

# Phylogeny of the *Polysphincta* group of genera (Hymenoptera: Ichneumonidae; Pimplinae): a taxonomic revision of spider ectoparasitoids

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**Abstract.** A cladistic analysis of the *Polysphincta* genus-group (= the 'Polysphinctini' of authors), a clade of koinobiont ectoparasitoids of spiders, was undertaken using ninety-six characters for seventy-seven taxa (sixty-five ingroup and twelve outgroup). The genus-group is monophyletic, nested within the Ephialtini as (*Iseropus* (*Gregopimpla* (*Tromatobia* ((*Zaglyptus* + *Clistopyga*) + (*Polysphincta* genus-group))))). Within the *Polysphincta* genus-group, the clade (*Piogaster* + *Inbioia*) is sister-lineage to all other genera. The cosmopolitan genus *Zabrachypus* is nonmonophyletic, and has been subdivided into a monophyletic Nearctic/Western Palaearctic *Zabrachypus* s.str. and an Eastern Palaearctic *Brachyzapus* **gen.n.**, comprising *B. nikkoensis* (Uchida) **comb.n.**, *B. tenuiabdormalis* (Uchida) **comb.n.** and *B. unicarinatus* (Uchida & Momoi) **comb.n.** An Afrotropical species placed in *Zabrachypus*, *Z. curvicauda* (Seyrig), belongs to *Schizopyga* **comb.n.** The monophyly of the cosmopolitan genus *Dreisbachia* is equivocal, and we consider that species assigned to it are best placed in an expanded *Schizopyga* (**syn.n.**). The monobasic Afrotropical genus *Afrosphincta* is also a synonym of *Schizopyga* (**syn.n.**). The newly delimited *Schizopyga* is the sister-lineage of *Brachyzapus*, and these two genera form the sister-lineage of *Zabrachypus* s.str. as the monophyletic clade (*Zabrachypus* + (*Schizopyga* + *Brachyzapus*)). The Holarctic genus *Sinarachna* is monophyletic if the Palaearctic species *S. anomala* (Holmgren) is excluded and transferred to *Zatypota* **comb.n.** The European species *Polysphincta nielseni* Roman belongs to the Palaearctic genus *Reclinervellus*, and (*Reclinervellus* + *Sinarachna*) is the sister-lineage to a monophyletic group of undescribed Asian species herein assigned to a new genus, *Chablisea* **gen.n.** All remaining polysphinctine genera form a strongly monophyletic clade, the *Polysphincta* clade, although the relationship between this clade and the *Chablisea* and *Zabrachypus* clades remains an unresolved trichotomy. The *Polysphincta* clade comprises three lineages as an unresolved trichotomy, a monophyletic *Oxyrrhexis*, a major group ('*Polysphincta*' (*Ticapimpla* (*Acrotaphus* + *Hymenoepimecis*))) and an *Acrodactyla* lineage. In the second group, '*Polysphincta*' is paraphyletic with respect to the other three genera. However, we retain '*Polysphincta*' as a genus because few species of this very large genus were included in our analysis. We suspect that, when the tropical fauna is better known, it will be possible to subdivide '*Polysphincta*' into two or more monophyletic taxa. In the third lineage, the *Acrodactyla* lineage, the Holarctic genus *Acrodactyla* is monophyletic if the European species *A. madida* (Haliday) is excluded. Consequently, we erect a new genus *Megaetaira* **gen.n.** for this species. The monobasic Afrotropical genus *Pterinopus* is the sister-lineage to the

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cosmopolitan genus *Eruga*. The very large cosmopolitan genus *Zatypota* seems to be monophyletic if two New World species, *Z. parva* (Cresson) and *Z. gerardoii* Gauld, Ugalde & Hanson, are transferred to *Flacopimpla* **comb.n.** The expanded *Flacopimpla* is the sister-group to the Indo-Australian genus *Eriostethus*, and these two in turn form the sister-group to (*Zatypota* + *Longitibia*). This complex forms an unresolved tetrachotomy with (*Pterinopus* + *Eruga*), *Acropimpla* and *Megaetaira*. Formal descriptions of all genera are included, together with an illustrated key to the genera. Brief notes are given about the recorded hosts of each genus.

## Introduction

The *Polysphincta* genus-group (= Polysphinctini *sensu* Townes, 1969) has long been recognized as a natural group of genera (e.g. Hellén, 1915; Townes, 1944), although recent work (Wahl & Gauld, 1998; Gauld *et al.*, 2002) has shown clearly that this monophyletic clade nests within the *Sericopimpla* genus-group of the tribe Ephialtini and thus, as it renders the remainder of the Ephialtini paraphyletic, the status as a separate tribe of Pimplinae should be discontinued. Biologically, this group (which, for convenience, we hereafter refer to as polysphinctines) is of particular interest because all species develop as ectoparasitoids of spiders – a unique trait within the Ichneumonidae (Fitton *et al.*, 1987). As far as is known, polysphinctines are unequivocally koinobionts, developing as larvae on active spiders (Fitton *et al.*, 1988; Eberhard, 2000a), and the spider host is killed prior to the ichneumonid's pupation.

The immature stages of some polysphinctines can modify the host's web-building behaviour (Eberhard, 2000a, b, 2001), and the group offers considerable potential for biological studies (e.g. Jiménez, 1987; Fincke *et al.*, 1990; Eberhard, 2000a, b). However, the study of the host utilization and behaviour of polysphinctines is seriously hampered by two problems. Generic limits are unclearly defined and several species have been assigned almost arbitrarily. Species currently placed together in genera such as *Zabrachypus* and *Sinarachna* (see Yu & Horstmann, 1997) have little in common structurally, and such genera are unlikely to be monophyletic. Further, phylogenetic relationships are poorly understood, and so it is impossible to evaluate the evolutionary biological trends that have been postulated (see Townes, 1969) for the genus-group as a whole. Here, we attempt to define monophyletic groups of species, and derive a testable phylogenetic hypothesis of the relationship for such groups in order to provide a basis for the future evaluation of current evolutionary scenarios.

## Materials and methods

### Taxonomic sampling

Seventy-seven taxa were used in this study, twelve related outgroup taxa and sixty-five species to represent the

diversity of the 190 or so described species of the *Polysphincta* genus-group (Appendix 1). Outgroups were chosen on the basis of earlier analyses (Wahl & Gauld, 1998; Gauld *et al.*, 2002), and include a basal member of the Pimplinae (*Delomerista diprionis*), a species of each of three genera of the relatively less derived Ephialtini (*Acropimpla*, *Iseropus* and *Gregopimpla*) (see Gauld *et al.*, 2002) and representatives of the three genera *Clistopyga*, *Tromatobia* and *Zaglyptus* which are closely related to the *Polysphincta* genus-group (Gauld *et al.*, 2002). The *Polysphincta* genus-group was represented by the type-species of the monobasic genera *Flacopimpla*, *Inbioia*, *Longitibia* and *Pterinopus*, and otherwise by a range of taxa embracing the widest morphological diversity we have perceived in each genus: *Acrodactyla* (six species, including the morphologically rather aberrant species *A. madida*); *Acrotaphus* (two species); *Dreisbachia* (seven species); *Eriostethus* (four species); *Eruga* (three species); *Hymenoepimecis* (two species); *Oxyrrhexis* (two species); *Piogaster* (two species); *Polysphincta* (six species); *Reclinervellus* (two species); *Schizopyga* (two species); *Sinarachna* (three species); *Ticapimpla* (two species); *Zabrachypus* (five species); and *Zatypota* (seven species). In addition, seven undescribed, unassigned or doubtfully assigned species (in AEIC and BMNH collections) were included: '*Dreisbachia*' sp. 4; '*Zabrachypus*' spp. 1 and 2; '*Oxyrrhexis*' sp. 1; *Ticapimpla* sp.n.; Wahl gen. incogn. sp. 1; and BM genus A sp. 1.

