flagellum of female lanceolate, with flagellomere 3 1.3–1.8× as long as wide; flagellum of male lacking tyloids. Clypeus flat and wide, apicolateral margin forming an angle of approximately 90°, punctures evenly distributed, apical 0.3 thinned, apical margin straight and with weak median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without paired median ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena swollen in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum strongly convex, often shelf-like, or strongly convex with planar surfaces and forming a more or less acute angle in lateral view; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced and partially to completely filled-in, latter state appearing as polished boss. Anterior transverse carina complete, median section not swollen; posterior transverse carina complete; lateral longitudinal carinae complete; median longitudinal carinae, basad anterior transverse carina, either close together on raised areas or fused into single carina; median longitudinal carinae, apicad anterior transverse carina, present or absent. First lateral area with regularly distributed punctures and second lateral area rugosopunctate, or both finely and contiguously punctate. Metapleuron weakly rugosopunctate. Juxtacoxal carina present or absent. Propodeal lateral profile steeply sloping or (in one species) evenly convex. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2 m-cu interception either at midpoint or apicad midpoint of posterior margin (vein 2/M 1.5–2.3× as long as vein 3/M).

MS1 in lateral view with petiole flattened, post-petiole convex; sclerotized anterior portion of S1 0.9–1.4× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole with or without basal convexity, median longitudinal carinae absent, median field present, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with fine contiguous punctures. T2-5 not basally constricted and without dorsolateral ridges. S2 divided and S3-5 entire, or S2-5 entire. Apex of female metasoma with T7-8 barely projecting beyond apex of T6; amblypygous

Autapomorphies. Propodeum with median longitudinal carinae anteriad apical transverse carina close together on raised area (#32–1); metapleuron with small contiguous/confluent punctures and without rugae (#36–2); cell 1 + 2Rs of fore wing with vein 2 m-cu interception apicad midpoint of posterior margin (#41–1).

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is feminine.

Species and distribution. There is one described species, *D. hansoni*, and nine undescribed species [AEIC, CCCP, IMLA, JHIC, NHML, UCDC], distributed from Mexico to Argentina.

Biology. The holotype and paratype specimens of *D. hansoni* (see below) were reared as larval-pupal parasitoids of the sphingid *Erinnyis ello* (L.). The hosts were collected as final-instar larvae on Euphorbiaceae (D. Janzen, pers. comm.). In addition, this parasitoid has been reared from *Manduca occulta* (Rothschild & Jordan) on *Cestrum glanduliferum* (Solanaceae) (Costa Rica: Area de Conservación Guanacaste, "91-SRNP-1260" [JHIC]), also collected in the final instar (D. Janzen, pers. comm.).

DOTHENIA HANSONI WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Callajoppa* genus-group by the characters given above in the generic description of *Dothenia*, and from the other species in the genus by the following combination of characters: fuscous to black overall colour without bluish tint or overtone, dark brown wings, brownish-red annulus of flagellum, concave clypeal apex, strongly convex and shelf-like scutellum (without planar surfaces that form an acute angle), basally convex postpetiole, strongly rugose S1,and divided S2 and entire S3-5.

Female. Structure. Clypeal apex concave. Scutellum strongly convex and shelf-like. Postpetiole of MS1 with basal convexity. First and second lateral areas finely and contiguously punctate, rugae absent. S1 strongly

rugose, appearing serrated in lateral view. S2 divided, S3-5 entire. Other characters as in generic description. *Colour*. Uniformly fuscous to black. Clypeus, paraocular area to level of antennal socket, and basal 0.8 of mandible, varying independently from fuscous to deep brownish red. Flagellomeres 9–21 of antenna brownish-red. Wings uniformly dark brown. *Length*. 24.4–27.1 mm (27.1 mm); fore wing 21.3–23.7 mm (21.3 mm).

Male. Structure. As for female. *Colour*. Similar to female except that flagellomeres 13–31 are brownish red. *Length*. 25.6–28.6 mm (28.2 mm); fore wing 21.8 mm-23.6 mm (22.1 mm).

Type material. Holotype ♀, COSTA RICA: *Guanacaste*, Area de Conservación Guanacaste, Sector Cacao, Estación Cacao, Lambert coord. 323150–375650, 1120 m, *ex Erinnyis ello* (host larva collected 4.ii.1999, wasp emerged from host pupa 29.iii.1999), '99-SRNP-107' (*Ramirez*) [AEIC]. Condition of holotype: intact. Paratypes: 2 ♀♀ and 2 ♂♂, same data as preceding except host larvae collected 4.ii.1999 and wasps emerged from host pupae 27.iii-31.iii.1999), '99-SRNP-92, 97, 98, and 106' (*Ramirez*) [AEIC, JHIC]; 1 ♂, same data as preceding except host larva collected 5.ii.1999 and wasp emerged from host pupa on 28.iii.1999, '99-SRNP-130' [JHIC]; 2 ♂♂, *Guanacaste*, Area de Conservación Guanacaste, Sector Santa Rosa, 17.vii.1978, Dry Hill (*Janzen*) [AEIC]; 1 ♂, *Guanacaste*: Area de Conservación Guanacaste, Sector Santa Rosa, Bosque San Emilio, Lambert coord. 313800–359800, 300 m, *ex Erinnys ello* (host larva collected 2.viii.1984, wasp emerged from host pupa 29.viii.1984), '84-SRNP-1624' (*Janzen*) [JHIC]

Etymology. Named after Paul Hanson, chalcidologist and indefatigable collector of Costa Rican Hymenoptera.

Comments. The brownish-red colouration of the male flagellum can be quite variable, in terms of presence (can be restricted to flagellomeres 18–25) and extent (ranging from absent to present only on the dorsal surface).

FACYDES CAMERON, 1901

Facydes Cameron, 1901: 278. Type-species: *Facydes purpureomaculatus* Cameron. Monotypic.
Species and distribution. There are two described species found in Japan, southern China, north-eastern India, and Burma (Yu & Horstmann 1997).
Autapomorphies. Epicnemial carina dorsally incomplete (#19–1); scutellum with lateral carinae extending to basal 0.5 scutellar length (#21–1); juxtacoxal carina absent (#22–1); posterior transverse carina of propodeum medially incomplete (#30–1).
Biology. Unknown.

GNAMPTOPELTA HOPPER, 1939

Gnamptopelta Hopper, 1939: 333. Type-species: *Trogus obsidianator* Brullé. Original designation.
Species and distribution. There is one species found in North America (Sime & Wahl 1998).
Autapomorphies. Apical margin of clypeus concave (#4–1); scutellum conical (#20–2); propodeum with median longitudinal carinae anteriad anterior transverse carina present (#32–0); median longitudinal carinae of T1 apically incomplete (#46–1); S2-3 divided, S4-5 entire (#55–1). Alternate combinations: (1) #s 4–1, 20–2, and 55–1, or (2) #s 4–1, 20–2, 32–0, and 55–1.
Biology. *G. obsidianator* is a larval-pupal parasitoid of Sphingidae; it has been reared from *Amphion floridensis* B.P. Clark attacked as third- and fifth-instars (Sime & Wahl, 1998). The association of male and female *G. obsidianator* with grapevines (Heinrich 1962, 1977) suggests that this species specializes on Vitaceae-feeding sphingids (of which there are at least 10 species in its range (Hodges 1971)), but the degree of specificity is unknown. Reports of *G. obsidianator* attacking *Papilio polyxenes* Fabricius (Papilionidae) and *Pyrrharctia isabella* (J.E. Smith) (Arctiidae) (Weed, 1888; Howard, 1889; Bischoff, 1915; Hopper, 1939) are not corroborated by voucher specimens or recent records; we consider them implausible.

HUMBERT WAHL & SIME, GEN. N.

Type-species. **Humbert humberti** sp. n.
Description. Flagellum of female lanceolate, with flagellomere 3 about 1.6× as long as wide; flagellum of male unknown. Clypeus flat and wide, apicolateral margin forming an angle of approximately 90°, punctures evenly distributed, apical 0.3 thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena swollen in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum strongly convex with planar surfaces and forming a more or less acute angle in lateral view; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced

Figures 7–16. (7, 8) Dorsal view of metasoma: (7) *Conocalama canadensis* (Provancher); (8) *Trogus pennator* (Fabricius). (9–12) Dorsal view of heads: (9) *Dimaetha* sp. 2; (10) *Stirojoppa thoracica* (Kriechbaumer); (11) *Tricyphus apicalis* Kriechbaumer; (12) ***Lagavula gauldi*** sp. n. (13) ***Lagavula gauldi***, lateral view of MS1. (14) *Conocalama brullei* (Cresson), lateral view of MS1. (15, 16) lateral view of propodeum and MS1: (15) *Catadelphops nasutus* (Heinrich); (16) ***Xanthosomnium froesei*** sp. n.

and partially filled-in. Anterior transverse carina complete, median section not swollen; posterior transverse carina medially incomplete; lateral longitudinal; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleuron rugosopunctate. Juxtacoxal carina absent. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception at midpoint of posterior margin.

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 0.9–1.4× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field absent, punctures scattered. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with fine punctures separated by about 0.5× their diameter to contiguous. T2-5 not basally constricted and without dorsolateral ridges. S2-5 entire. Apex of female metasoma with T7-8 barely projecting beyond apex of T6; amblypygous.

Autapomorphies. Apical margin of clypeus simple (#5–0); posterior transverse carina of propodeum medially incomplete (#30–1); postpetiole of T1 without distinct median field (#47–1), with fine and delicate punctures and lacking rugae (#48–1).

Etymology. The genus is after the hapless Humbert Humbert of Nabokov's novel, *Lolita*. Its gender is masculine.

Species and distribution. There is one species, *Humbert humberti*, found in Brazil.

Biology. Unknown.

HUMBERT HUMBERTI WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Callajoppa* genus-group by the characters given above in the generic description of *Humbert*, and by the striking colour combination of a black body with metallic blue and green tints and fuscous wings.

Female. Structure. As in generic description. *Colour.* Head and mesosoma black with metallic blue tints,

except for dark brown of antenna, fore tibia, and tarsi. Metasoma black with metallic green tints. Wings uniformly dark brown. *Length.* 22.9–24.8 mm (22.9 mm); fore wing 20.1–20.6 mm (20.1 mm).

Male. Unknown.

Type material. Holotype ♀, BRAZIL: *Nova Teutonia*, Santa Catarina, xi.1970 (*Plaumann*) [AEIC]. Condition of holotype: intact except left antenna broken beyond flagellomere 17 and left forewing with tear in cell R. Paratype: 1 ♀, same data as holotype [AEIC].

Etymology. Named after the aforementioned Humbert Humbert.

LADERRICA WAHL & SIME, GEN. N.

Type-species. ***Laderrica feenyi*** Wahl & Sime, sp. n.

Description. Flagellum of female lanceolate, with flagellomere 3 2.9× as long as wide; flagellum of male unknown. Clypeus flat and wide, apicolateral margin forming an angle of approximately 40°, punctures evenly distributed, apical 0.3 not thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena convex in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum conical; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced, completely filled-in and appearing as polished boss. Anterior transverse carina absent; posterior transverse carina complete; lateral longitudinal carinae present; median longitudinal carinae absent. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleuron rugosopunctate. Juxtacoxal carina absent. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception apicad

midpoint of posterior margin (vein 2/M 2.5× as long as vein 3/M).

MS1 in lateral view evenly curved with highest point at middle, petiole laterally compressed (similar to Fig. 24); sclerotized anterior portion of S1 about 0.9× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; median longitudinal carinae absent, median field present, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 with longitudinal rugae restricted to median basal 0.2 of T2, absent on other tergites. T2-4 evenly convex, with normal punctures separated by about 0.5× their diameter. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma with T7-8 projecting well beyond apex of T6; amblypygous.

Autapomorphies. Scutellum conical (#20–2); median longitudinal carinae of propodeum absent (#33–1); MS1 in profile evenly curved with highest point at middle, petiole laterally compressed (#42–1).

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is feminine.

Species and distribution. There is one species, *Laderrica feenyi*, found in Brazil.

Biology. Unknown.

LADERRICA FEENYI WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Callajoppa* genus-group by the characters given above in the generic description of *Laderrica*.

Female. Structure. As in generic description. *Colour.* Overall colour brownish yellow. Following areas dark brown: antenna except for medial surface of scape; supra-antennal area; vertex; dorsal 0.3 of gena; dorsal 0.3 of lateral area of pronotum except for dorsal posterior corner; mesoscutum; fore and middle tarsi; dorsal surface of middle tibia; hind leg: posterior condyles of coxa, apical 0.7 of femur, tibia, basal 0.2 and apical 0.2 of basitarsus, and tarsomeres 2–5. Following areas fuscous: basal 0.5 of T3 except for apical lateral corners, T4-7, and S5-6. Wings clear except for light brown of apical 0.2 of fore wing. *Length.* 15.6 mm; fore wing 13.7 (mm).

Male. Unknown.

Type material. Holotype ♀, BRAZIL: *Nova Teutonia*, 27°11′ S, 52°23′ W; 8.ii.1939, "B.M. 1939–181" (*Plaumann*) [NHML]. Condition of holotype: intact.

Etymology. Named after Paul Feeny, in recognition of his outstanding contributions to the study of the biology of swallowtail butterflies.

LAGAVULA WAHL & SIME, GEN. N.

Type-species. **Lagavula gauldi sp. n.**

Description. Flagellum of female lanceolate, with flagellomere 3 1.8× as long as wide; flagellum of male with tyloids present (weak) or absent. Clypeus flat and wide, apicolateral margin forming an acute angle of approximately 40°, punctures evenly distributed, apical 0.3 not thinned, apical margin straight and with weak median projection present or absent. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena flat and sharply receding in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete or incomplete. Scutellum weakly convex; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola small (about 3.0× as wide as long, not reduced to boss) or absent. Anterior transverse carina complete or incomplete, median section not swollen when complete; posterior transverse carina complete or absent; lateral longitudinal carinae complete or absent; median longitudinal carinae absent basad anterior transverse carina, present or absent apicad anterior transverse carina. First lateral area with punctures ranging from uniformly distributed to widely scattered; second lateral area with scattered punctures. Metapleuron with surface sculpture ranging from widely scattered punctures to rugosopunctate. Juxtacoxal carina absent. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception apicad midpoint of posterior margin (vein 2/M 2.1–5.8× as long as vein 3/M).

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 0.9× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field absent, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with fine punctures separated by 0.5× their diameter to contiguous. T2-5 not basally constricted and without dorsolateral ridges. S2 divided and S3-5 entire, or S2-5 entire. Apex of female metasoma with T7-8 projecting well beyond apex of T6; amblypygous.

Autapomorphies. Occipital carina with ventral region above mandible produced as low flange (#17–1); areola small (about 3.0× as wide as long) but not reduced to boss (#27–0); first lateral area with punctures ranging from uniformly distributed to scattered or absent, second lateral area with scattered punctures (#35–2); postpetiole of T1 with median field absent (#47–1), and with fine and dense punctures, no trace of rugae (#48–2).

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is feminine.

Species and distribution. There is one described species, *Lagavula gauldi*, and four undescribed species [AEIC, IMLA, INBC], distributed from Costa Rica to Argentina.

Biology. Lagavula gauldi has been reared from *Aleuron iphis* (Walker) (Sphingidae) on *Tetracera volubilis* L. (Dilleniaceae) (Costa Rica: *Guanacaste* (see paratype data, below), '94-SRNP-10018' [AEIC]). It is a larval-pupal parasitoid; the host was collected in the penultimate instar (D. Janzen, pers. comm.).

LAGAVULA GAULDI WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Callajoppa* genus-group by the characters given above in the generic description of *Lagavula*, and from the other species in the genus by the following combination of characters: ventral 0.5 of mesopleuron with punctures on polished surface, punctures separated by about 1–2× their diameter (vs. ventral 0.5 with closely spaced vertical rugae); areola present albeit weakly defined; base of propodeum strongly elevated; predominately brownish yellow colour of body; banded fore wing (Fig. 73).

Female. Structure. Ventral 0.5 of mesopleuron with punctures on polished surface, punctures separated by about 1–2× their diameter. Areola present albeit weakly defined. Base of propodeum strongly elevated. Other characters as in generic description. *Colour.* Overall colour brownish yellow. Following areas fuscous/black: two parallel stripes on supraclypeal area; supra-antennal area; vertex; dorsal 0.7 of gena and region bordering eye; dorsal 0.4 of occiput; antenna; pronotum except for extreme posterior ventral corner; mesoscutum; scutellum except for apical 0.2; mesopleuron except for posterior 0.5 of hypoepimeron, ventral 0.5 of epicnemium, and ventral posterior corner; hind leg except for basal 0.7 of coxa and apical 0.5 of femur (except for extreme apex); apical 0.2 of T3, and T4-6; S4-6. Fore and hind legs with following dark brown: ovoid near apex of posterior face of femur, tarsomeres 2–4 of fore leg, and middle tarsus. Ground colour of wings light yellow: fore wing with two dark brown bands (Fig. 73), hind wing with extreme apex dark brown. *Length.* 17.9 mm; fore wing 14.9 mm.

Male. Structure. As in female. *Colour.* As in female except: supraclypeal area, with exception of paraocular area, can be fuscous to dark brown; fuscous of mesopleuron can be restricted to dorsal 0.5, leaving epicnemium entirely brownish yellow; S4 brownish yellow. *Length.* 15.2–17.9 mm; fore wing 13.4–14.9 mm.

Type material. Holotype ♀, COSTA RICA: *Guanacaste*, Area de Conservación Guanacaste, Sector Orosi, Estación Maritza, Lambert coord. 326900–373000, 600 m 1990, 'INBIO CRI000713326' [INBC]. Condition of holotype: intact except left antenna broken beyond flagellomere 3, and right antenna broken beyond flagellomere 12. Paratypes: COSTA RICA, 1 ♂, same data as holotype except collected viii.1990 'INBIO CRI000289722' [INBC]; 1 ♂, *Guanacaste*: Area de Conservación Guanacaste, Sector El Hacha, Agua Buena, Lambert coord. 334900–364100, 220 m, *ex Aleuron iphis* (host larva collected 14.xi.1994, wasp emerged from host pupa 31.xii.1994), '94-SRNP-10018' (*Janzen*) [AEIC].

Etymology. Named after Ian Gauld, ichneumonologist of the first rank.

MOKAJOPPA WAHL & SIME, GEN. N.

Type-species. Tricyphus respinozai Ward & Gauld

Description. Flagellum of female lanceolate, with flagellomere 3 1.6–1.9× as long as wide; flagellum of male without tyloids. Clypeus flat and wide, apicolateral margin forming an angle of approximately 90°, punctures evenly distributed, apical 0.3 not thinned, apical margin concave, and with median projection present or absent. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena swollen in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum moderately convex; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced and completely filled-in, appearing as polished boss. Anterior transverse carina absent; posterior transverse carina complete or absent; lateral longitudinal carinae absent; median longitudinal carinae absent basad anterior
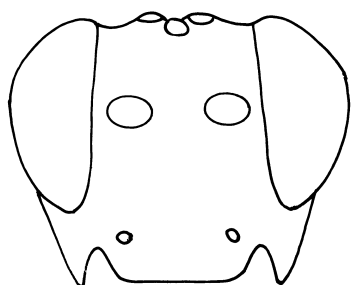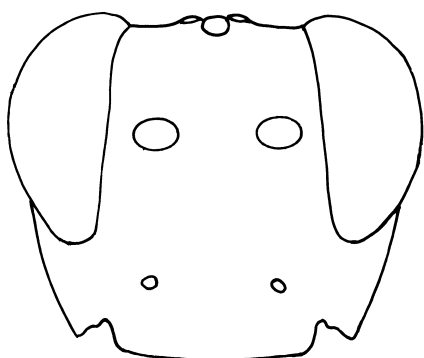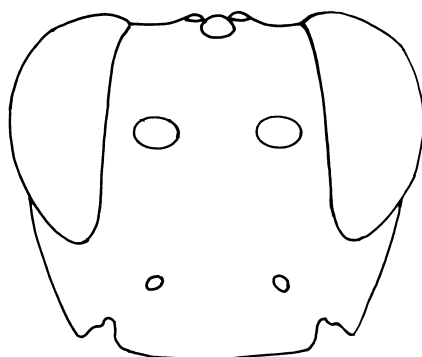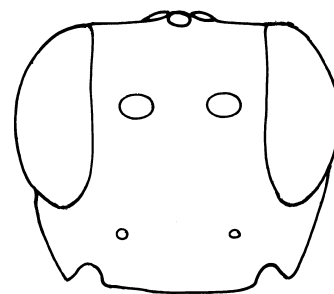
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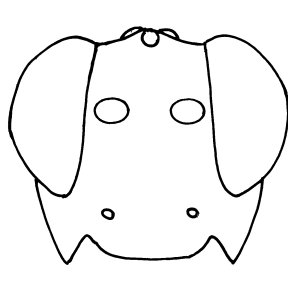
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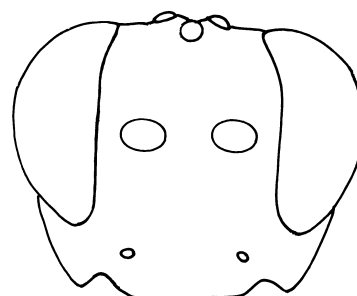
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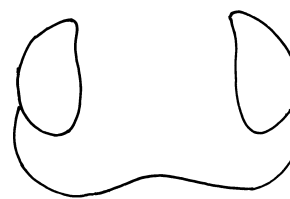**21**
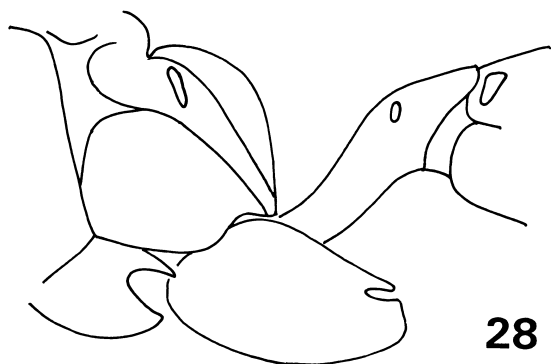
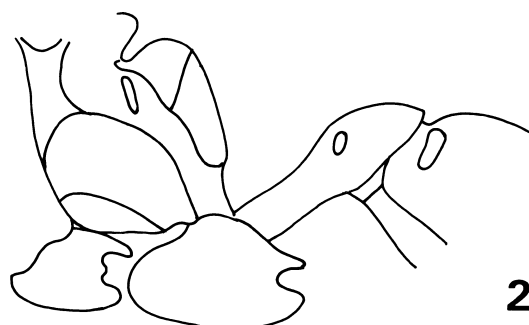**22**

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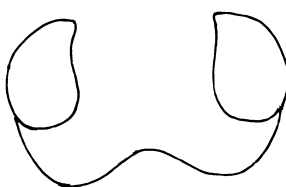
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Figures 17–29. (17–22) Frontal view of heads: (17) *Charmedia chavarriai* **sp. n.**; (18) *Laderrica feenyi* **sp. n.**; (19) *Saranaca elegans* (Cresson); (20) *Callajoppa exaltatoria* (Panzer); (21) *Quandrus pepsoides* (Smith); *Catadelphus atrox* (Cresson). (23–25) Lateral view of MS1: (23) *Tricyphus nigriventris* Kriechbaumer; (24) *Saranaca elegans*; (25) *Charmedia chavarriai*. (26, 27) Dorsal view of heads: (26) *Callajoppa cirrogaster* (Schrank); (27) *Catadelphus arrogator* (Fabricius). (28, 29) Lateral view of propodea and MS1: (28) *Dothenia* sp. 8; (29) *Quandrus pepsoides*.

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transverse carina, present or absent apicad anterior transverse carina]. First lateral area with punctures uniformly distributed, second lateral area with punctures ranging from large and uniformly spaced to scattered. Metapleuron ranging from rugosopunctate to punctate. Juxtacoxal carina present. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception at midpoint or apicad midpoint of posterior margin (vein 2/M about 4.8× as long as vein 3/M).

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 1.1× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field present, rugosopunctate. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with fine punctures separated by 0.3–0.5× their diameter. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma with T7-8 barely projecting beyond apex of T6; amblypygous.

Autapomorphies. Apical margin of clypeus concave (#4–1); juxtacoxal carina present (#22–0); lateral longitudinal carinae of propodeum absent (#31–1); first lateral area with punctures uniformly distributed, second lateral area with punctures ranging from large and uniformly spaced to scattered (#35–2); apex of female metasoma with T7-8 barely projecting beyond apex of T6 (#56–1).

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is feminine.

Species and distribution. There is one described species, *Mokajoppa respinozai*, and one undescribed species [AEIC, INBC, JHIC]. Both are from Costa Rica.

Comments. M. respinozai was formerly placed in *Tricyphus* (see Taxonomy, above).

Biology. Species of *Mokajoppa* evidently specialize on Sphingidae. *Mokajoppa respinozai* is well established as attacking *Manduca dilucida* Hübner (57 records [JHIC]; Ward & Gauld 1987). The undescribed species has been reared twice from *Cautethia spuria* (Boisduval) collected in the penultimate instar on *Exostema mexicanum* A. Gray (Rubiaceae) (Costa Rica: Area de Conservación Guanacaste '91-SRNP-1906', '93-SRNP-7532' [JHIC]) (D. Janzen, pers. comm.). Both are larval–pupal parasitoids.

According to Ward & Gauld (1987) and D. Janzen (pers. comm.), *M. respinozai* is obligately univoltine, remaining dormant in the pupa through the dry season and emerging usually by May or early June. It shows no apparent preferences among the food plants of this host, and has been reared from larvae found on Bignoniaceae (*Amphilophium*, *Tabebuia*), Annonaceae (*Annona*, *Sapranthus*) and Verbenaceae (*Rehdera*). Observations in Costa Rica indicate that this species is specific to *M. dilucida*: at least five other *Manduca* species are often collected on the same food plants but have never yielded *Mokajoppa* (D. Janzen, pers. comm.). The wasp has been reared from hosts collected in the field as young as the second instar. The biology of the undescribed species differs somewhat from that of *M. respinozai* (D. Janzen, pers. comm.). The adult emerges within about a month of host pupation, and its host, *C. spuria*, unlike the relatively polyphagous *Manduca dilucida*, is a specialist on just two species of Rubiaceae. It pupates in the leaf litter, rather than underground.

MYOCIOUS WAHL & SIME, GEN. N.

*Type-species. **Myocious orientalis** sp. n.*
Description. Flagellum of female unknown; flagellum of male with tyloids present. Clypeus flat and wide, apicolateral margin forming an angle of approximately 90°, punctures evenly distributed, apical 0.3 not thinned, apical margin straight and with weak median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena convex in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible produced as a low flange.

Pronotal flange low and with posterior face convex. Epicnemial carina dorsally incomplete. Scutellum strongly convex; lateral carinae absent. Central convexity of metanotum not widened and lateral

depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced and completely filled-in, appearing as polished boss. Anterior transverse carina complete, median section not swollen; posterior transverse carina complete; lateral longitudinal carinae complete; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First and second lateral area with fine contiguous punctures. Metapleuron weakly rugosopunctate. Juxtacoxal carina absent. Propodeal lateral profile steeply sloping. Scopa unknown. Cell 1 + 2Rs of fore wing pointed, vein 2/Rs < 3r-m, vein 2m-cu interception at midpoint of posterior margin.

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 1.4× as long as distance from posterior margin of anterior portion to apex of T1, basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field present, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with fine punctures separated by 0.3–0.5× their diameter. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma not known.

Autapomorphies. Apical margin of clypeus with weak median tooth (#5–1); occipital carina with ventral region above mandible produced as low flange (#17–1); scutellum moderately convex (#20–0), and first and second lateral areas finely and contiguously punctate (#35–1). Alternate combination: #s 17–1, 20–0, and 35–1.

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is masculine.

Species and distribution. There is one described species, *Myocious orientalis*, found in northern India.

Biology. Unknown.

MYOCIOUS ORIENTALIS WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Callajoppa* genus-group by the characters given above in the generic description of *Myocious*.

Female. Unknown.

Male. Structure. As in generic description. *Colour.* Head yellow, the following fuscous: median 0.3 of supra-antennal area; vertex; gena adjacent to occipital carina and mandibular base. Antenna with scape and pedicel dorsally fuscous; flagellum with ventral surface brown, dorsal surface dark brown. Overall colour of mesosoma fuscous, the following yellow: propleuron; flange, dorsal margin, and ventral posterior

corner of pronotum; following areas of mesopleuron: anterior margin, subalar ridge, posterior 0.5 of epicnemium, triangular area comprising ventral 0.2 of mesepisternum and extending for 0.5× its length; mesopleural venter; two lines extending from notauli to their convergence at mesoscutal apex; median 0.5 of scutellum; anterior margin and central convexity of metanotum; following areas of propodeum: carinae, most of second lateral area, and apical margin. Head and mesosoma with often with reddish yellow region between fuscous and yellow areas. Hind leg overall brownish red; dorsal surface and apical 0.5 of ventral surface of coxa, apical 0.3 of ventral surface of femur, apical 0.1 of tibia, and tarsus except for basal 0.2 of basitarsus, dark brown to fuscous; anterior surfaces of trochanter and trochantellus, basal 0.2 of basitarsus, brownish yellow. Metasoma overall brownish red; basal 0.7 of petiolar dorsum dark brown; T2-5 with pattern of basal fuscous and apical yellow on brownish red ground, fuscous comprising basal 0.5 of T2 and progressively reduced to basal 0.2 on T5. Wings light yellow except for light brown of apical 0.2 of fore wing and apical 0.1 of hind wing. *Length.* 18.7–20.7 mm (18.7 mm); fore wing 14.5–15.6 mm (14.5 mm).