The specimens examined in this study were borrowed from or deposited in the following collections: AEIC, American Entomological Institute, Gainesville, Florida; BMNH, The Natural History Museum, London; INBio, Instituto Nacional de Biodiversidad de Costa Rica, Santo Domingo de Heredia; MNHN, Muséum National d'Histoire Naturelle, Paris; MRAC, Musée Royal d'Afrique Centrale Tervuren; ZAU, Zhejiang Agricultural University, Hangzhou, China; ZMTU, Zoological Museum, University of Turku, Finland.

Two described genera are excluded. *Afrosphincta*, described from a single male specimen from Zaire (Benoit, 1953) remains known only from this specimen. The examined holotype in MRAC undoubtedly belongs to the *Dreisbachia*/*Schizopyga* clade as defined below, but lacks association with a female. The second genus, *Aravenator*, was described from a female from Japan and a male from Mongolia (Momoi, 1973). The female holotype is in the private collection of Professor S. Momoi, and we have been

unable to borrow it. The original description fails to differentiate this genus unambiguously, and is best considered as genus incertae sedis. Sex associations amongst species of polysphinctines can be very difficult, even if sympatric and the association of a single Japanese female with a single Mongolian male requires confirmation.

The morphological terminology used is that of Gauld (1991). Throughout this work, when discussing the cladogram and the characters supporting the various nodes, we prefix the character number by a hash mark (#). Diagnostic synapomorphies are indicated by an asterisk (\*).

### Characters

Ninety-six morphological adult characters were observed for the analysis. Larval characters were not used due to the large amount of missing data. Multistate characters have been treated as nonadditive and all the characters are equally weighted. Comments are included where appropriate. The distribution of the character states over the taxa is shown in Appendix 2.

1. *Mandible*: (0) moderately large, weakly and evenly tapered; (1) moderately large, but evenly tapered so apex is <0.5 base; (2) slender and very strongly tapered so apex is needlelike. There is considerable variation in the form of the mandible excluding the teeth. The ground plan condition for the Pimpliformes is to have a rather large and weakly tapered mandible, but in many taxa it is more strongly narrowed (#1.1), but still robust. In most taxa in the *Polysphincta* genus-group, the mandible is altogether more slender, with needlelike sharp pointed teeth (#1.2).
2. *Mandibular teeth length*: (0) upper tooth subequal to the lower; (1) upper tooth conspicuously the longer, the lower tooth small, <0.5 of length of upper tooth; (2) the upper tooth greatly lengthened and up-curved.
3. *Mandibular teeth breadth*: (0) upper tooth similar to or very slightly broader than the lower; (1) lower slightly flattened and broadened to form a blade; (2) as (1) but with lower tooth very strongly broadened; (3) upper tooth broadened and blunt.
4. *Axis of mandible*: (0) not twisted; (1) weakly twisted 10–40°; (2) twisted more than 45°.
5. *Outer surface of mandible*: (0) more or less punctate or slightly rugulose; (1) with a weakly swollen, polished subapical region.
6. *Malar space*: (0) without a subocular sulcus; (1) with a deep subocular sulcus.
7. *Malar space*: (0) short, to moderately long, 0.2–0.8 times basal mandibular width; (1) long, > basal mandibular width; (2) obliterated, lower margin of eye more or less touching base of mandible.
8. *Lobe of maxilla*: (0) normal, not occluding oral fossa; (1) enlarged to occlude oral fossa at rest.
9. *Palpal formula*: (0) 5 : 4; (1) 4 : 3. We choose to make this a single character because a reduction in the number of palpomeres almost always occurs in both maxillary and labial palps within the Ichneumonidae. In all the small polysphinctines in which we have seen reduction in one set, it is invariably accompanied by reduction in the other set. Thus, we believe that treating this as two independent characters is unwarranted.
10. *Clypeus towards distal apex*: (0) flat or slightly incurved; (1) with margin slightly flared outwards.
11. *Clypeus centrally and towards base*: (0) basally slightly swollen, then slightly concave centrally, so in median longitudinal section it would be slightly sinuous; (1) from flat to weakly but evenly convex; (2) very strongly convex; (3) basally ridged.
12. *Clypeofacial suture*: (0) impressed; (1) absent.
13. *Apical margin of clypeus*: (0) with central part weakly sclerotized and more or less notched, laterally bilobed; (1) transverse, at most very slightly concave or convex. In the Ephialtini, the ground plan appears to be that the central part of the clypeal margin is weakly sclerotized and tending to invaginate. Often (as in most species of *Iseropus*, *Gregopimpla* and *Scambus*), this forms a deep notch, that is emphasized as the lateral lobes are slightly extended. The more or less truncated form of most polysphinctines is here considered to be derived, although this condition is widespread outside the Pimplinae.
14. *Inner margin of eye*: (0) weakly concave opposite antennal socket; (1) with a deep, more or less V-shaped invagination opposite antennal socket.
15. *Colour of frontal orbit of ♀*: (0) more or less concolorous with remainder of frons; (1) pallid, contrasting strongly with remainder of frons.
16. *Occipital carina*: (0) more or less complete, dorsally evenly convex or slightly flattened, normally raised; (1) quite narrowly absent dorsally, but ventrally present; (2) entirely absent; (3) more or less complete, dorsally evenly convex, flangelike.
17. *Head in profile at vertex*: (0) moderately long, weakly and evenly rounded down to occipital carina; (1) long and convex, usually with occipital carina rather low on head; (2) precipitously declivous behind posterior ocelli, concave.
18. *Occipital notch*: (0) present, ranging from a deep cleft with raised lobes laterally to a weak impression just above the foramen; (1) absent. Wahl & Gauld (1998) demonstrated that the presence of this notch (Fig. 4A, B) is a ground plan feature of the Pimpliformes. In some members of the *Polysphincta* genus-complex, it is lacking, and this absence is considered to be derived. In many taxa in the *Polysphincta* group, the notch is shallow and displaced ventrally, so it is immediately above the foramen, but this shift in position is very difficult to quantify and we have not tried to do this here.
19. *Foramen magnum*: (0) with a narrow flange dorsally; (1) with a broad dorsal flange.