Type material. Holotype ♂, INDIA: *Uttar Pradesh*, Barkot, 4000 ft., 21.v.1967, 'no. 281' (*Ram*) [AEIC]. Condition of holotype: intact except left antenna broken beyond flagellomere 25, tarsomeres 4–5 of right fore leg missing, tarsomeres 2–5 of left hind leg missing, and tarsomere 5 of right hind leg missing. Paratype ♂, INDIA: *Uttar Pradesh*, Kashi, Ranajeet, 21.v.1967, 'no. 280' (*Gupta*) [AEIC].

Etymology. From the Latin *orientalis*, of the east, in reference to the specimens' place of origin.

PEPSIJOPPA HEINRICH, 1936

Pepsijoppa Heinrich, 1936: 199. Type-species: *Trogus gryps* Morley. Original designation.

Species and distribution. There is one species, *Pepsijoppa gryps*, from sub-Saharan Africa.

Autapomorphies. Anterior margin of propodeum forming normal groove with metapostnotum (#25–0); areola large and well-defined by constituent carina (#27–0), triangular in shape; propodeum with median longitudinal carinae anteriad anterior transverse carina present (#32–0); propodeum in lateral view with distinguishable dorsal and postero-dorsal faces which meet at an angle (37–0). Alternate combination: #s 25–0, 27–0, and 37–0.

Comments. Heinrich (1967) discussed the defining characters of Trogini, emphasizing propodeal structure and areolet shape (see above, Classificatory History). *Pepsijoppa* was 'rather problematic' (Heinrich 1967: 238) as it was 'closest in general appearance' to the Callajoppina, lacked the characteristic

evenly convex propodeal outline and reduced areola (which thus seemed to 'indicate some relationship to the Protichneumonini'), but yet had cell 1 + 2Rs in the usual callajoppine configuration. Heinrich thought the genus was 'best placed in the Trogini, without attributing it to one of the two named subtribes. It may perhaps represent an ancient form.' The analysis, however, shows it to be placed well within the traditional Callajoppina. The species is highly derived and characterized by a suite of reversals.

Biology. Unknown.

QUANDRUS WAHL & SIME, GEN. N.

Type-species. Trogus pepsoides Smith

Description. Flagellum of female lanceolate, with flagellomere 3 1.5× as long as wide; flagellum of male with tyloids present. Clypeus flat and wide, apicolateral margin forming an angle of approximately 90°, punctures evenly distributed, apical 0.3 thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena convex in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum conical; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced and partially filled-in. Anterior transverse carina complete, median section not swollen; posterior transverse carina complete; lateral longitudinal carinae complete; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleuron rugosopunctate. Juxtacoxal carina present. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception apicad midpoint of posterior margin (vein 2/M about 1.3× as long as vein 3/M).

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 about 1.1× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field present, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 with longitudinal rugae restricted to median basal 0.1 of T2, absent on other tergites. T2-4 evenly convex, with fine contiguous punctures. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma with T7-8 barely projecting beyond apex of T6; amblypygous.

Autapomorphies. Apical margin of clypeus simple (#5–0); scutellum conical (#20–2); metapleuron with small, contiguous punctures and without rugae (#36–2); cell 1 + 2Rs of fore wing with vein 2m-cu interception apicad midpoint of posterior margin (#41–1). Alternate combination: #s 20–2, 36–3, and 41–1.

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is masculine.

Species and distribution. There is one species, *Quandrus pepsoides*, found in China, Japan, Korea, and Taiwan.

Comments. Q. pepsoides was formerly placed in *Callajoppa* (see Taxonomy, above).

Biology. Quandrus pepsoides is a larval-pupal parasitoid of Sphingidae, possibly limited to Sphingini. Mell & Heinrich (1931) report as hosts *Acherontia lachesis* (Fabricius), *A. styx* (Westwood), *Meganoton rufescens* (Butler), and *Psilogramma menephron* (Cramer); Uéda (1956) adds *Psilogramma increta* (Walker). These hosts use an unusually broad array of plants, including Annonaceae, Verbenaceae, Oleaceae, Convolvulaceae, and Solanaceae (Mell, 1922). In southern China, *Q. pepsoides* is a particularly common parasitoid of *M. rufescens*, with parasitism rates as high as 45% (15 of 33 pupae; Mell & Heinrich, 1931). References (e.g. Townes *et al.*, 1965) to *Papilio xuthus* L. (Papilionidae) as a host are apparently based on a single report (Ohtsuka, 1947) which should be viewed skeptically: *P. xuthus* is exceptionally well studied (Watanabe, 1981), and among frequent reports of other parasitoids there are no additional records of *Q. pepsoides* attacking this host.

SARANACA WAHL & SIME, GEN. N.

Type-species. Trogus elegans Cresson.

Description. Flagellum of female lanceolate, with flagellomere 3 about 2.0× as long as wide; flagellum of male with tyloids present. Clypeus flat and wide, apicolateral margin forming an angle of approximately 40°, punctures evenly distributed, apical 0.3 not thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina.
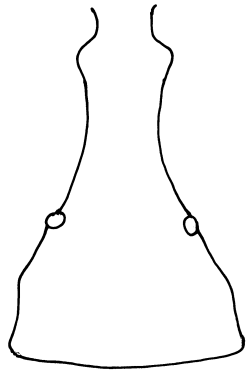
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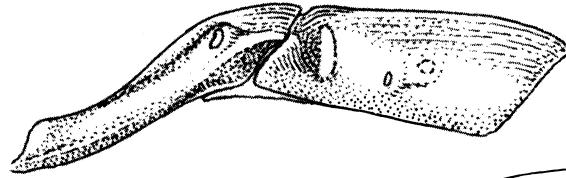
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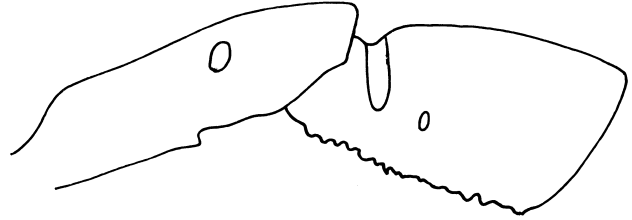
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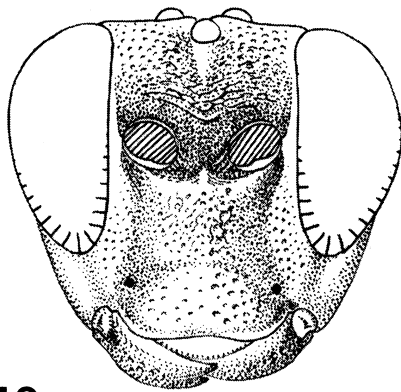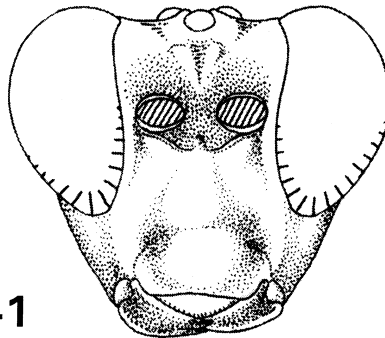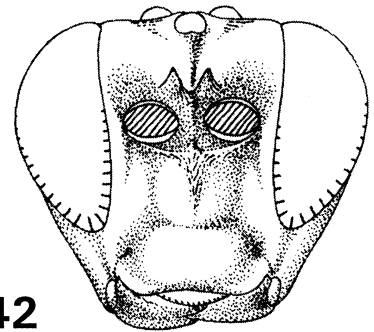**42**

Figures 30–42. (30) *Macrojoppa pulcherrima* (Ashmead), dorsal view of T1. (31, 32) Lateral view of MS1 and T2: (31) *Macrojoppa concinna* (Brullé); (32) *Macrojoppa rufa* (Brullé). (33) **Daggoo philoctetes sp. n.**, fore and hind wings. (34, 35) Lateral view of MS1: (34) *Pedinopelte latipennis* (Cresson); (35) **Daggoo philoctetes**. (36–39) Lateral view of heads: (36) *Psilomastax pyramidalis* Tischbein; (37) *Queequeg* sp. 1; (38) *Holcojoppa bicolor* (Radoszkowski); (39) *Neofacydes* sp. 3. (40–42) Frontal view of heads: (40) *Ctenichneumon funereus* (Geoffroy); (41) *Macrojoppa concinna*; (42) *Trogus lapidator* (Fabricius).

Gena convex in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum strongly convex with planar surfaces and forming a more or less acute angle in lateral view; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola reduced and completely filled-in, appearing as polished boss. Anterior transverse carina complete, median section not swollen; posterior transverse carina complete; lateral longitudinal carinae complete; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleuron rugosopunctate. Juxtacoxal carina present. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception apicad midpoint of posterior margin (vein 2/M 2.8× as long as vein 3/M).

MS1 in lateral view evenly curved with highest point at middle (Fig. 24), petiole laterally compressed; sclerotized anterior portion of S1 about as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; median longitudinal carinae absent, median field present, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with fine punctures separated by about 0.3× their diameter to contiguous. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma with T7-8 barely projecting beyond apex of T6; amblypygous.

Autapomorphies. MS1 in profile evenly curved with highest point at middle, petiole laterally compressed (#42–1).

Etymology. The generic name is a euphonious combination of letters with no meaning. Its gender is feminine.

Species and distribution. There are four described species from North America: *apicalis* (Cresson), *ater*

(Hopper), *elegans* (Cresson), and *floridanus* (Heinrich) (Heinrich, 1977).

Comments. The four species in this genus were formerly placed in *Tricyphus* (see Taxonomy, above).

Biology. Two independent reports indicate that *Saranaca* is a genus of sphingid parasitoids, though the records themselves are mediocre by our criteria. *Saranaca apicalis* is reported to attack *Sphinx kalmiae* J.E. Smith (the sole record appears originally in Schaffner & Griswold (1934)) and *S. elegans* to attack *Darapsa myron* (Hopper, 1939; we examined a specimen labelled as such [NMNH] that lacked host remains). The wasp exits from the host pupa; we have no data on which stage is attacked.

STIROJOPPA CAMERON, 1911

Camarota Kriechbaumer, 1898: 32. Type-species: *Camarota thoracica* Kriechbaumer. Preoccupied by *Camarota* Meigen, 1830.

Stirojoppa Cameron, 1911: 160. Type-species: *Stirojoppa violaceipennis* Cameron. Monotypic.

Camarotella Morley, 1917: 193. New name for *Camarota*. Synonymized by Townes & Townes (1966).

Hymenocamarota Cushman 1922: 1. New name for *Camarota*. Synonymized by Townes & Townes (1966).

Camarotana Strand, (1926) 1928: 52. New name for *Camarota*. Synonymized by Townes & Townes (1966).

Autapomorphies. Punctures of first lateral area sparse and scattered (#34–1); S2-3 divided, S3 partly divided, S4-5 entire (#55–1).

Species and distribution. There are two described species (Yu & Horstmann, 1997), and at least three undescribed species [AEIC], from Central and South America.

Biology. Unknown.

TMETOGASTER HOPPER, 1939

Conocalama subgenus *Tmetogaster* Hopper, 1939: 321. Type-species: *Trogus nubilipennis* Haldeman. Monotypic and original designation.

Autapomorphies. Clypeus uniformly thick (#6–0); pronotal flange low and with posterior face convex

(#18–1); juxtacoxal carina present (#22–0); metapleuron rugosopunctate, with long and transverse rugae (#36–1).

Species and distribution. There is one species, *Tmetogaster nubilipennis*, from eastern North America.

Biology. Several records establish *T. nubilipennis* as a larval–pupal parasitoid of Sphingidae. We have examined two specimens [NMNH] reared from *Paonias myops*. Hopper (1939) lists '*Ampelophaga* sp.', apparently an erroneous reference either to the species *ampelophaga* Walker (synonym *Eumorpha pandorus* (Hübner)) or to the genus *Ampeloeca* (*Darapsa*). Heinrich 1962 used the latter interpretation and supported the record with an observation of a female captured at *Vitis* plants infested with *D. myron* (Cramer) larvae. Hopper (1939) also provides an unverifiable record of *Sphecodina abbottii* (Swainson), another Vitaceae-feeding sphingid (Hodges, 1971). His reports of *T. nubilipennis* attacking *Pyrrharctia isabella* (Arctiidae) and *Papilio polyxenes* (Papilionidae) (Hopper, 1939) are also not corroborated by specimens or biological data and must be considered implausible.

TRICYPHUS KRIECHBAUMER, 1898

Tricyphus Kriechbaumer, 1898: 30. Type-species: *Tricyphus cuspidiger* Kriechbaumer. Designated by Viereck 1913).

Description. Flagellum of female lanceolate, with flagellomere 3 2.0–2.2× as long as wide; flagellum of male with tyloids present. Clypeus flat and wide, apicolateral margin forming an angle of approximately 40°, punctures evenly distributed, apical 0.3 not thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena flat and sharply receding in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum strongly convex, sometimes with planar surfaces and forming a more or less acute angle in lateral view; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Basal area and areola separated by anterior transverse carina. Areola reduced and completely filled-in, appearing as polished boss. Anterior transverse carina absent; posterior transverse carina complete; lateral longitudinal carinae present or absent; median longitudinal carinae absent basad anterior transverse carina, present or absent apicad anterior transverse carina. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleuron regularly punctate. Juxtacoxal carina present. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception apicad midpoint of posterior margin (vein 2/M 2.2–4.2× as long as vein 3/M).

MS1 in lateral view evenly curved with highest point at middle (Fig. 23), petiole cylindrical; sclerotized anterior portion of S1 0.5–0.6× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field absent, punctures fine and dense and without rugae. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with fine punctures separated by about 0.3× their diameter to contiguous. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma with T7-8 projecting well beyond apex of T6; amblypygous.

Autapomorphies. Juxtacoxal carina present (#22–0); MS1 in profile evenly curved with highest point at middle, petiole cylindrical (#42–2); sclerotized anterior portion of S1 0.5–0.6× as long as distance from posterior margin of anterior portion to apex of T1 (#43–1).

Species and distribution. There are three described species (*apicalis* Kriechbaumer, *cuspidiger* Kriechbaumer, and *nigriventris* Kriechbaumer) and two undescribed species [NHML]. They are found in Brazil, Paraguay, and Peru.

Comments. As interpreted by Townes (Townes & Townes 1966: 324) and Ward & Gauld (1987), the limits of *Tricyphus* were extremely vague and it was, in essence, a wastebasket group for New World sphingid parasitoids. The present study has radically redefined the genus and a new description is provided above. The North American species are placed in a new genus, *Saranaca*, and *Tricyphus respinozai* is moved to the new genus *Mokajoppa*.

The holotype of *cuspidiger* could not be located in the Naturhistorisches Museum Wien and is presumed lost. Morley (1915: 86) discussed a specimen in the Natural History Museum that he considered to be *cuspidiger*, although it is unlikely that he compared it with the type. It was collected by H.W. Bates 'on the Amazon and received in 1862' (Morley, *ibid.*). That specimen has been located and it is in the same genus as *apicalis* and *nigriventris*. In the interest of nomenclatural stability, it is here designated as the neotype of *cuspidiger*. The label data are as follows: '62.56' [handwritten, round label]; 'Amaz.' [handwritten, rectangular label]. *T. cuspidiger* may be

distinguished from other species in the genus by the following combination of characters: juxtacoxal carina distinct and complete; median longitudinal carinae of the propodeum obsolete posteriad anterior transverse carina; black mesoscutum (except for brownish-yellow of notaular areas) and scutellum; brownish-yellow hind coxa.

Vagaries of preservation have lead to some specimens appearing to have an undivided S2. Careful examination will show the sternite to be divided into two sections.

Biology. Unknown.

XANTHOSOMNIUM WAHL & SIME, GEN. N.

Type-species. **Xanthosomnium froesei sp. n.**

Description. Flagellum of female lanceolate, with flagellomere 3 about 1.8× as long as wide; flagellum of male unknown. Clypeus flat and wide, apicolateral margin forming an angle of approximately 40°, punctures evenly distributed, apical 0.3 thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth turned under dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena swollen in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about 0.5× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange low and with posterior face concave. Epicnemial carina dorsally complete. Scutellum moderately convex; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola completely filled-in, appearing as polished boss. Anterior transverse carina absent; posterior transverse carina weak but present; lateral longitudinal carinae weak but complete; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First lateral area with regularly distributed punctures; second lateral area weakly rugosopunctate. Metapleuron rugosopunctate. Juxtacoxal carina absent. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception apicad midpoint of posterior margin (vein 2/M about 2.1× as long as vein 3/M).

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 about 1.5× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carina absent, median field absent, punctures large and scattered. Ventral margin of T2 simple. T2-4 without longitudinal rugae. T2-4 evenly convex, with normal punctures separated by 0.5–1.0x their diameter. T2-5 not basally constricted and without dorsolateral ridges. S2 divided, S3-5 entire. Apex of female metasoma with T7-8 projecting well beyond apex of T6; amblypygous

Autapomorphies. Apical 0.3 of clypeus thinned (#6–1); ventral mandibular tooth turned under (#12–1); basal area and areola confluent, anterior transverse carina absent (#26–1); postpetiole of MS1 without median field (#47–1).

Etymology. The genus is named after the musical group Tangerine Dream, the choice of discriminating ichneumonologists. From the Greek *xanthos*, yellow or yellowish-red (the closest equivalent to 'tangerine' in a classical language) and the Latin *somnium*, dream. The gender is neuter.

Species and distribution. There is one species, *Xanthosomnium froesei*, found in Costa Rica.

Biology. The holotype of *X. froesei* was reared as a larval-pupal parasitoid of the sphingid *Cautethia spuria* (see holotype data, above; '98-SRNP-3514' [AEIC]). The host was collected as a penultimate instar feeding on an unidentified species of *Chiococca* (Rubiaceae). The locality is at the upper elevational limit of lowland dry forest below Cerro Pedregal, in Area de Conservación Guanacaste, Costa Rica. Although over 500 Sphingidae of 17 species have been reared within one kilometer of this site, no other specimens of *X. froesei* have been encountered (D. Janzen, pers. comm.).

XANTHOSOMNIUM FROESEI WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Callajoppa* genus-group by the characters given above in the generic description of *Xanthosomnium*, and by the uniformly brownish red colouration and light brown wings.

Female. Structure. As in generic description. *Colour.* Uniformly brownish-red except for dark brown of flagellomeres 14–42, and fuscous gastrocoelus. Wings uniformly light brown. *Length.* 20.2 mm; fore wing 15.6 mm.

Male. Unknown.

Type material. Holotype ♀, COSTA RICA: *Guanacaste*, Area de Conservación Guanacaste, Sector Cacao, Cerro Pedregal, 1000 m, *ex Cautethia spuria* (host larva collected 2.ix.1998, wasp emerged from host pupa 17.x.1998), '98-SRNP-3514' (*Pereira*) [AEIC]. Condition of holotype: intact except right antenna broken beyond flagellomere 12 (flagellomeres 13–37 mounted on point below specimen).

Etymology. Named after Edgar Froese, the founder and continuity behind Tangerine Dream.

YEPPOONA GAULD, 1984

Yeppoona Gauld, 1984: 220. Type-species: *Yeppoona grandis* Gauld. Original designation.

Autapomorphies. Cell 1 + 2Rs of fore wing anteriorly truncate (#39–0); postpetiole of T1 without distinct median field (#47–1).

Species and distribution. There is one described species, and five undescribed species [AEIC], all found in northeastern Australia and New Guinea.

Comments. The female specimen used by Gauld (1984) for his generic description could not be located and so all the specimens at hand were male. Consequently, the amblypygous hypopygium could not be entered into the data matrix.

Biology. Unknown.

(THE *TROGUS* SUBGROUP)

DAGGOO WAHL & SIME, GEN. N.

Type-species. **Daggoo philoctetes sp. n.**

Description. Flagellum of female bristle-shaped, with flagellomere 3 3.1× as long as wide; flagellum of male without tyloids. Clypeus narrow, basally with two lateral concavities, median concavity just above apical margin, apicolateral margin forming a rounded angle of approximately 40°, punctures evenly distributed, apical 0.3 not thinned, apical margin straight and without median projection. Mandible long and evenly tapered to apex, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median paired ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena flat and receding in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange high and with posterior face flat. Epicnemial carina absent. Scutellum conical; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola not distinguishable, only anterior transverse carina appears to be present. Anterior transverse carina complete, median section swollen; posterior transverse carina absent; lateral longitudinal carinae absent; median longitudinal carinae present, sections basad anterior transverse carina separated by low carina. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleural sculpture regularly punctate. Juxtacoxal carina absent. Propodeal lateral profile steeply sloping. Scopa

absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception at midpoint of posterior margin.

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 1.2× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field absent, regularly punctate. Ventral margin of T2 simple. T2-4 with weak longitudinal rugae over entire surface of each tergite. T2-4 laterally weakly flattened, with normal punctures separated by about 0.3× their diameter to contiguous. T2-5 basally constricted and without dorsolateral ridges. S2-4 divided, S5 entire. Apex of female metasoma with T6-8 barely projecting beyond apex of T5; amblypygous.

Autapomorphies. Anterior transverse carina of propodeum medially swollen (#29–1); cell 1 + 2Rs of fore wing with vein 2m-cu interception apicad midpoint of posterior margin (#41–1); postpetiole of T1 without distinct median field (#47–1).

Etymology. The genus is named after one of the harpooners in Melville's novel *Moby Dick*.

Species and distribution. There is one described species, and one undescribed species [AEIC], both found in El Salvador.

Biology. *Daggoo philoctetes* has been reared from *Parides photinus* (Doubleday) (Papilionidae: Troidini) (El Salvador: Ahuachapán [NMNH]; see holotype data, below), and the undescribed species has been reared from *Parides montezuma* (Westwood) (El Salvador, Aug. 1995 [AEIC]). Both wasps emerged from the pupae; no other biological data are available. Given the toxicity and chemical uniqueness of the Troidini (*Aristolochia*-feeding Papilionidae), it is likely that *Daggoo* is restricted to this group, if not to *Parides* alone (Miller & Feeny 1989; Gauld & Gaston 1994). The hosts reported here feed on a variety of *Aristolochia* species (Tyler *et al.* 1994).

DAGGOO PHILOCTETES WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Trogus* subgroup by the characters given above in the generic description of *Daggoo*, and from the other undescribed species in the genus by the following combination of characters: petiole with distinct flattened sides, apical 0.5 punctate (vs. petiole cylindrical and with apical 0.7 punctate); dorsal 0.4 of pronotum, mesoscutum, and central section of dorsal 0.5 of mesepisternum, fuscous (vs. size of dark areas reduced, and colour dark to light brown).

Female. Structure. Petiole with distinct flattened sides, apical 0.5 punctate. Other characters as in

generic description. *Colour*. Overall colour whitish yellow. Following areas fuscous: median 0.5 of supra-antennal area, vertex, dorsal 0.3 of gena, dorsal 0.4 of lateral area of pronotum, central area of dorsal 0.5 of mesepisternum (excluding epicnemium), hind femur, apical 0.6 of hind tibia, hind tarsus, T5-7, and S5-6. Antenna dark brown except for except for light brown of ventral surface. Fore and middle legs beyond trochantellus brownish-red except for brown of tarsomeres 2–5. Wings yellow with brown banding as in Fig. 33. *Length*. 17.9 mm; fore wing 16.3 mm.
Male. Unknown.
Type material. Holotype ♀, EL SALVADOR: *Ahuachapán*, El Corozo, El Imposible, 9.vii.1987, '#10 *ex Parides photinus* at 500 m' (*Serrano*) [NMNH]. Condition of holotype: intact.
Etymology. Named after Philoctetes, the Greek archer who slew Paris.

HOLCOJOPPA CAMERON, 1902B

Holcojoppa Cameron 1902b: 180. Type-species: (*Holcojoppa flavipennis* Cameron) = *Psilomastax orientalis* Kriechbaumer. Monotypic.
Pedinojoppa Heinrich 1960: 109. Type-species: (*Pedinopelte orientalis* Szépligeti) = *Holcojoppa pyrina* Townes, Townes, & Gupta. Original designation. Synonymized by Townes *et al.* (1961).
Autapomorphies. Supra-antennal area medially with two low vertical ridges (#13–1); vertex with posterior section 1.0–1.3× as long as ocellar triangle, strongly convex (#14–1); epicnemial carina dorsally incomplete (#19–1).
Species and distribution. There are nine described species in the genus, distributed from eastern Russia south to Java, Sumatra, and the Celebes. An undescribed species (*Holcojoppa* sp. 2) is found in El Salvador [AEIC].
Comments. As discussed above (see Taxonomy), four species have been moved from *Trogus* to *Holcojoppa*: *bicolor* (Radoszkowski), *heinrichi* (Uchida), *mactator* (Tosquinet), and *tricephalus* (Uchida).
Biology. *Holcojoppa* species are larval–pupal parasitoids of Papilionidae. Species for which reliable records exist appear all but one to specialize on Rutaceae-feeding *Papilio* species: *H. coelopyga* (Morley) on *Papilio helenus* L. (Morley 1915), *H. formosana* (Matsumura) on *P. polytes* L. (Konishi, pers. comm.), *H. heinrichi* (Uchida) on *P. memnon* L. and *P. protenor* Cramer (Mell & Heinrich 1931), *H. pyrina* (Townes, Townes, & Gupta) on *P. demolion* Cramer (Waterston 1926) and *P. polytes* (Bascombe *et al.* 1999), and *H. tricephalus* (Uchida) on *P. bianor* Cramer and *P. xuthus* (Mell & Heinrich 1931). The exception is *H. mactator*, which has been reared from *Graphium sarpedon* (L.) feeding on *Cinnamonum* (Lauraceae)

(Iwata 1961) and possibly from the umbellifer-feeder *P. machaon* (Uchida 1924, 1926; 1955), in addition to the Rutaceae-feeders *P. xuthus* (Watanabe 1979), *P. maackii* Ménétriés (Tosquinet, 1889), and *P. bianor* (Bischoff, 1915). *Holcojoppa mactator* is particularly well known from ecological studies as a common parasitoid of *P. xuthus*, often emerging from 30 to 50% of field-reared pupae (Tsubaki, 1973; Watanabe, 1979, 1981; Hirose *et al.,* 1980). It oviposits into and has been successfully reared from all instars of this host (Omata, 1984).

MACROJOPPA KRIECHBAUMER, 1898

Macrojoppa Kriechbaumer, 1898: 21. Type-species: *Trogus blandita* Cresson. Designated by Ashmead (1900b).
Cryptopyge Kriechbaumer, 1898: 21. Type-species: *Joppa picta* Guérin. Designated by Ashmead (1900b). **Syn. n.**
Ischnopus Kriechbaumer, 1898: 25. Type species: (*Ischnopus longiceps* Kriechbaumer) = *Ischnopus rufus* Brullé. Designated by Ashmead (1900b). Preoccupied by *Ischnopus* Amyot, 1846 and *Ischnopus* Faust, 1894. **Syn. n.**
Cryptopyga Schulz, 1906: 130. Emendation of *Cryptopyge*.
Araeoscelis Schulz, (1909) 1911: 38. Replacement name for *Ischnopus* Kriechbaumer 1898. **Syn. n.**
Areoscelis of authors. *Lapsus*.
Aglaojoppidea Viereck, 1913: 368. Type-species: *Trogus fascipennis* Cresson. Original designation. Synonymized with *Macrojoppa* by Hopper (1939).
*Autapomorphies*. Clypeal punctures sparse or absent (#10–1); supra-antennal area medially with two low vertical ridges (#13–1); juxtacoxal carina absent (#22–1); anterior transverse carina of propodeum swollen medially (#29–1); lateral longitudinal carinae absent (#31–1); first lateral area with punctures scattered or absent (#34–1); petiole of MS1 basally with dorsal bulge (#44–1); S2-5 divided (#55–5); apex of female metasoma with T7-8 barely projecting beyond apex of T6 (#56–1).
Species and distribution. With the addition of *Araeoscelis* and *Cryptopyge*, and the removal of *latipennis* Cresson, *Macrojoppa* has 46 described species distributed from the United States (southern Texas) to Argentina (Yu & Horstmann, 1997). There are numerous undescribed species.
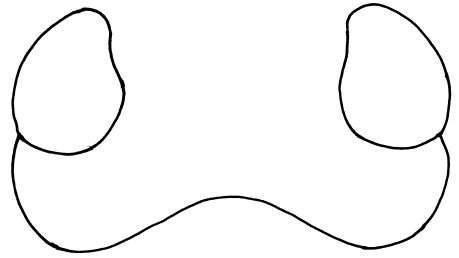   Morley (1915: 55) recorded *Macrojoppa subbifasciata* Szépligeti (as *Ischnopus subfasciatus*) from 'Araucania' in southern Chile, a locale that cannot be located on gazetteers. This record is suspect for several reasons. Extensive collections from Chile (AEIC, CCCP, CNCI) have not yielded specimens of the *rufa* species-group (=*Araeoscelis*). Other than the
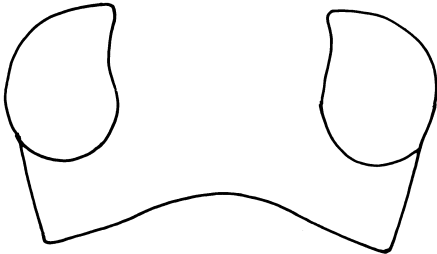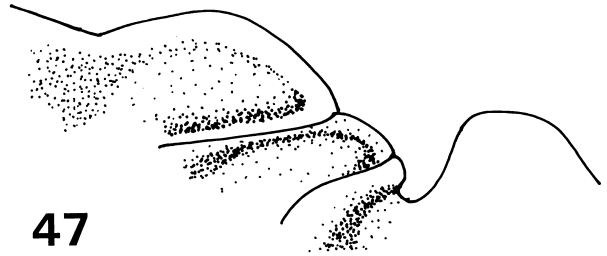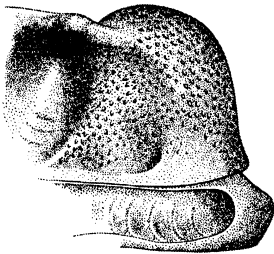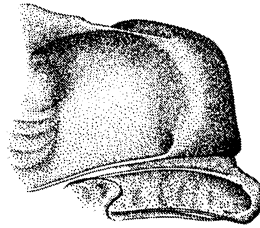
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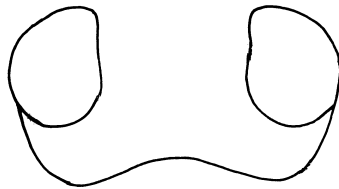
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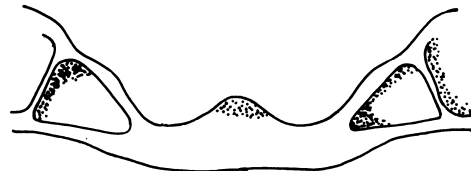**47**
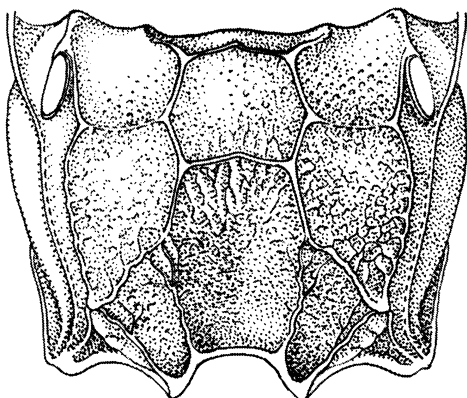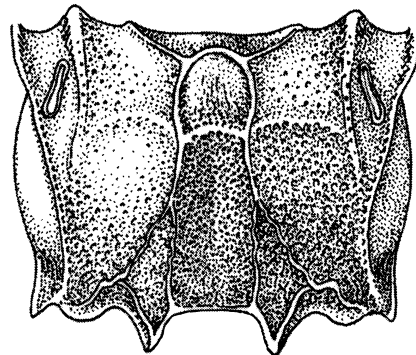