20. *Surface of eye*: (0) glabrous or with inconspicuous hairs; (1) with long conspicuous pubescence.
21. *Ocelli*: (0) of normal size, separated from eye margin by about minimum diameter or more; (1) greatly enlarged, more or less contiguous with margin of eye.
22. *Pedicel*: (0) conspicuously smaller than scape, not inflated, and only of slightly greater diameter than first flagellomere; (1) strongly inflated, almost as broad as scape and distinctly broader than first flagellomere.
23. *Pronotum in profile*: (0) moderately long, 0.8–1.0 times as long as deep, collar not close to mesoscutum; (1) long, >1.1 times as long as deep, collar not close to mesoscutum but mediodorsal region still rather short and furrowed; (2) long, but with mediodorsal region horizontal and lengthened.
24. *Anterior margin of pronotum*: (0) simple; (1) mediodorsally reflexed, and directed backwards as a strong pointed tubercle; (2) with a very weak posteriorly directed median indentation.
25. *Posterior part of pronotum near midline*: (0) slightly thickened; (1) with horizontal ‘shelf’; (2) with ‘shelf’ very long and laterally closed to form a pocketlike structure (Fig. 4F); (3) with a weak median ridge extending forwards from the hind margin; (4) with a high median longitudinal lamella.
26. *Upper anterior margin of pronotum*: (0) simple; (1) with epomialike ridge extending to margin and with margin slightly produced to form a low tooth.
27. *Epomia*: (0) complete, forming a weak ridge shaped like the numeral 7; (1) with only the upper oblique part present and short; (2) with only upper (vertical) part present, but this is long and strong; (3) entirely absent.
28. *Anterior transverse notaular crest*: (0) absent; (1) present.
29. *Mesoscutal sculpture*: (0) finely punctate; (1) smooth and impunctate; (2) very coarsely punctate, with punctures separated *inter se* by about their own diameter.
30. *Mesoscutum centrally*: (0) evenly pubescent; (1) glabrous.
31. *Mesoscutum with lateral flange posteriorly*: (0) complete to anterior end of scutellum; (1) evanescent, not reaching the scutellum.
32. *Mesoscutum with lateral flange postero-centrally*: (0) narrow, not or only barely broader than it is anteriorly; (1) strongly broadened, at least twice as wide as it is anteriorly.
33. *Epiconial carina*: (0) complete, extending above level of lower corner of pronotum, with upper end remote from anterior margin of pleuron; (1) present only ventrally; (2) absent; (3) curved.
34. *Mesopleural sulcus*: (0) angled opposite mesepisternal scrobe, usually with a shallow horizontal impression extending from this angulation to the scrobe; (1) more or less straight.
35. *Central part of mesosternal region immediately behind fore coxae*: (0) simply transverse; (1) produced forwards in a blunt angulation.
36. *Submetapleural carina*: (0) complete, low, posteriorly usually bifid with outer branch directed towards outer margin of hind coxal insertion; (1) incomplete but discernible anteriorly; (2) entirely absent.
37. *Pleural carina of propodeum*: (0) complete; (1) incomplete or absent.
38. *Posterolateral angle of propodeum*: (0) evenly rounded; (1) swollen.
39. *Anterior transverse carina of propodeum*: (0) discernible, especially laterally; (1) absent.
40. *Posterior transverse carina of propodeum*: (0) discernible, low, more or less complete; (1) absent, except sometimes for lateral vestiges; (2) strong, horseshoe-shaped.
41. *Lateromedian longitudinal carinae of propodeum*: (0) present anteriorly as raised lines that extend at least 0.1 of length of propodeum; (1) absent, or their position indicated by faint ridges, or by small nubs on anterior margin of propodeum.
42. *Propodeal sculpture*: (0) smooth, sometimes with scattered rugae and/or isolated punctures; (1) uniformly finely granulate.
43. *Propodeum in profile*: (0) fairly evenly rounded, declivous posteriorly; (1) with dorsal surface weakly and evenly declivous, before being abruptly declivous near hind end, so the whole propodeum is somewhat more tubular than normal.
44. *Metasternum centrally*: (0) medially flat with a weak median longitudinal groove; (1) with a raised anterior longitudinal crest.
45. *Hind coxal socket*: (0) separated from metasomal foramen by a strongly sclerotized area; (1) confluent with metasomal foramen, or separated from same by a very thin, inconspicuous and unsclerotized tissue.
46. *Fore femur of ♀*: (0) ventrally unspecialized; (1) anteriorly concave beneath, and with a central blunt prominence.
47. *Fore tibia of ♀*: (0) simple; (1) enlarged and inflated; (2) slender and bowed to fit around angularly produced femur.
48. *Fore leg of ♀ with second tarsomere*: (0) elongate and slender, >2.0 times as long as broad; (1) short, <1.5 times as long as broad.
49. *Fore leg of ♀ with third tarsomere*: (0) elongate, >1.5 times as long as broad; (1) short, subquadrate to transverse, <1.2 times as long as broad.
50. *Fore leg of ♀ with fourth tarsomere*: (0) elongate, >1.5 times as long as broad; (1) short, subquadrate to transverse, <1.2 times as long as broad.
51. *Fore leg of ♀ with fifth tarsomere*: (0) slender, of similar thickness to other tarsomeres; (1) exceptionally swollen.
52. *Tarsal claws of ♀*: (0) all simple; (1) all with a basal lobe.
53. *Hind femur ventrally*: (0) simple; (1) with a blunt tooth.

54. *Hind tibia with internal surface*: (0) unspecialized, weakly convex and evenly hirsute; (1) with a more or less glabrous longitudinal groove.
55. *Hind leg of ♀ with second to fourth tarsomeres ventrally*: (0) with pubescence that is similar to the dorsal pubescence; (1) with strong stout spines that are obviously thicker than the dorsal pubescence.
56. *Ventral surface of distal hind tarsomere of ♀*: (0) simple, with isolated fine bristles; (1) with a triangular field of long stout bristles.
57. *Hind tarsus with pulvillus*: (0) of normal dimensions, not projecting beyond apex of claw; (1) enlarged, projecting conspicuously beyond apex of claw.
58. *Fore wing with 3rs-m*: (0) present, enclosing an obliquely rhombic areolet; (1) entirely absent.
59. *Fore wing with 2rs-m*: (0) clearly shorter than abscissa of *M* between it and *2m-cu*; (1) more or less equal in length or longer than abscissa of *M* between it and *2m-cu*; (2) obliterated.
60. *Hind wing with basal abscissa of M + Cu*: (0) evenly bowed; (1) basally straight, and quite abruptly bowed in distal 0.3 or 0.4; (2) distally straight.
61. *Hind wing with distal abscissa of Cu*: (0) tubular; (1) more or less absent.
62. *Hind wing with subbasal cell*: (0) of normal width, with anterodistal corner slightly to very obtuse; (1) broad with anterodistal corner acute.
63. *Body predominant coloration*: (0) black or dark brownish; (1) yellowish; (2) whitish with black speckling.
64. *Tergite I of ♀ in profile*: (0) anteriorly rounded, posteriorly fairly flat; (1) markedly humped.
65. *Tergite I of ♀ in dorsal view*: (0) elongate, from about 1.5–3.5 times as long as posteriorly wide; (1) subquadrate.
66. *Sternite I of ♀*: (0) about 0.4–0.5 of length of tergite; (1) very short, <0.3.
67. *Sternite I of ♀ centrally*: (0) not ornamented; (1) with a low rounded swelling; (2) with a pointed tubercle.
68. *Tergite II of ♀ in dorsal view*: (0) 1.3–2.5 times as long as posteriorly broad; (1) subquadrate to transverse.
69. *Tergite II of ♀ anterolaterally*: (0) simple, with no impression behind thyridium; (1) with a shallow very oblique impression behind thyridium, this impression subtending an angle of >45° to longitudinal axis of tergite; (2) with a long deep oblique impression reaching back to second thyridium, this impression subtending an angle of <40° to longitudinal axis of tergite.
70. *Tergite II of ♀ centrally*: (0) with deep close punctures; (1) evenly granulate; (2) smooth and polished with few isolated punctures; (3) finely microreticulate/granulopunctate.
71. *Tergite II of ♀ posterolaterally*: (0) simple, without a transverse impression; (1) with a transverse impression (sometimes with this only present laterally and not meeting on mid-line), but it more or less delineates a raised median area.
72. *Posterior 0.2 of tergites II–IV of ♀*: (0) with sculpture differing from rest of tergite, usually smooth and impunctate; (1) not sculpturally differentiated from anterior part of tergite, at most with extreme posterior margin of tergite impunctate.
73. *Laterotergite II of ♀*: (0) more or less absent; (1) moderately broad, 0.25–0.4 times as wide as long, and strongly sclerotized.
74. *Tergite III of ♀ centrally*: (0) more or less evenly convex, without raised areas; (1) with weak to strong lateromedian rounded swellings; (2) with a flat median rhombic raised area.
75. *Laterotergite III of ♀*: (0) more or less absent; (1) moderately broad, 0.25–0.4 times as wide as long, and strongly sclerotized.
76. *Tergite III of ♀ anteriorly*: (0) with a shallow transverse groove, which may have a small inconspicuous ridge or swelling on midline; (1) with a large convex central swelling; (2) occluded.
77. *Tergite III of ♀ posteromedially*: (0) simple; (1) with a distinct swelling.
78. *Tergite III of ♀ posterolaterally*: (0) with vestigial to strong more or less straight impressions; (1) with impressions curving forwards and meeting centrally on midline.
79. *Laterotergite IV of ♀*: (0) more or less absent; (1) moderately broad, 0.25–0.4 times as wide as long, and strongly sclerotized.
80. *Metasoma of ♀ with tergite VII*: (0) similar size to tergite VI, sometimes partially retraced under it, but not very noticeably smaller; (1) conspicuously longer than tergite VI.
81. *Metasoma of ♀ with tergites VIII and IX*: (0) laterally separated, with tergite VIII forming a lateral plate either side of tergite IX; (1) with tergites VIII and IX completely fused laterally. The condition in many outgroups is for these tergites to be divided (see Gauld *et al.*, 2002: figs 98–101).
82. *Apex of metasoma*: (0) simple; (1) with paired, branched intersegmental processes.
83. *Subgenital plate of ♀*: (0) inconspicuous, slightly transverse; (1) elongate, strongly sclerotized and slightly convex.
84. *Cercus of ♀*: (0) small, fingerlike; (1) flattened, disclike.
85. *Ovipositor sheath centrally*: (0) with short hairs, the longest hairs being shorter than the breadth of the ovipositor sheath; (1) with very long pubescence, the longest hairs exceeding the breadth of the ovipositor sheath.
86. *Ovipositor length*: (0) moderately long, from 0.9 to 2.0 times as long as metasoma; (1) shorter, from 0.3 to 0.8 times as long as metasoma; (2) exceedingly short, <0.3 times as long as metasoma.
87. *Axis of shaft of ovipositor*: (0) more or less straight; (1) up-curved towards apex; (2) uniformly curved upwards.
88. *Base of upper valve of ovipositor*: (0) simple with a small basal boss, without an impressed area; (1) swollen, with a large weakly impressed triangular area laterally.

89. *Base of ovipositor, ventrally*: (0) simple; (1) expanded; (2) greatly expanded, protruding at rest.
90. *Ovipositor in profile*: (0) parallel sided then abruptly tapered to apex; (1) apically elongately tapered and with enlarged submedian region of lower valve.
91. *Apex of ovipositor in dorsal view*: (0) evenly tapered; (1) subapically slightly expanded and flattened.
92. *Median ovipositor swelling*: (0) absent; (1) present but weak; (2) strong.
93. *Ovipositor sculpture*: (0) smooth, apparently unsculptured; (1) matt; (2) at least lower valve weakly to strongly wrinkled.
94. *Ovipositor shaft subapically*: (0) subcylindrical, or weakly compressed; (1) strongly compressed.
95. *Apex of lower valve of ovipositor*: (0) with distinctly oblique moderately interspaced teeth; (1) without discernible teeth.
96. *Ovipositor apex with basal tooth*: (0) unspecialized or absent; (1) enlarged and forming barb.

#### Phylogenetic analyses

All analyses were performed with PAUP\*4b10 (Swofford, 2002) with the same set of options (no limit to the number of trees kept in memory [*maxtrees=200 increase=auto autoinc=200*]; heuristic search with starting trees for branch swapping obtained by random stepwise addition sequence, followed by TBR (tree bisection-reconnection) branch-swapping searching; 100 replicates carried out [*hsearch start=stepwise addseq=random nreps=100 swap=tbr*]; branches with null maximum length collapsed and duplicate trees deleted [*condense collapse=maxbrlen deldupe=yes*]). For each analysis, we computed the strict consensus (*contree/strict=yes*) and described the tree to access the list of transformations and apomorphies (*describetrees/plot=phylogram labelnode=yes apolist=yes chglist=yes diag yes*). All these descriptions were realized using the default optimization option (*opt=acctrans*). Because of the number of analyses and the use of the default optimization option, only nonambiguous synapomorphies found in all the analyses were kept for the discussion.

We carried out a total of nine analyses. The first was an unweighted parsimony analysis, and the eight others were weighted parsimony analyses. Three successive weighting analyses (SW) (Farris, 1969) were performed, each using one of the three different possible indices [consistency index (CI) (Kluge & Farris, 1969), retention index (RI) and rescaled consistency index (RC) (Farris, 1989)]. Iterations were performed until the inferred weights were stabilized (*reweight index=ci/ri/rc*). For the last five analyses, we used the implied weighting method (IW) (Goloboff, 1993) with a concavity parameter, *k*, ranging from one to five (note that it is not the *conc* parameter in Goloboff's Pee-Wee program, which is equal to  $k + 1$  [*PSet Goloboff=yes GK=1/2/3/4/5 GUninf=exclude GPeeWee=no*]). The fit was measured with a concave function. The curve of the fit vs. extra-steps would be steeper for fewer extra-steps; the same

difference in numbers of steps is less important if occurring between trees with more steps.

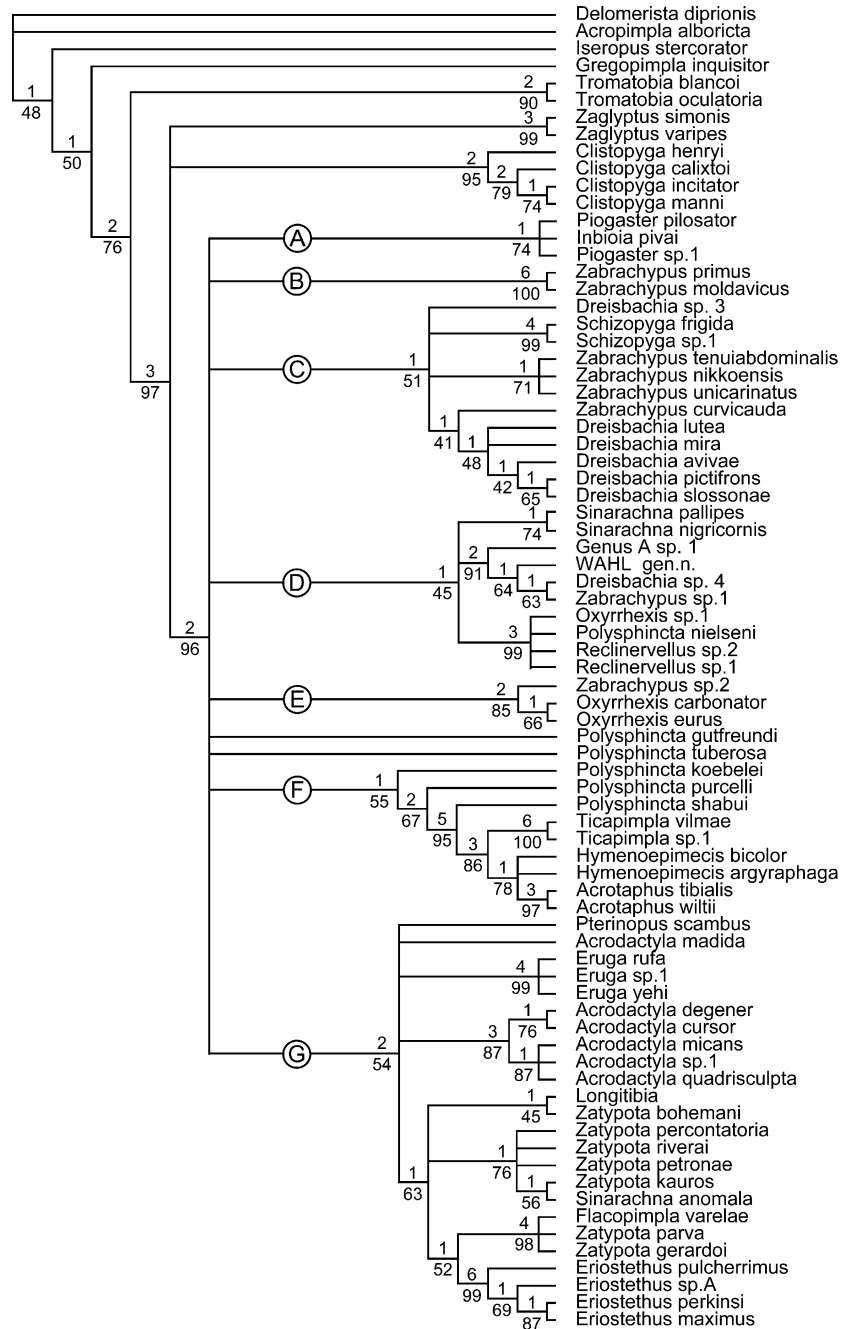
All of these analyses were performed within the frame of a sensitivity analysis (Wheeler, 1995). Because the choice of an index for weighting is problematic (Farris, 1989; Goloboff, 1993), we decided to estimate the sensibility of the analysis to variation on the parameter values. Therefore, we carried out different weighting schemes (SW and IW) with different parameter values (CI, RI, RC and  $k = 1-5$ ), and applied the optimality criterion of taxonomic congruence to discuss the validity of the different results obtained. If a clade is found in many analyses, it means that the phylogenetic signal is rather strong and the topology is less prone to variations of the parameter values. We show here the strict consensus tree resulting from the equally weighted parsimony analysis (Fig. 1) and the 50% majority rule consensus tree resulting from the different weighted analyses (Fig. 2).