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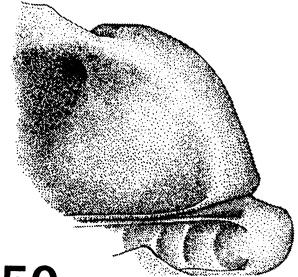
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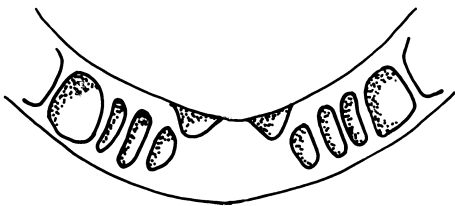
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Figures 43–54. (43) *Holcojoppa* sp. 2, mandible. (44–46) Dorsal view of heads: (44) *Saranaca elegans*; (45) *Conocalama brullei*; (46) *Holojoppa grandis* Szépligeti. (47–50) Lateral views of scutella: (47) **Lagavula gauldi**; (48) *Conocalama copei* (Cresson); (49) *Catadelphus semiruber* Hopper; (50) *Catadelphops nasutus*. (51, 52) Dorsal view of metanota: (51) *Macrojoppa bogatensis* Kriechbaumer; (52) *Macrojoppa rufa*. (53, 54) Dorsal view of propodea: (53) *Cratichneumon luteiventris* (Gravenhorst); (54) *Protichneumon grandis* (Brullé).

◄——

Chilean record, *M. subbifasciata* has been collected from Bolivia, Chile, French Guiana, and Peru (Townes & Townes, 1966); ichneumonid distributions do not, in general, encompass both the Neantarctic (Porter, 1991) and Neotropical regions.

Comments. As discussed above (see Taxonomy), *Araeoscelis* and *Cryptopyge* are synonymized with *Macrojoppa*. Since these are morphologically and biologically distinct clades within *Macrojoppa*, the species formerly placed in *Araeoscelis* should be referred to as the *rufa* species-group and the species formerly placed in *Cryptopyge* be referred to as the *picta* species-group.

Biology. Apart from the *rufa* species-group, host records for *Macrojoppa* indicate parasitism of Nymphalidae. Three specimens with associated host remains have been reared from subfamily Nymphalinae: *M. inclyta* (Cresson) from *Junonia evarete* (Cramer) (Costa Rica: *Guanacaste*, Parque Santa Rosa, 20 June 1978 (*DeVries*) [NHML]), *M. blandita* (Cresson) from an unidentified nymphaline pupa (no label data [CUIC]), and an undescribed species from *Colubura dirce* (L.) (Venezuela: Yaracuy [AEIC]). Yet another undescribed species has been reared from an undetermined nymphalid in Costa Rica (Costa Rica: *Guanacaste*, Area de Conservación Guanacaste, Sector Santa Rosa, Sendero Natural, Lambert coord. 313100–359900, 250 m (host larva collected 5.vi.1999, wasp emerged from host pupa 17.vi.1999) '99-SRNP-8799' [JHIC]). One species (*M. pulchripennis* (Smith) of the *picta* species-group) has been reared from a host in subfamily Charaxinae, *Siderone marthesia* (Cramer) (El Salvador: *Ahuachapán*, El Imposible; 4 Aug. 1986, F. Serrano [NMNH]). All wasps emerged from the host pupae; no other biological data are available.

The biology of the *rufa* species-group is better known. Members of this clade are larval-pupal parasitoids apparently specializing on the papilionid *Battus polydamas* (L.). Published reports are available for *M. rufa* (Schrottky, 1909; Tyler *et al.,* 1994), and we have new records for *M. pulcherrima* (Ashmead) in Costa Rica (23 specimens [JHIC]) and an undescribed species (3 specimens from El Salvador (*Serrano*) [NMNH]). *Battus polydamas* is notable as the most widespread and most polyphagous of the neotropical troidine papilionids (Gonzales & Rodgers, 1996), and the parasitoids have been reared from caterpillars feeding on a variety of *Aristolochia* species. They attack larvae at least as young as third instar (Tyler *et al.,* 1994). Behavioural and field observations indicate that the wasps do not attack *Parides* species or even other *Battus* species feeding on some of the same food plants (D. Janzen, pers. comm. for *M. pulcherrima*; A. Morais, pers. comm. for *M. rufa*, Brazil).

METALLICHNEUMON WAHL & SIME, GEN. N.

Type-species. **Metallichneumon neurospastarchus sp. n.**

Description. Flagellum of female lanceolate, with flagellomere 3 2.7× as long as wide; flagellum of male unknown. Clypeus narrow, basally with two lateral concavities, median concavity just above apical margin, apicolateral margin forming a rounded angle of approximately 40°, punctures evenly distributed, apical 0.3 not thinned, apical margin concave and without median projection. Mandible short and quadrate, ventral tooth in same plane as dorsal tooth. Supra-antennal area without median ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena flat and receding in dorsal profile. Juncture of hypostomal and occipital carinae separated from mandible by about 0.6× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange high and with posterior face flat. Epicnemial carina dorsally complete. Scutellum conical; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola not distinguishable, only anterior transverse carina appears to be present. Anterior transverse carina complete, median section swollen; posterior transverse carina absent; lateral longitudinal carinae complete; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First lateral area with regularly distributed punctures; second lateral area rugosopunctate. Metapleuron regularly punctate. Juxtacoxal carina present. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing petiolate, vein 2/Rs < 3r-m, vein 2m-cu interception apicad midpoint of posterior margin (vein 2/M about 2.5× as long as vein 3/M).

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 1.2× as long as distance from posterior margin of anterior portion to apex of T1; petiole, basally without dorsal or lateral bulges; postpetiole without basal convexity, median longitudinal carinae absent, median field present, rugosopunctate. Ventral margin of T2 denticulate. T2-4 with weak longitudinal rugae extending down midline of each tergite. T2-4 laterally weakly flattened, with normal punctures separated by about 0.2× their diameter. T2-5 basally constricted, T3-4 without dorsolateral ridges. S2-4 divided, S5 entire. Apex of female metasoma with T7-8 projecting well beyond apex of T6; oxypygous.

Etymology. The genus is named after the musical group Metallica. The coupling of a descriptive word with the stem '-ichneumon' is a common form of generic name in the Ichneumoninae. The gender is masculine.

Autapomorphies. Flagellomere 3 of female 2.7× as long as wide (#2–0); apical margin of clypeus concave (#4–1); cell 1 + 2Rs of fore wing with vein 2 m-cu interception apicad midpoint of posterior margin (#41–1); T2-4 with weak longitudinal rugae extending down midline of each tergite (#50–1).

Species and distribution. There is one species, *Metallichneumon neurospastarchus*, found in Peru.

Biology. Unknown.

METALLICHNEUMON NEUROSPASTARCHUS WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Trogus* subgroup by the characters given above in the generic description of *Metallichneumon*.

Female. Structure. As in generic description. *Colour.* Head and mesosoma black with metallic purple tint, except for brown of apical 0.5 of flagellum, whitish yellow of lateral 0.3 of supraclypeal area. Wings uniformly dark brown with metallic purple tint. *Length.* 22.1 mm; fore wing 19.8 mm.

Male. Unknown.

Type material. Holotype ♀, PERU: 'Quiroz, Rio Paucartambo' [AEIC]. Condition of holotype: intact except left antenna broken beyond flagellomere 41, tarsomere 5 of right middle leg broken off (mounted on label), and tarsomere 5 of left hind leg missing.

Etymology. From the Greek *neurospasta*, puppet, and *archos*, ruler, hence 'ruler of puppets: a tribute to the Metallica album *Master of Puppets* and a comment upon the weak and mindless nature of lepidopterous larvae.

Comment. There are several towns by the name of Quiroz in Peru, but none is in the vicinity of the Rio Paucartambo (which is in the Department of Cuzco).

The type locality must remain a mystery for the present.

NEOFACYDES HEINRICH, 1960

Neofacydes Heinrich, 1960: 107. Type-species: *Neofacydes sinensis* Heinrich. Original designation.

Autapomorphies. Juncture of hypostomal and occipital carinae separated from mandibular base by about 0.5× basal mandibular width; cell 1 + 2Rs of fore wing anteriorly pointed (#39–1); apex of female metasoma with T7-8 barely projecting beyond apex of T6 (#56–1).

Species and distribution. After the removal of *flavibasalis* Uchida to *Queequeg*, there are eight described species (Yu & Horstmann, 1997) and at least four undescribed species [AEIC]. They are distributed from north-eastern India to New Guinea, and as far north as Japan.

Biology. Host information is available only for the holotype, which emerged from *Oxyambulyx sericeipennis* Butler (Sphingidae) reared on Myricaceae in southern China (Mell & Heinrich, 1931). We consider this report reliable and have treated *Neofacydes* as a genus of sphingid parasitoids. This account indicates that the host was attacked as a larva, but more exact information on stage attacked is not available as the host was collected shortly before pupation. Although *Neofacydes* species are oxypygous, which suggests that they should oviposit into pupae (Hinz, 1983; but see Biology above), *O. sericeipennis* pupates in a tunnel in the ground (Mell, 1922) and is unlikely to be accessible to a pupal parasitoid.

PEDINOPELTE KRIECHBAUMER, 1898

Pedinopelte Kriechbaumer, 1898: 26. Type-species: (*Ichneumon gravenhorstii* Guérin) = *Ichneumon gravenstii* Guérin. Monotypic.

Autapomorphies. Apical margin of clypeus concave (#4–1); postpetiole of T1 with basal convexity (#45–1); median longitudinal carinae of T1 apically incomplete (#46–1).

Species and distribution. With the addition of *latipennis* (Cresson), there are 3 described species (Yu & Horstmann, 1997) and at least two undescribed species [AEIC, JHIC, NHML]. They are found in Central and South America.

Comments. P. latipennis was formerly placed in *Macrojoppa* (see Taxonomy, above).

Biology. Published host records for *P. gravenstii* (Guerin) are vague: neither the Brazilian reports from '*Automeris* sp.' (Saturniidae) and *Papilio anchisiades* Esper (Sauer, 1946) nor the report from *Papilio thoas* L. (or *P. lycophron* Hübner; identification was uncertain) in Argentina (Schrottky, 1910) can be traced to

any insect remains or contain supporting natural history information. However, on the more convincing evidence of several series of reared specimens, we consider *Pedinopelte* to be a genus of larval-pupal parasitoids of *Papilio*. One series consists of 18 specimens of an undescribed species reared from *Papilio anchisiades* in Costa Rica [AEIC, JHIC]. A second series consists of five specimens of another undescribed species reared from *P. anchisiades* in Costa Rica ('99-CALI-480') [JHIC]; the host larvae were collected on *Xanthophylus* sp. (*Rutaceae*). The host larvae were collected as penultimate or final instars on *Xanthoxylum setulosum* P. Wilson (Rutaceae). The third series establishes *P. latipennis* as a parasitoid of Central American *Papilio* species feeding on Piperaceae as well as Rutaceae. It includes five specimens reared from *Papilio thoas*; three of the host larvae were collected on *Piper marginatum* Jacquin, one on *Piper pseudofuligineum* C.DC., and one on *Piper peltatum* L. ('81-SRNP-1046A', '81-SRNP-1320', '82-SRNP-742', '93-SRNP-7857', '95-SRNP-11365', respectively [AEIC, JHIC]). Another four specimens were reared from the Rutaceae-feeder *Papilio cresphontes* Cramer; three of these hosts were collected on *Citrus limetta* (introduced) and one on *Angostura nicaraguiensis* Standl. & Williams ('93-SRNP-2253', '93-SRNP-2283', '96-SRNP-3057', '96-SRNP-3056' [AEIC, JHIC]). All *P. latipennis* specimens were reared from hosts collected as final and penultimate instars in Area de Conservación Guanacaste, Costa Rica (D. Janzen, pers. comm.).

In addition, two specimens of another undescribed *Pedinopelte* species have been reared from *Papilio caiguanabus* Poey (Cuba, 1932; M.E. Fontaine [NHML]), a rare Cuban species that is suspected to feed on Rutaceae, although no certain food-plant records have been published (Tyler *et al.,* 1994).

PSILOMASTAX TISCHBEIN, 1868

Psilomastax Tischbein, 1868: 255. Type-species: *Psilomastax pyramidalis* Tischbein. Monotypic.
Cercodinotomus Uchida, 1940: 9. Type-species: (*Psilomastax pictus* Kriechbaumer) = *Psilomastax pyramidalis* Tischbein. Original designation. Synonymized by Townes (1957).
Autapomorphies. Epicnemial carina present only on mesothoracic venter (#19–2); S2-5 divided (#55–5).
Species and distribution. There is one described species, *Psilomastax pyramidalis*, distributed from western Europe to Japan.
Biology. Reports of *P. pyramidalis* attacking *Apatura iris* (L.) date back over 100 years (e.g. Tischbein, 1868). It is a larval–pupal parasitoid, attacking all instars (Mell & Heinrich, 1931), and specializes on apaturine nymphalids throughout its range. In the western

Palearctic, *P. pyrimidalis* is reported almost exclusively as a parasitoid of *A. iris*. Although three species of *Apatura* occur in this region, we have just one record from *A. ilia* (Denis & Schiffermüller) (National Museum of Scotland; M. Shaw pers. comm.). This apparent preference for a single host species could be an artifact of the rarity of rearings: for example, from over 1300 *A. iris* collected in the field and reared to pupation, Friedrich (1977) reared just one *P. pyrimidalis*. In the east, *P. pyrimidalis* has been reliably reported as a parasitoid of *Hestina assimilis* (L.) (Mell & Heinrich, 1931) and *H. japonica* (C & R Felder) (Iwata, 1961).

Morley (1915) reports viewing a specimen labelled as a parasitoid of *Psilogramma* (*Dicranura*) *increta* (Sphingidae) in Taiwan. Weighing this single report against the number of apaturine records, we consider it unlikely that *Psilomastax* routinely, if ever, parasitizes Sphingidae.

QUEEQUEG WAHL & SIME, GEN. N.

Type-species. Gathetus flavibasalis Uchida
Description. Flagellum of female lanceolate, with flagellomere 3 3.0–3.8× as long as wide; flagellum of male with tyloids present. Clypeus narrow, basally with two lateral concavities, median concavity just above apical margin, apicolateral margin forming a rounded angle of approximately 40°, punctures ranging from evenly to sparsely distributed, apical 0.3 not thinned, apical margin straight or concave and without median projection. Mandible short and quadrate, ventral tooth in same plane as dorsal tooth. Supra-antennal area simple or with two denticles. Vertex with posterior section about 1.5× as long as ocellar triangle, steeply sloping to occipital carina. Gena flat and receding in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by 0.5–0.9× basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange high and with posterior face flat. Epicnemial carina incomplete dorsally or present only on mesothoracic venter. Scutellum weakly conical; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola not distinguishable, only anterior transverse carina appears to be present. Anterior transverse carina complete or absent, median section not swollen when present; posterior transverse carina absent; lateral longitudinal carinae complete or absent; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First lateral area with punctures regularly

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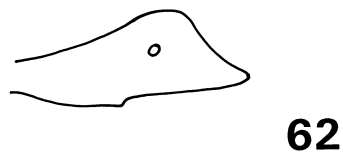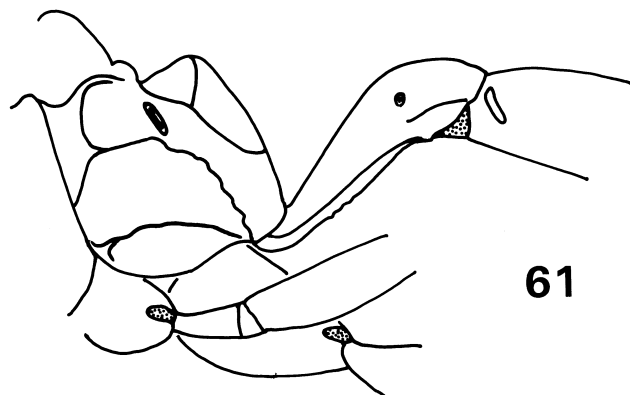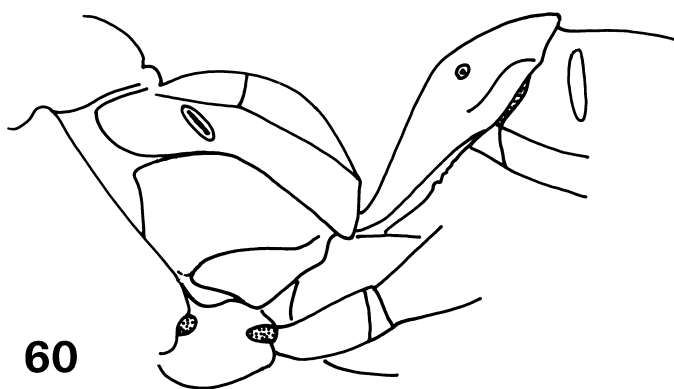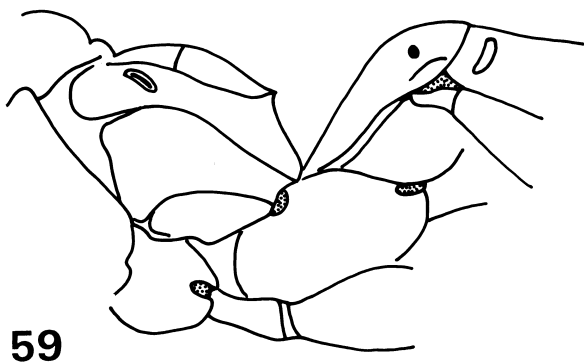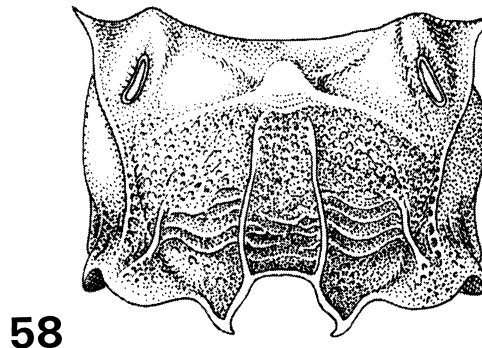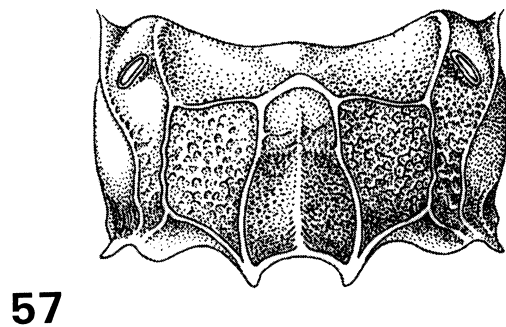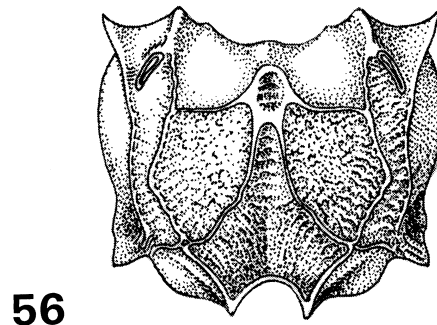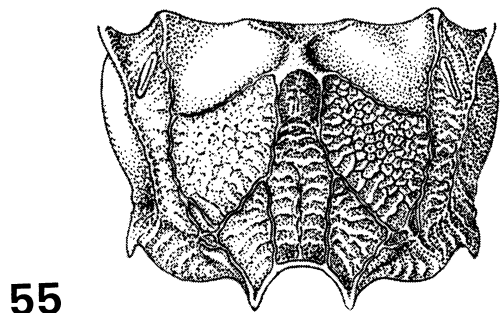
Figures 55–62. (55–58) Dorsal view of metanota: (55) *Gnamptopelta obsidianator* (Brullé); (56) *Catadelphus atrox*; (57) *Trogus lapidator*; (58) *Macrojoppa concinna*. (59–61) Lateral view of propodea and MS1: (59) *Cratichneumon* sp.; (60) *Coelichneumon* sp.; (61) *Gnamptopelta obsidianator*. (62) **Tashtego janzeni sp. n.**, lateral view of MS1.

distributed or absent; second lateral area rugosopunctate. Metapleuron with few (<10) punctures or rugosopunctate. Juxtacoxal carina present or absent. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing truncate, pointed or petiolate, vein 2/Rs ≤ 3r-m, vein 2m-cu interception at midpoint of posterior margin.

MS1 in lateral view with petiole flattened, postpetiole convex; sclerotized anterior portion of S1 0.8–1.3× as long as distance from posterior margin of anterior portion to apex of T1; petiole basally without dorsal or lateral bulges; postpetiole with or without basal convexity, median longitudinal carinae absent, median field present, rugosopunctate or with scattered punctures. Ventral margin of T2 simple. T2-4 with strong longitudinal rugae over entire surface of each tergite. T2-4 laterally strongly flattened, either mostly impunctate or with normal punctures separated by 0.3–1.0× their diameter to contiguous. T2-5 basally constricted, T3-4 with strong dorsolateral ridges that may or may not project posterodorsally. S2-4 divided, S5 entire. Apex of female metasoma with T6-8 barely projecting beyond apex of T5; oxypygous.
Autapomorphies. Vertex with posterior section about 1.5× as long as ocellar triangle, steeply sloping to occipital carina (#14–2); T3-4 with dorsolateral ridges, ridges with some degree of posterior development (#54–3); apex of female metasoma with T6-8 barely projecting beyond apex of T5.
Etymology. The genus is named after one of the harpooners in Melville's novel *Moby Dick*.

Species and distribution. *Q. flavibasalis* is found in Taiwan. Two undescribed species are found in southern China (Hainan Dao) [AEIC] and Malaysia [AEIC].
Comments. *Q. flavibasalis* was formerly placed in *Neofacydes* (see Taxonomy, above).
Biology. Unknown.

TASHTEGO WAHL & SIME, GEN. N.

Type-species. **Tashtego janzeni sp. n.**
Description. Flagellum of female lanceolate, with flagellomere 3 3.8× as long as wide; flagellum of male with tyloids present. Clypeus narrow, basally with two lateral concavities, median concavity just above apical margin, apicolateral margin forming a rounded angle of approximately 40°, punctures sparse, apical 0.3 not thinned, apical margin concave and without median projection. Mandible short and quadrate, ventral tooth in same plane as dorsal tooth. Supra-antennal

area without median ridges or denticles. Vertex with posterior section about as long as ocellar triangle, gently sloping to occipital carina. Gena flat and receding in dorsal view. Juncture of hypostomal and occipital carinae separated from mandible by about basal mandibular width. Occipital carina with ventral region above mandible not produced as a low flange.

Pronotal flange high and with posterior face flat. Epicnemial carina present only on mesothoracic venter. Scutellum strongly convex with planar surfaces and forming a more or less acute angle in lateral view; lateral carinae absent. Central convexity of metanotum not widened and lateral depressions not reduced. Base of propodeum rising steeply and abruptly. Areola not distinguishable, only anterior transverse carina appears to be present. Anterior transverse carina complete or absent, median section not swollen when present; posterior transverse carina absent; lateral longitudinal carinae absent; median longitudinal carinae absent basad anterior transverse carina, present apicad anterior transverse carina. First lateral area without punctures; second lateral area rugosopunctate. Metapleuron with few (<10) punctures. Juxtacoxal carina absent. Propodeal lateral profile steeply sloping. Scopa absent. Cell 1 + 2Rs of fore wing truncate, vein 2/Rs ≤ 3r-m, vein 2m-cu interception at midpoint of posterior margin.

MS1 in lateral view as in Fig. 62; sclerotized anterior portion of S1 about as long as distance from posterior margin of anterior portion to apex of T1; petiole, basally without dorsal or lateral bulges; postpetiole with basal convexity, median longitudinal carinae present, median field present, impunctate and with four strong longitudinal rugae. Ventral margin of T2 simple (area immediately above margin strongly and coarsely punctate, superficially resembling denticulate condition). T2-4 impunctate with relatively few (*c*. 20) strong longitudinal rugae over entire surface of each tergite. T2-4 laterally strongly flattened. T2-5 basally constricted, T3-4 with strong dorsolateral ridges. S2-4 divided, S5 entire. Apex of female with T7-8 strongly projecting beyond apex of T6; oxypygous.
Autapomorphies. Apical margin of clypeus concave (#4–1); clypeal punctures sparse (#10–1); scutellum strongly convex with planar surfaces and forming a more or less acute angle in lateral view (#20–1); juxtacoxal carina absent (#22–1); anterior transverse carina of propodeum absent (#28–1); punctures of first lateral area absent (#34–1); cell 1 + 2Rs of fore

wing anteriorly truncate (#39–0) and with veins 2/Rs and 3r-m of equal length (#40–0); postpetiole of T1 with basal convexity (#45–1); median longitudinal carina of T1 complete and extending to apex (#46–0); postpetiole of T1 impunctate (#48–2) and with four strong longitudinal rugae; T2-4 with dorsolateral ridges (#54–1).

Etymology. The genus is named after one of the harpooners in Melville's novel *Moby Dick*.

Species and distribution. T. janzeni is found in Costa Rica.

Biology. Unknown.

TASHTEGO JANZENI WAHL & SIME, SP. N.

Diagnosis. This species can be distinguished from other members of the *Trogus* subgroup by the characters given above in the generic description of *Tashtego.*
Female. Structure. As in generic description. *Colour.* Overall colour light yellowish brown, with metapleuron and metasoma shading to whitish yellow. Following areas black/fuscous: head except for yellow of gena adjacent to mandibular base, basal 0.5 of mandible, maxillus, and labium; median 0.3 of lateral area of pronotum; mesoscutum, ranging from basal 0.3 of median lobe to entire structure except for small squarish area at apex and small patches adjacent to tegula; mesopleuron, ranging from only hypoepimeron and areas below subalar ridge to dorsal 0.3; basal 0.7 of scutellum; metanotum except for median convexity (it can also be entirely yellowish brown); metapostnotum; fore and middle legs: apical 0.7 of posterior surface of femur, posterior surface of tibia, and tarsus; hind leg: apical 0.4 of femur, tibia, and tarsus; T5-7; S5-6. Wings uniformly light fuscous.
Length. 12.2–13.4 mm (13.0 mm); fore wing 10.7–11.8 mm (11.8).
Male. Structure. As in female. *Colour.* Similar to female except for greater extent of mesosomal black/fuscous markings in some specimens: pronotum with median 0.3 and dorsal 0.5 of lateral area, dorsal 0.3 of mesopleuron, scutellum, metanotum (except for central convexity), metapostnotum, and propodeum (excluding metapleuron). *Length.* 10.9–12.6 mm; fore wing 9.5–11.5 mm.
Type material. Holotype ♀, COSTA RICA: *Cartago,* Area de Conservación Amistad, Parque Nacional Amistad, Quebrada Segunda, Lambert coord. 194000–559800, 1150 m, vi.1994, 'INBIO CRI001907226' (*Mora*) [INBC]. Condition of holotype: intact. Paratypes: COSTA RICA: 1 ♂, same data as holotype except collected vii.1994, 'INBIO CRI001885494' [INBC]; 1 ♀, *Cartago,* Parque Nacional Tapanti, Quebrada Segunda, Lambert coord. 194000–560000, 1250 m, iv.1992, 'INBIO CRI000459497' (*Vargas*) [AEIC]; 1 ♀, *Cartago,* Parque

Nacional Tapanti, Quebrada Segunda, Lambert coord. 194000–560000, 1150 m, v.1994, 'INBIO CRI001819956' (*Vargas*) [INBC]; 1 ♂, *Puntarenas,* Area de Conservación Amistad, Buenos Aires, Estación Altamira, Lambert coord. 331700–572100, 1500 m, 30.viii.1992, 'INBIO CRI001977521' (*Delgado*) [INBC]; 1 ♂, *Puntarenas,* Estación Pittier, Lambert coord. 330900–577400, 1670 m, 26.i.1995, 'INBIO CRI002209324' (*Chinchilla*) [AEIC]; 1 ♀, *Puntarenas,* Coto Brus, Estación Las Alturas, Lambert coord. 322500–591300, 1500 m, xi.1991, 'INBIO CRI000400402' (*Zumbado*) [INBC]; 1 ♀, *Puntarenas,* Monteverde, San Luis, Lambert coord. 250850–449250, 1040 m, viii.1992, 'INBIO CRI000754704' (*Fuentes*) [AEIC]. ECUADOR: 1 ♀, 'Orte.' (possibly Ortega = Hacienda Quillán, 1°14′S, 78°32′W), 'Rio Zuñag' (Rio Zuñac, 1°25′S, 78°11′W), 9.x.1968 (*Peña*) [AEIC].