Bremer indices were calculated using PAUP\* and TREEROT (Sorenson, 1999). Default options were used, except we ran a heuristic search with 100 random addition sequences for all constrained nodes. Jackknife was performed with different settings because of computational limits (10 000 max-trees; deletion of 36.79% of the characters (Farris *et al.*, 1996); 1000 pseudoreplicates; resample normal; one random addition sequence per pseudoreplicate; and TBR swapping [*jackknife pctdelete=36.79 nreps=1000 resample=normal conlevel=50 keepall=yes search=heuristic/addseq=random nrep=1 swap=tbr*]).

#### Results

The uniformly weighted analysis yielded 2935 equally parsimonious trees with a length of 371 steps, CI = 0.358 and RI = 0.774. The results and tree statistics of all the analyses are summarized in Table 1.

These analyses confirm that the *Polysphincta* group of genera is strongly monophyletic (supported by four synapomorphies, #8.1\*, 22.1, 51.1\*, 57.1\*), and is the sister-lineage to (*Clistopyga* + *Zaglyptus*). Furthermore, all groups of pimelines that utilize araneomorph spiders or their egg sacs as larval provender form a monophyletic clade within the Ephialtini as (*Tromatobia* + ((*Zaglyptus* + *Clistopyga*) + the *Polysphincta* genus-group)), supported by two synapomorphies (#13.1\*, 41.1). The close relationship of this lineage to genera such as *Acropimpla*, *Iseropus* and *Gregopimpla* is consistent with the evolutionary scenario described by Townes (1969: 97–98) and elaborated by others (e.g. Fitton *et al.*, 1988; Gauld *et al.*, 2002) – that parasitism of spiders arose once, as a host-switch from ovipositing on lepidopterous larvae or pupae in dense cocoons (such as Psychidae), as done by the ephialtines *Acropimpla*, *Gregopimpla*, *Iseropus* and *Sericopimpla*, to ovipositing into the structurally somewhat similar egg sacs of spiders such as Segestridae and Salticidae (by *Clistopyga*), Araneidae, Tetragnathidae, Philodromidae and Linyphiidae (by *Tromatobia*), and



**Fig. 1.** Strict consensus tree of 2935 equally parsimonious trees yielded by the equally weighted parsimony analysis (length = 371 steps, CI = 0.358, RI = 0.774). Bremer index values and jackknife values are indicated above and below the branches, respectively. Each of the generic groups A–G is indicated.

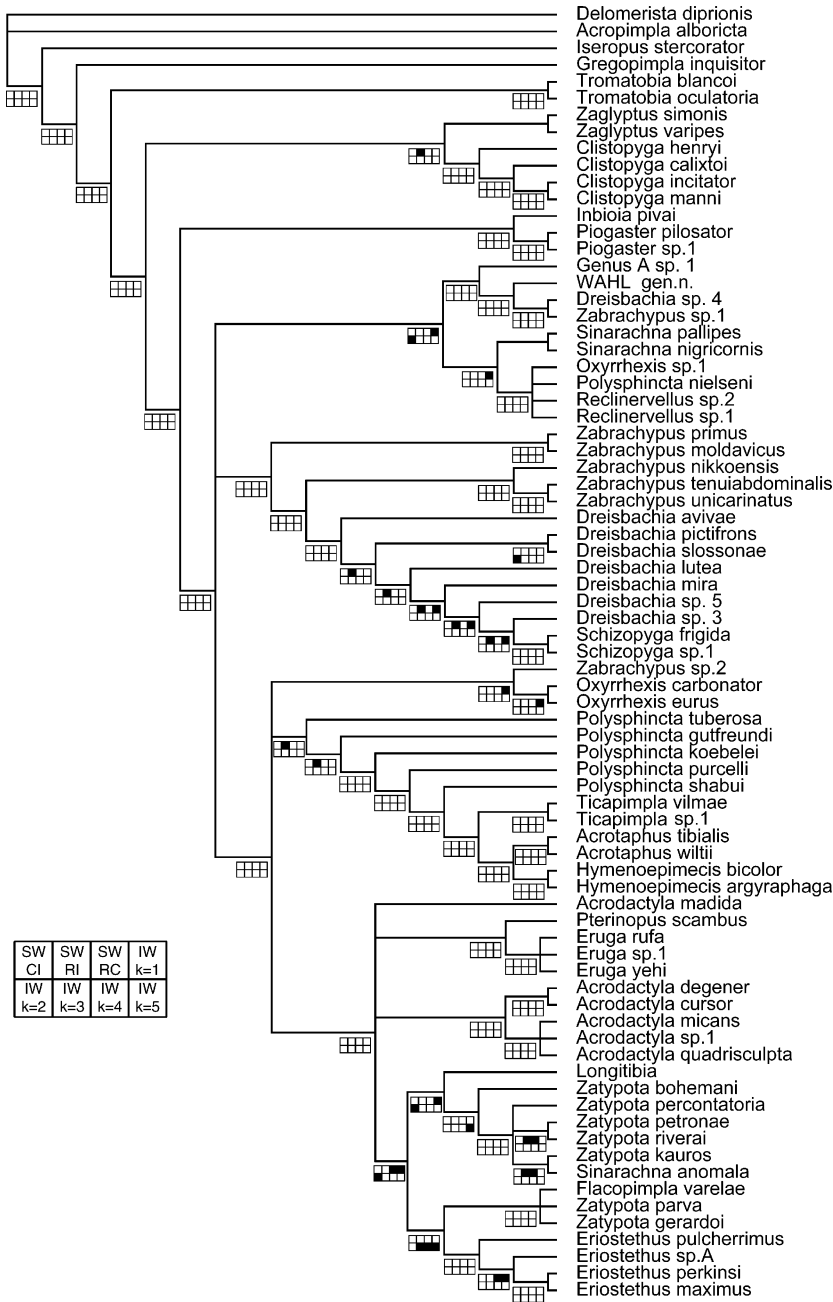
Clubionidae, Miturgidae and Salticidae (by *Zaglyptus*). Like the larvae of species of *Sericopimpla* (Smithers, 1956) and *Tromatobia*, *Clistopyga* and *Zaglyptus*, those of polysphinctines are furnished with dorsal warts bearing strongly curved setae, that enable the larvae to move around on silken strands within a silken bag (Nielsen, 1935; Smithers, 1956). No subsequent switch to another group of hosts has occurred within the polysphinctine clade.

All analyses (see the strict consensus tree, Fig. 1) consistently revealed the presence of seven groups of species in the *Polysphincta* genus-group:

Group A: the *Piogaster* genus-complex – (*Piogaster pilosator* + *P. sp. 1* + *Inbioia pivai*).