Etymology. It is a great pleasure to name this species after Daniel Janzen, in honor of a lifetime of research on the Neotropical biota.

TROGUS PANZER, 1806

Trogus Panzer, 1806: 80. Type-species: (*Ichneumon coerulator* Fabricius) = *Ichneumon lapidator* var. *coerulator* Fabricius. Monotypic.

Dinotomus Förster, 1869: 188. Type-species: (*Ichneumon coerulator* Fabricius) = *Ichneumon lapidator* var. *coerulator* Fabricius. Designated by Viereck (1914). Synonymized by Dalla Torre (1902).

Autapomorphies. Apical margin of clypeus concave (#4–1).

Species and distribution. After the removal of four species to *Holcojoppa* (see above, Taxonomy), there are nine described species distributed in the Palearctic and the New World.

Biology. Trogus is perhaps the biologically best-known of the *Callajoppa* genus-group. Several species are common parasitoids of familiar swallowtails, notably *T. lapidator* (Fabricius) on *Papilio machaon* (e.g. Kaltenbach, 1874; Morley, 1901) and *T. pennator* (Fabricius) on *P. polyxenes, P. glaucus* L., and *Eurytides marcellus* (Cramer), among others (Heinrich, 1962; Feeny *et al.,* 1985; Damman, 1986). Most species have been reared, some of them hundreds of times, and all reliable reports are from the papilionid genera *Papilio* and *Eurytides*. There is some variation among *Trogus* species in degree of polyphagy. *Trogus pennator* attacks some 10 species on nine food-plant families; *T. lapidator* attacks at least five swallowtails on three plant families (Heinrich, 1962; Mitchell, 1979, 1983). Apparently more specialized are *T. violaceus* (Mocsáry) on *Papilio hospiton* and *P. machaon* (Prota, 1962; M. Shaw, pers. comm.), *T. flavipennis* Cresson on *P. multicaudatus* Kirby (two records

[CNCI, DNHC]), *T. edwardsii* Cresson on *P. eurymedon* Lucas (Heinrich, 1962), *T. thoracicus* Cresson on *Eurytides epidaus* (Doubleday) and *E. philolaus* (Boisduval) (D. Janzen, pers. comm. [JHIC]), and, less certainly, the poorly known *T. pompeji* (Kriechbaumer) on *P. scamander* Boisduval (two specimens [NHML]). All are larval–pupal parasitoids; *T. pennator* successfully attacks hosts as young as the first instar (KRS, pers. obsv. in field and laboratory).

None of the records of nonpapilionid hosts for *Trogus* species merits attention. In collections, we have seen *Apatura iris* (Nymphalidae) pupal remains placed with a specimen of *Psilomastax* misidentified as *T. lapidator*, and a specimen of the latter placed with pupal remains labelled as '*Argynnis*' but clearly those of a *Papilio*; we thus have very little confidence in isolated records. Early published reports from the nymphalids *Vanessa atalanta* (L.), *V. cardui* (L.), *A. iris*, and *Argynnis pandora* (Denis & Schiffermüller) and the arctiid *Pyrrharctia isabella* (Howard, 1889; Morley, 1901, 1903; Bischoff, 1915; Schmiedeknecht, 1930) have neither been repeated in recent years nor can they be traced to materials in collections.

KEY TO THE GENERA OF THE *CALLAJOPPA* GENUS-GROUP

1. T2-5 not or hardly basally constricted (Fig. 7) 2
– T2-5 strongly basally constricted (Fig. 8) (*Trogus* subgroup) 28
2. Scutellum with lateral carinae extending at least 0.5× scutellar length 3
– Scutellum with lateral carinae absent or extending at most 0.2–0.3× scutellar length..............................5
3. Hypostomal and occipital carinae meeting at mandibular base; clypeus concave, apical 0.2 thin and translucent; thyridia wide, space between them about 0.5× width of thyridium; distribution: Japan, southern China, north-eastern India (Meghalaya), Burma ....*Facydes*
– Hypostomal and occipital carinae meeting above mandibular base; clypeus flat to gently convex, uniformly thick; thyridia narrower, space between them about equal to width of thryridium 4
4. Genae in dorsal view flat and sharply receding (Fig. 9); scutellum flattened to weakly convex; distribution: north-eastern India (Meghalaya) to Sulawesi..*Dimaetha*
– Genae in dorsal view convex (Fig. 10); scutellum strongly convex (ranging from shelf-like to forming a more or less acute angle in lateral view); distribution: Central and South America ....*Stirojoppa*
5. Genae in dorsal view flat or strongly receding (Figs 11,12) 6

– Genae in dorsal view convex (Figs 44, 45) 8
6. Thyridium/gastrocoelus reduced to narrow linear transverse impression at extreme base of T2; cell 1 + 2Rs truncate anteriorly; distribution: Australia and New Guinea ....*Yeppoona*
– Thyridium/gastrocoelus not reduced, set back from base of T2; cell 1 + 2Rs petiolate 7
7. MS1 in lateral view evenly convex with highest point at middle (Fig. 23); sclerotized anterior portion of S1 0.5–0.6x as long as distance from posterior margin of anterior portion to apex of T1; scutellum strongly convex and shelf-like; distribution: South America (Brazil, Paraguay, Peru) ....*Tricyphus* (part)
– MS1 in lateral view with petiole flattened and postpetiole weakly convex (Fig. 13); sclerotized anterior portion of S1 0.9× as long as distance from posterior margin of anterior portion to apex of T1; scutellum usually flattened (weakly convex in one species); distribution: Central and South America (Costa Rica to Brazil, Peru) ....*Lagavula*
8. Ventral 0.5 of occipital carina produced as low flange (section above mandible about 0.6× as wide as 5th maxillary palpomere); oxypygous; distribution: sub-Saharan Africa, Madagascar ....*Afrotrogus*
– Occipital carina not produced as low flange; oxypygous or amblypygous 9
9. Propodeum in lateral profile with distinguishable dorsal and postero-dorsal faces which meet at an angle, its base not rising steeply or abruptly to anterior margin of areola (similar to Fig. 59); apex of 2nd lateral area produced as low, broad apophysis; thyridium/gastrocoelus absent; distribution: sub-Saharan Africa ....*Pepsijoppa*
– Propodeum in lateral profile evenly convex or steeply sloping, base rising steeply and abruptly to anterior margin of areola; areola reduced, partially or completely filled in, usually appearing as polished boss (as in Figs 55, 56); apex of 2nd lateral area not produced; thyridium/gastrocoelus present................10
10. Postpetiole conical/pyramidal in lateral view (Fig. 14). 11
– Postpetiole ranging from moderately convex to flattened in lateral view (Figs 15, 16, 24, 25)...........13
11. Areola large and well-defined; thyridia wide, space between them about 0.4x width of thyridium; distribution: southern China to Sulawesi. ....*Cobunus*
– Areola reduced to polished boss; thyridia narrower, space between them about equal to width of thryridium..14
12. Juxtacoxal carina present; metapleuron rugosopunctate, rugae strong and nearly vertical; scutellum forming a more or less acute angl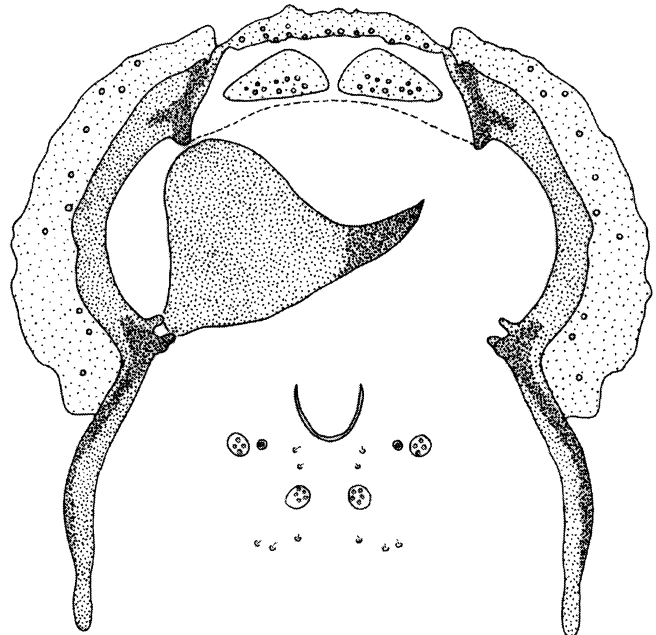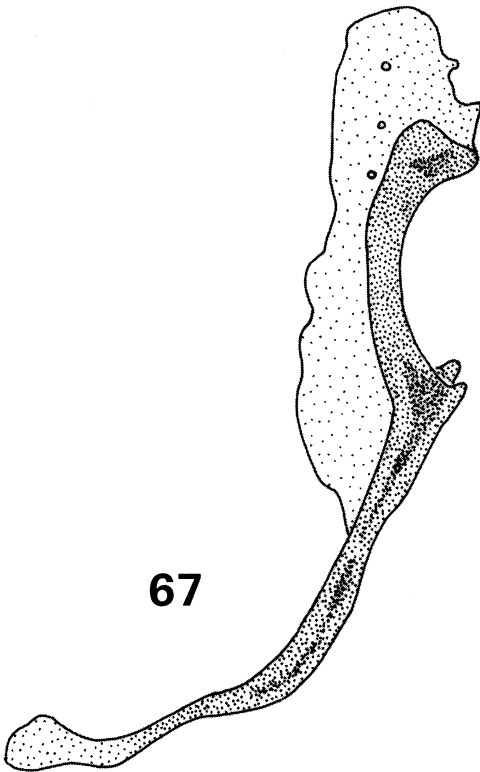e in lateral view; distribution: eastern North America. ....*Tmetogaster*
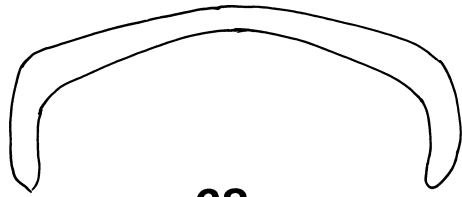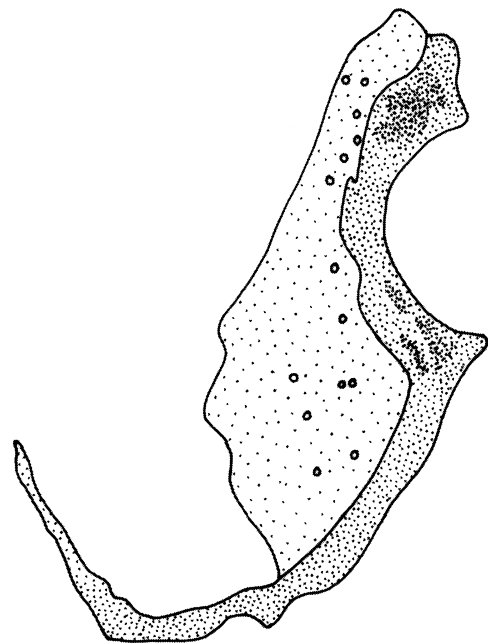
63
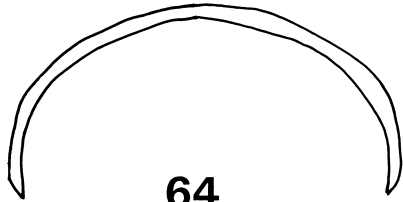
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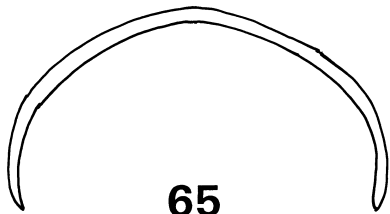
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Figures 63–68. (63–65) Posterior view of T3: (63) *Cobunus pallidiolus* (Matsumura); (64) *Macrojoppa picta* (Guerin); (65) *Macrojoppa rufa*. (66) *Gnamptopelta obsidianator*, cephalic sclerites of mature larva [from Sime & Wahl (1998)]. (67, 68) Pleurostoma and hypostoma of mature larva: (67) *Pedinopelte* sp. 2 (AEIC: DBW 28.viii.97b); (68) *Trogus thoracicus* Cresson (NMNH: DBW 3.viii.97d).