Group B: the *Zabrachypus sensu stricto* complex – (*Zabrachypus primus* + *Z. moldavicus*).

Group C: the *Dreisbachia/Schizopyga* genus-complex – (*Zabrachypus nikkoensis* + *Z. unicarinatus* +



**Fig. 2.** Fifty per cent majority rule consensus tree from the eight strict consensus trees resulting from the weighted analyses. Stability plots (Giribet, 2003) are given below the nodes. Each square represents a weighted analysis: an open square indicates that the clade is found to be monophyletic in the strict consensus tree resulting from this analysis; a filled square indicates that the clade does not exist in this analysis. SW, successive weighting approximation (Farris, 1969); IW, implied weighting (Goloboff, 1993); CI, consistency index; RI, retention index; RC, rescaled consistency index; k, concavity constant.

*Z. tenuiabdominalis*) + (*Z. curvicauda* + *Dreisbachia avivae* + *D. pictifrons* + *D. slossonae* + *D. lutea* + *D. mira* + *D. sp. 3* + (*Schizopyga frigida* + *S. sp. 1*)).

Group D: the *Sinarachna*/*Reclinervellus* genus-complex - ((*Sinarachna pallipes* + *S. nigricornis*) + (*Reclinervellus sp. 1* + *R. sp. 2* + *Oxyrrhexis sp. 1* + *Polysphincta nielsenii*) + (Genus A sp. 1 + (Wahl, new genus + (*Dreisbachia sp. 4* + *Zabrachypus sp. 1*))).

Group E: the *Oxyrrhexis* complex - ((*Oxyrrhexis carbonator* + *O. eurus*) + *Zabrachypus sp. (2)*).

Group F: the *Polysphincta* genus-complex - (*Polysphincta koebelei* + *P. purcelli* + *P. shabui* + (*Ticapimpla vilmae* +

*T. sp. 1*) + (*Hymenoepimecis bicolor* + *H. argyraphaga* + (*Acrotaphus tibialis* + *A. wiltii*))).

Group G: the *Eruga*/*Acrodactyla*/*Zatypota* genus-complex - (*Pterinopus scambus* + *Acrodactyla madida* + (*Eruga rufa* + *E. yehi* + *E. sp.1*) + ((*A. degener* + *A. cursor*) + (*Acrodactyla micans* + *A. quadrisculpta* + *A. sp. 1*)) + *Longitibia sinica* + *Zatypota bohemani* + (*Z. percontatoria* + *Z. petronae* + *Z. riverai* + *Z. kauros* + *Sinarachna anomala*) + (*Flacopimpla varelae* + *Z. parva* + *Z. gerardoi*) + (*Eriostethus pulcherrimus* + (*E. sp. A* + (*E. perkinsi* + *E. maximus*))).



**Table 1.** Results of the nine analyses, including tree length and tree statistics. For the three successive weighting analyses, tree statistics are given after having put back the character weights to one.

	Analysis								
	UW	SW CI	SW RI	SW RC	IW $k = 1$	IW $k = 2$	IW $k = 3$	IW $k = 4$	IW $k = 5$
No. of trees before condensation	2941	18	12	12	2064	319	18	18	6
No. of trees after condensation	2935	18	12	12	2025	315	18	18	6
No. of iterations before stabilization	–	4	3	3	–	–	–	–	–
Tree length	371	133	259.19	105.59	391	382	376	376	375
CI	0.358	0.558	0.406	0.628	0.340	0.348	0.354	0.354	0.355
RI	0.774	0.858	0.811	0.891	0.755	0.764	0.769	0.769	0.77
G-Fit	–58.48	–40.92	–50.17	–38.5	–54.47	–59.45	–63.05	–65.82	–68.02
Number of nodes Unweighted value	49	68	68	67	64	65	68	68	69
Tree length	–	375	372	378	–	–	–	–	–
CI	–	0.355	0.358	0.352	–	–	–	–	–
RI	–	0.77	0.773	0.767	–	–	–	–	–
G-Fit	–	–59.24	–58.82	–59.27	–	–	–	–	–

UW, unweighted analysis; SW, successive weighting approximation (Farris, 1969); IW, implied weighting (Goloboff, 1993); CI, consistency index; RI, retention index; RC, rescaled consistency index; G-Fit, Goloboff fit;  $k$ , concavity constant.

Two species of *Polysphincta* (*P. tuberosa* and *P. gutfreundi*) were unassociated in the strict consensus tree (Fig. 1), but in most weighted analyses these species were found to form a monophyletic group with the *Polysphincta* genus-complex (Fig. 2).

## Discussion

The results obtained show that several of the currently accepted genera (namely *Schizopyga*, *Ticapimpla*, *Acrotaphus*, *Eruga*, *Eriostethus*) are demonstrably monophyletic groups retrievable by all analytical procedures. All are supported by several synapomorphies and a Bremer Index (BI) ranging from three to six. Using various weighting options, we have obtained more resolution and clarification of the status and relationships of some other genera (Fig. 2), but a few remain problematic. All of these are discussed below.

Within Group A, the relationship between *Inbioia* and *Piogaster* remains equivocal, although the two genera together form a very distinctive monophyletic clade in all analyses. Re-analysis of the dataset using various weighting options (Fig. 2) always placed this clade as the sister-lineage to all other taxa, and consistently yielded *Piogaster* as monophyletic and the sister-group to *Inbioia* as (*Inbioia pivai* + (*Piogaster pilosator* + *P. sp. 1*)).

Within Groups B and C, we never retrieved *Zabrachypus* (sensu Townes, 1969) as a monophyletic group, although consistently we retrieved two monophyletic groups of *Zabrachypus* species: (*Z. primus* + *Z. moldavicus*) and (*Zabrachypus nikkoensis* + *Z. uncarinatus* + *Z. tenui-abdominalis*). Other species placed tentatively in this genus, *Z. curvicauda* (which in one collection had been identified as a *Dreisbachia* species), *Z. sp. 1* and *Z. sp. 2*,

were always associated with species of other genera, and these are discussed below under their respective groups. Re-analysis of the dataset applying various weighting options (Fig. 2) consistently showed that the two species-groups of *Zabrachypus* formed two monophyletic basal lineages to *Dreisbachia* + *Schizopyga*. However, *Zabrachypus* in the current sense (see included species listed in Yu & Horstmann, 1997) clearly is a heterogeneous assemblage of species definable only by the symplesiomorphy: 'having the mesoscutum rather densely hairy all over' (#30.0) (Townes, 1969). Our analysis clearly shows that most described species comprise two discrete species-groups: a Holarctic group (the *primus* species-complex) with weakly tapered, untwisted mandibles (#1.1), a basally very strongly convex clypeus (#11.3\*) and a dorsally strongly basally broadened ovipositor (#88.1\*) (Fig. 6B), and an east Asian set (the *tenuiabdominalis* species-complex) with twisted mandibles (#4.2), very weakly convex, apicolaterally angulate clypeus (#11.1) and an elongate narrow face. The generic name *Zabrachypus* cannot continue to be applied in this very ill-defined sense and, as the type-species *Z. primus* and a few other taxa form a distinctive monophyletic clade, we restrict the name *Zabrachypus* to the *Z. primus* species-complex. The other group of species, the *tenuiabdominalis* species-complex, warrants distinction as a separate genus, which it has been accorded below as *Brachyzapus*. The other species of 'Zabrachypus' in the data matrix are placed elsewhere. One of these, *Z. sp. 2*, consistently formed a monophyletic clade with the two species of *Oxyrrhexis* (group E above). Re-examination of this species has convinced us that it is better treated as a new species of *Oxyrrhexis*. Making this generic re-assignment now creates a distinctive and monophyletic *Oxyrrhexis*.

*Schizopyga* always was found to be monophyletic, but its relationship with *Dreisbachia* is equivocal. In the weighted analyses, *Schizopyga* + *Dreisbachia* was retrieved as a

monophyletic group, the sister-group to the *Zabrachypus tenuiabdominalis* species-complex, with these two, in turn, the sister-group to *Zabrachypus* s.str. (Fig. 2). However, in one case (successive weighting approximation using the retention index, SW RI), *Dreibachia* (including *Zabrachypus curvicauda*) is a distinct monophyletic group, the sister-lineage to *Schizopyga*, whilst, in other cases, *Dreibachia* is a paraphyletic basal grade with respect to the highly derived *Schizopyga* (Fig. 2). In this analysis, *Dreibachia* monophyly is supported by two synapomorphies: an obliterated malar space and the fore wing with the *3rs-m* present (#7.2, 58.0). We accord little taxonomic importance to the first, homoplastic, character which shows fifteen changes all along the tree on a maximum of twenty and six independent appearances. This analysis also groups together all the species on the basis of an enclosed areolet (#58.0), a character used widely in the precladistic literature to define *Dreibachia* (e.g. Townes, 1969). However, this is the sole character supporting this grouping and not all the species of *Dreibachia* have it (e.g. *D. lutea* Gauld and *D. aperta* Momoi) (see Discussion by Gauld, 1984).

The difference between the two hypotheses is the position of the root of the *Dreibachia*–*Schizopyga* species-complex. Mostly, the complex is rooted on the *D. avivae* branch, rendering *Dreibachia* paraphyletic in respect of a highly derived *Schizopyga*, but under SW RI, the root is located on the branch uniting *Schizopyga* and *D. sp. 3*, rendering *Dreibachia* monophyletic. The position of the root also is questionable in the unweighted analysis, *Schizopyga*, *Dreibachia* and the *Zabrachypus tenuiabdominalis* species-group forming a polytomy.

*Schizopyga* comprises a cluster of highly derived species – two were included in the analysis, but six other described species (Yu & Horstmann, 1997) all are *Dreibachia*, sharing derived features such as a strongly convex face and a very short ovipositor. Recognition of these as a separate genus renders *Dreibachia* paraphyletic. Indeed, it is possible to arrange the species included in the analysis more or less into a continuum from the relatively less derived *D. avivae* through to the highly modified *S. frigida*. The unique male of *Afrosphincta* apparently nests within this continuum. The Afrotropical species, *Zabrachypus curvicauda*, also clearly belongs to this complex. Given the demonstrably monophyletic nature of *Dreibachia* + *Schizopyga*, and the equivocal relationship of these two groups of species, all species should be included in a single genus, *Schizopyga*, and this classification has been adopted formally below.

Group D, the *Sinarachna*/*Reclinervellus* genus-complex, was not always recovered as a monophyletic group in all weighted analyses (see IW  $k = 1$ ,  $k = 2$ ; Fig. 2), although the monophyly of these three genera is well supported by three synapomorphies (#25.4\*, 66.1, 95.1). The composition of *Sinarachna* warrants comment as it comprises only the two species *Sinarachna pallipes* and *S. nigricornis*. As mentioned above, *Sinarachna* previously has been defined rather tenuously as ‘lacks distal abscissa of *Cul* in the hind

wing and has the mesoscutum hirsute all over’ (Townes, 1969). Some species attributed to it are placed better elsewhere. The Holarctic species *S. anomala* never clustered with the first two species and was always nested within a group of *Zatypota* species. The most striking autapomorphy of the clade comprising *Sinarachna pallipes* and *S. nigricornis* is the presence of a very narrow median discontinuity in an otherwise very sharply raised occipital carina (#16.1) (Fig. 4B) (although some species of both *Zatypota* and *Eriostethus* also lack the occipital carina dorsally, these taxa have the entire upper part of the carina vestigial or absent). Unlike true *Sinarachna*, the Holarctic species *S. anomala* has the occipital carina mediodorsally complete and has a sharply impressed posteromedian transverse groove on tergite III. This sharp groove (which in dorsal view varies from smoothly concave to almost V-shaped and defines a flattened area anteriorly – #74.2) seems to be one of the main defining features of the *Zatypota* lineage (*Zatypota*, *Flacopimpla*, *Eriostethus*); therefore, it appears most logical to transfer *S. anomala* to *Zatypota*, leaving a more tightly defined, monophyletic *Sinarachna* (#16.1, 25.3, 26.1, 68.0).

*Reclinervellus* has been referred to previously only in its original description and included only the type-species *R. dorsiconcavus* (He & Ye, 1998). However, several undescribed species of this genus are present in the BMNH collections (such as *Reclinervellus* spp. 1 and 2), although these had been placed under *Sinarachna* previously. In our analyses, these two species of *Reclinervellus* always formed a monophyletic group with a species determined in the AEIC collections as *Oxyrrhexis* sp. 1, and with the Palaearctic species *Polysphincta nielsenii*, a species that always has been treated as a species of *Polysphincta* (Roman, 1923; Sedivý, 1963; Aubert, 1969; Fitton *et al.*, 1988), although we never found it clustering with other *Polysphincta* species. All four, plus *Reclinervellus dorsiconcavus* He & Ye, have the subbasal cell in the hind wing rather broad and with *Cul* and *cu-a* strongly oblique (#62.1) (Fig. 6J), and a posteromedian swelling on tergite III (#78.1\*), indicating a monophyletic group warranting recognition as a distinct genus, as advocated by He & Ye (1998).

In most analyses (Fig. 2), a monophyletic set of four species (Genus A sp. 1 + (Wahl, new genus + (*Dreibachia* sp. 4 + *Zabrachypus* sp. 1))) was sister-lineage to *Sinarachna* + *Reclinervellus*. These species have never been recognized previously as comprising a single group. One, ‘Wahl gen.n.’ (in AEIC), was tentatively labelled as a ? new genus by Dr David Wahl, but another species was placed provisionally in *Dreibachia* (as ‘*D.*’ sp. 4). A third AEIC species was placed in *Zabrachypus* (‘*Z.*’ sp. 1), whilst a fourth species (in the BMNH) originally had been assigned to *Sinarachna*, although one of us (IDG) had appended a note that it did not belong in there. Seen together, and as demonstrated by the analysis, these four species represent a demonstrably monophyletic group (#4.1, 32.1), which is treated below as a distinct genus, *Chablisea*. In one weighted analysis (IW  $k = 2$ ), this genus

was found to be the sister-group of the *Schizopyga* genus-group, but this was based on an alternative interpretation of the character supporting the monophyly of *Chablisea* in all the other analyses. These characters (#4.1, 32.1) are shared also by some species of *Dreisbachia* and by the *Zabrachyus tenuiabdinalis* group, respectively. In this weighted topology (IW  $k = 2$ ), they are reinterpreted as synapomorphies of the *Chablisea* + *Schizopyga* genus-group, and the synapomorphies of the *Reclinervellus* genus-group in the other analyses (#25.4\*, 66.1, 95.1) become, in this weighted topology, the synapomorphies of *Chablisea* and then convergences of the characters uniting *Sinarachna* + *Reclinervellus*. We do not accept this grouping, and favour the first hypothesis (*Chablisea* + (*Sinarachna* + *Reclinervellus*)) for the following reasons: (i) this hypothesis is most parsimonious and is repeated in all the analyses except one; (ii) characters supporting this hypothesis are more numerous and less homoplastic than those supporting the second hypothesis (*Chablisea* + *Schizopyga* genus-group). Unlike almost all other species in the *Schizopyga* clade, all the species of *Chablisea* have the hind coxal cavities confluent with the metasomal foramen (#45.1) (Fig. 6G).