◄———————————————————————————

– Juxtacoxal carina absent; metapleuron rugosopunctate, rugae randomly orientated; scutellum strongly convex and shelf-like; distribution: North America to southern Mexico. ....*Conocalama*

13. Mandible appearing unidentate in frontal aspect (ventral tooth absent or turned under). 14

– Mandible appearing bidentate in frontal aspect (as in Fig. 43). 15

14. Ventral tooth of mandible absent; propodeum in lateral view evenly convex (Fig. 28) **or** strongly sloping; propodeal carinae strong, with at least median longitudinal carinae present; distribution: western North America. ....*Catadelphops*

– Ventral tooth of mandible present but turned under; propodeum in lateral view strongly sloping (Fig. 61); propodeal carinae absent or obsolescent; distribution: Central America (Costa Rica). ....*Xanthosomnium*

15. S2 entire. 16

– S2 divided, consisting of two sections separated by a membranous or weakly sclerotized longitudinal area. 17

16. Cell 1 + 2Rs with interception of 2m-cu at midpoint of posterior margin (vein 2/M about as long as vein 3/M); postpetiole centrally with a few scattered punctures on smooth surface; distribution: South America (Brazil). ....*Humbert*

– Cell 1 + 2Rs with interception of 2m-cu apicad midpoint of posterior margin (vein 2/M 1.5–2.3 as long as vein 3/M); postpetiole regularly and closely punctate; distribution: Central and South America (southern Mexico to Argentina). ....*Dothenia* (most species)

17. Apical margin of clypeus concave. 18

– Apical margin of clypeus straight. 20

18. Scutellum conical; juxtacoxal carina present; apical margin of clypeus without median tooth; distribution: central and eastern North America. ....*Gnamptopelta*

– Scutellum moderately to strongly convex (shelf-like; Figs 48–59); juxtacoxal carina absent; apical margin of clypeus with or without median tooth.....19

19. Propodeal carinae either completely absent or with only posterior transverse carina and posterior 0.5 of median longitudinal carina present; overall colour brown to light brownish

red, wings light brown; distribution: Central America (Costa Rica). ....*Mokajoppa*

– Propodeal carina complete; overall colour black, wings dark brown; distribution: Central America (Costa Rica). ....*Dothenia hansoni*

20. Clypeus with apicolateral margin forming an angle of about 40° relative to apical margin (Figs 17–19). 21

– Clypeus with apicolateral margin forming an angle of about 90° relative to apical margin (Figs 20–22). 24

21. S3 entire; scutellum conical and sharply pointed; distribution: South America (Brazil)............*Laderrica*

– S3 divided; scutellum strongly convex (ranging from shelf-like to forming a more or less acute angle in lateral view). 22

22. MS1 in lateral view with petiole flattened and postpetiole weakly convex (Fig. 25); distribution: Central America (Costa Rica, Panama). ....*Charmedia*

– MS1 in lateral view evenly convex with highest point at middle (Figs 23,24). 23

23. Petiole basally cylindrical or weakly laterally compressed with gently rounded margins, impunctate or with a few scattered punctures; sclerotized anterior portion of S1 0.5–0.6× as long as distance from posterior margin of anterior portion to apex of T1 (Fig. 23); distribution: South America (Brazil, Paraguay, Peru). ....*Tricyphus* (part)

– Petiole strongly laterally compressed and with strong angled margins, strongly rugosopunctate laterally; sclerotized anterior portion of S1 about as long as distance from posterior margin of anterior portion to apex of T1 (Fig. 24); distribution: central and eastern North America ....*Saranaca*

24. S3 divided, consisting of two sections separated by a membranous or weakly sclerotized longitudinal area. 25

– S3 entire 26

25. Propodeum in lateral view evenly convex (similar to Fig. 60); genae in dorsal view moderately convex (Fig. 26); wings uniformly brown; distribution: Palearctic. ....*Callajoppa* (part)

– Propodeum in lateral view strongly sloping (similar to Fig. 61); genae in dorsal view inflated (Fig. 27); wings clear with yellowish tint; distribution: Holarctic. ....*Catadelphus*

26. Propodeum in lateral view evenly convex (Fig. 28); scutellum strongly convex, shelf-like
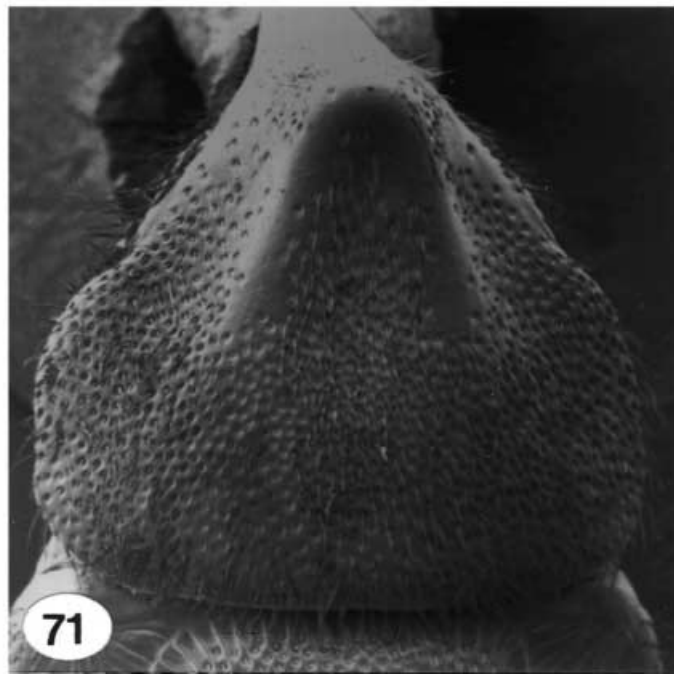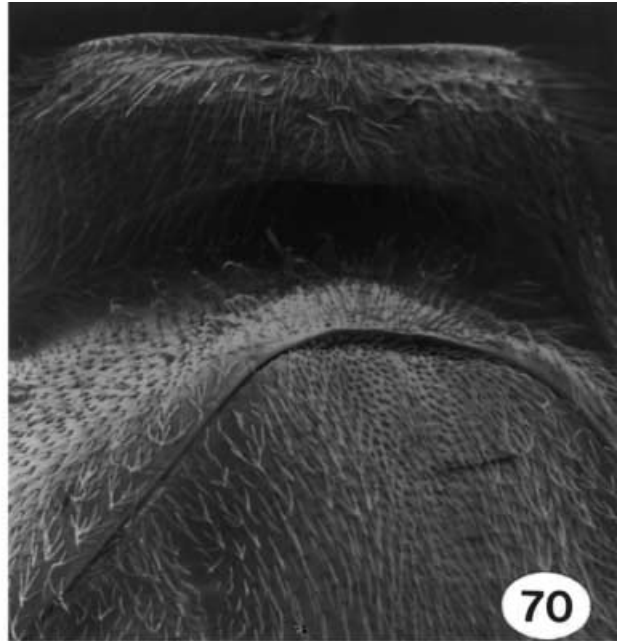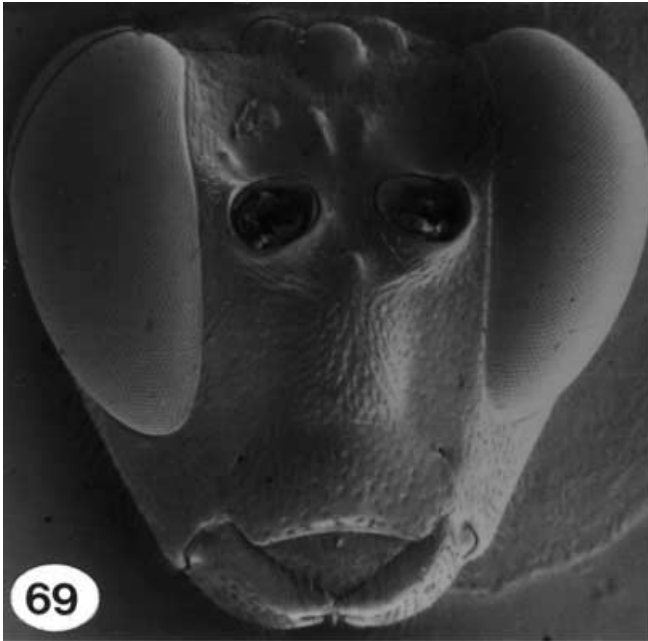
Figures 69–71. (69) *Trogus pennator* (Fabricius), frontal view of head. (70) *Gnamptopelta obsidianator*, dorsal view of pronotum and anterior of mesoscutum. (71) *Conocalama brullei*, dorsal view of postpetiole.

in lateral view; distribution: South America (Argentina)..................................*Dothenia* (one species)
– Propodeum in lateral view strongly sloping (as in Fig. 29); scutellum conical.............................27
27. Cell 1 + 2Rs with interception of 2m-cu at midpoint (2/M about as long as 3/M); centre of metapleuron rugosopunctate; distribution: Palearctic. ....*Callajoppa* (part)

– Cell 1 + 2Rs with interception of 2m-cu near 3r-m (vein 2/M about 1.3× as long as vein 3/M); centre of metapleuron with large and contiguous punctures, without discrete rugae; distribution: Japan, Korea, China, Taiwan. ....*Quandrus*
28. Juxtacoxal carina absent. 29
– Juxtacoxal carina present......................................34
29. Base of petiole with either lateral (Fig. 30) or

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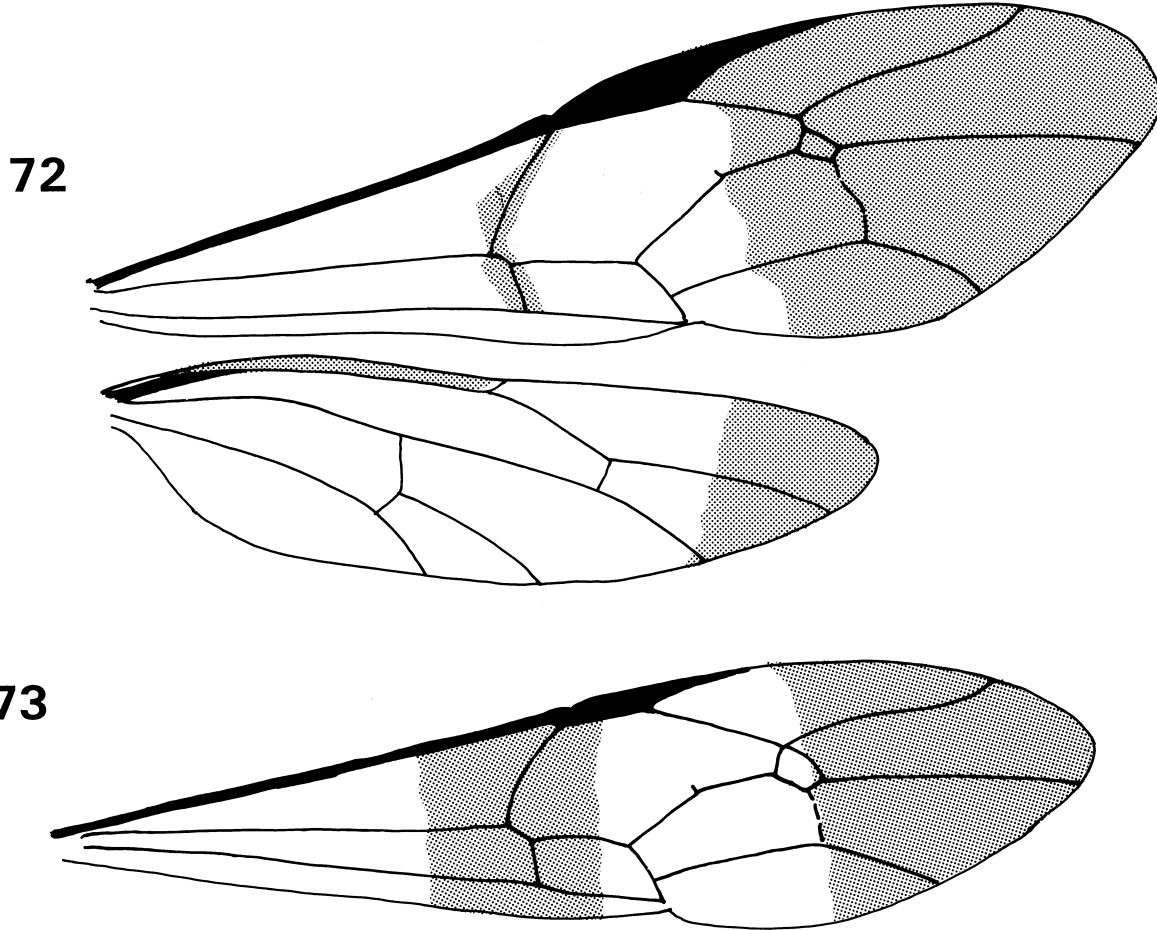
Figures 72–73. (72) *Charmedia chavarriai*, fore and hind wings. (73) *Lagavula gauldi*, fore wing.

dorsal bulges (Fig. 31); ventral margin of T2 denticulate (Fig. 32). 30
– Base of petiole without lateral or dorsal bulges; ventral margin of T2 simple. 32
30. Metasoma in dorsal view with 5 visible tergites (T6-8 retracted under T5); distribution: Central and South America. ....*Macrojoppa* (*picta* species-group)
– Metasoma in dorsal view with 6–7 visible tergites (T6-8 not completely retracted under T5).................31
31. Epicnemial carina absent or present only on mesothoracic venter; petiole with lateral bulges (Fig. 30); distribution: Central and South America. ....*Macrojoppa* (*rufa* species-group)
– Epicnemial carina varying from dorsally incomplete to complete (reaching either mesopleural dorsal or anterior margins); petiole with dorsal bulge (Fig. 31); distribution: New World (southern North America to Argentina). ....*Macrojoppa* (part)
32. Epicnemial carina present only on mesothoracic venter; metapleuron with only a few scattered punctures; T2-4 impunctate and with strong

longitudinal rugae over entire surface of tergite, dorsolateral ridges present; distribution: Central and South America (Costa Rica to Ecuador).........*Tashtego*
– Epicnemial carina absent; metapleuron more or less regularly punctate; T2-4 with regularly distributed punctures and with rugae either weak or confined to midline of each tergite, dorsolateral ridges absent...33
33. Apical margin of clypeus concave; T2-4 with weak longitudinal rugae restricted to midline of each tergite; MS1 in lateral view with highest point at base of postpetiole (Fig. 34); wings uniformly dark brown except some species with lighter oval in cell 1M+R1 of fore wing; distribution: Mexico to South America, Cuba. ....*Pedinopelte*
– Apical margin of clypeus straight; T2-4 with longitudinal rugae extending over entire surface of each tergite; MS1 in profile with postpetiole evenly convex (Fig. 35); fore wing patterned as in Fig. 33; distribution: Central America (El Salvador)..*Daggoo*

34. Epicnemial carina present only on mesothoracic
venter. 35
– Epicnemial carina varying from dorsally
incomplete to complete (reaching either mesopleural
dorsal or anterior margins). 36
35. T2-4 with longitudinal rugae restricted to
midline of each tergite, dorsolateral ridges absent;
vertex posteriorly short and sloping (Fig. 36);
supra-antennal area with two denticles (as in
Fig. 42); distribution: Palearctic. ....*Psilomastax*
– T2-4 with longitudinal rugae extending over
entire surface of each tergite, dorsolateral ridges
present; vertex posteriorly elongate and vertical
(Fig. 37); supra-antennal area with or without
denticles; distribution: Malay Peninsula,
Hainan Island, Taiwan...................................*Queequeg*
36. Ventral margin of T2 denticulate (as in Fig. 32);
T2-4 laterally weakly flattened and with
longitudinal rugae restricted to midline of
each tergite; distribution: South America
(Peru). ....*Metallichneumon*
– Ventral margin of T2 simple; T2-4 laterally
strongly flattened and with longitudinal rugae
extending over entire surface of each tergite...........37
37. Apical margin of clypeus concave; S3-5 entire;
supra-antennal area usually with two denticles
(as in Fig. 42); distribution: Palearctic, New World
(incl. Cuba)..*Trogus*
– Apical margin of clypeus straight; at least S3
divided (S4 entire or divided); supra-antennal area
without denticles, simple or with only two low ridges
present (as in Fig. 41). 38
38. Vertex posteriorly strongly convex (Fig. 38);
female flagellum bristle-shaped; amblypygous;
distribution: Central America (El Salvador),
eastern Russia south to Celebes, Java,
Sumatra. ....*Holcojoppa*
– Vertex posteriorly flat (Fig. 39); female flagellum
lanceolate; oxypygous; distribution: Sikkim,
north-eastern India (Meghalaya) to Philippines,
Borneo. ....*Neofacydes*

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