Groups E, F and G (the *Oxyrrhexis* complex, the *Polysphincta* genus-complex and the *Eruga*/*Acrodactyla*/*Zatypota* genus-complex) were united into a monophyletic clade in many weighted analyses. The monophyly of this clade is supported by two synapomorphic characters of the ovipositor shape (#89.1\*, 92.2). We place considerable importance on the expanded ovipositor base, which seems to be a functional modification to allow the egg to exit basally from the ovipositor rather than travel down the ovipositor lumen (Eberhard, 2000b). In most weighted analyses, the integrity of the three genus-complexes (E–G) is maintained, although the two unassociated species of *Polysphincta* (*P. tuberosa* and *P. gutfreundi*) (Fig. 1) often clustered in group F with most other *Polysphincta* species (Fig. 2).

The major problem with these groups concerns the genus ‘*Polysphincta*’, another traditionally ill-defined genus, which mostly has been characterized by symplesiomorphies such as ‘abdominal tergites with sparse punctures or almost smooth’ (#70.2) (Townes & Townes, 1960) and ‘a long ovipositor’ (#86.1) (Townes, 1969), or derived characters shared by all the members of the *Polysphincta* genus-group, and a general absence of derived characters that define other genera (Townes, 1969). Most of our analyses suggest that ‘*Polysphincta*’ is a paraphyletic grade-group relative to (*Ticapimpla* (*Hymenoepimecis* + *Acrotaphus*)). All analyses revealed that the terminal group of taxa (*P. shabui*, *Ticapimpla*, *Hymenoepimecis* and *Acrotaphus*) forms a very strongly delineated, robust clade supported by five characters (#18.1, 22.0, 24.2, 27.3, 33.1) and a BI value of five. The two genera, *Ticapimpla* and *Acrotaphus*, are monophyletic in all analyses, and in all weighted analyses *Hymenoepimecis* was recovered also as a monophyletic group as the sister-group to *Acrotaphus*. In all these analyses, *Polysphincta shabui* was sister-lineage to (*Ticapimpla* + (*Hymenoepimecis* + *Acrotaphus*)). *P. shabui*

was placed by Gauld (1991) in the *P. dizardi* species-group, and the other members of this species-group that we have seen (*P. dizardi* Gauld and an undescribed species from Brazil) clearly will cluster with *P. shabui*, as all three share the same set of derived features defining the placement of the group in our analysis. Almost certainly the *P. dizardi* species-group should be recognized as a separate genus, but we refrain from according it such status until the Neotropical fauna is better collected, and the broader problem of the paraphyletic ‘*Polysphincta*’ is resolved.

Including more *Polysphincta* species in a further analysis did not help, as we always obtained a similar hierarchy, with the Holarctic species (represented by *P. tuberosa* in the cladogram; Fig. 2) occupying a basal position with respect to a paraphyletic set of tropical taxa (represented by *P. gutfreundi*, *P. koebeleri* and *P. purcelli* in the cladogram). These findings confirm some earlier suggestions (Gauld, 1991; Gauld *et al.*, 2002) that ‘*Polysphincta*’, as it is recognized currently, is a set of polysphinctine species that lacks the defining features of the other, demonstrably monophyletic, genera. This problem cannot be resolved yet, because the fauna of the tropics is so incompletely known, but we suspect that representative material will allow the definition of a series of monophyletic genera, and that *Polysphincta* will be restricted to include mainly the Holarctic species.

Group G, the *Eruga*/*Acrodactyla*/*Zatypota* genus-complex, is defined in the analysis by two unambiguous characters (#59.2, 60.1), and includes seven genera (*Acrodactyla*, *Eriostethus*, *Eruga*, *Flacopimpla*, *Longitibia*, *Pterinopus* and *Zatypota*) and one species placed previously in *Sinarachna* (*S. anomala*) which, for the reasons given above, seems better placed in *Zatypota*. Even accepting that *S. anomala* should be placed in *Zatypota*, the arrangement of the remaining taxa was inconsistent with the current classificatory system. *Eruga* is a clearly monophyletic taxon characterized by six apomorphies (#18.1, 27.3, 41.1, 73.1\*, 75.1\*, 79.1\*), as is *Eriostethus* (#4.1, 29.1, 59.0, 60.2\*) and the monobasic genus *Pterinopus* (#46.1, 68.0, 85.1, 95.1). However, consistently, we failed to retrieve *Acrodactyla*, *Flacopimpla* or *Zatypota* as monophyletic groups.

The problems with the monophyly of *Flacopimpla* and *Zatypota* arise because two species of the latter genus (*Z. parva* and *Z. gerardoi*) cluster with *Flacopimpla varelae*. These three taxa form a strongly monophyletic group supported by four apomorphies (#10.1\*, 37.1, 42.1, 70.3), of which the very characteristic, apically flared clypeus (#10.1\*) is diagnostic. Furthermore, unlike other species of *Zatypota*, both *Z. parva* and *Z. gerardoi* have a strongly impressed longitudinal groove internally on the hind tibia of the female (#54.1). A similar groove is only elsewhere found in *Flacopimpla* and *Eriostethus* species. Thus, it is clear that *Z. parva* and *Z. gerardoi* should be transferred to an expanded *Flacopimpla*, as has formally been performed below. The sister-group relationship between *Flacopimpla* and *Eriostethus* seems to be very robust, as it is supported not only by the presence of the tibial groove (Fig. 4C, D), but species of both taxa have similar very slender mandibles with an elongate, up-curved upper tooth (#2.2).

*Acrodactyla*, as recognized currently (Yu & Horstmann, 1997), was never retrieved as a monophyletic group, because the European species *A. madida* was excluded primarily because it lacks several features characteristic of the remaining *Acrodactyla* species – having an epomia-like ridge extending to the anterior margin of the pronotum (usually with margin slightly produced to form a low tooth) (#26.1) and a vertical crest present across the anterior end of the notaulus (#28.1\*). Conceivably, a trace of the mesoscutal crest may be present – sometimes there is slight wrinkling on the mesoscutum – and this has been used as justification for placing *A. madida* with the other species. However, close examination failed to show that this wrinkling was homologous with the crest. The unspecialized epomia (#27.0) also excludes *A. madida* from *Acrodactyla*, and so we feel confident that it is best excluded from *Acrodactyla*. A separate status for *A. madida* is also supported by other features (#11.0, 30.0, 61.1), including the weak, transversely ridged, impression on the inner surface of the female hind tibia. Whether this is homologous with the deep groove present in *Flacopimpla* + *Eriostethus* is debatable, as this groove has never been found to be transversely ridged in *Eriostethus*. Although coded as homologous for all species (#54.1), analysis suggests that it was derived independently in *A. madida*. The parchmentlike cocoons of *Acrodactyla* species are unusual in being almost quadrate in cross-section, but the cocoon of *A. madida* is fusiform, coarsely and densely woven and circular in cross-section. Consequently, we exclude *A. madida* from *Acrodactyla* s.str., and treat it as belonging to a separate new genus, *Megaetaira*.

The status of *Colpomeria* (type-species *A. quadrisculpta*) warrants some mention. Whilst generally treated as a junior synonym of *Acrodactyla* (e.g. by Townes, 1969; Fitton *et al.*, 1988), sometimes it has been recognized as a distinct genus (e.g. by Aubert, 1969). Typically, females attributed to *Colpomeria* have the fore and middle femora enlarged with a toothlike promontory beneath (#46.1), have the mandibles somewhat twisted, the clypeus flat, the metapleuron rather rugose, and are rather polished, impunctate and glabrous insects. These species may simply be a rather derived group of *Acrodactyla*, but we found very weak evidence suggesting that the *degener* species-complex (*Acrodactyla* s.str.) may be monophyletic. At present, we do not recognize *Colpomeria* as a distinct genus, preferring instead to retain it as a species-group within *Acrodactyla*, but more study, especially of the biology of the two complexes (they seem to have different host foci), may necessitate revision of this opinion.

*Longitibia* has only been referred to in its original description (He & Ye, 1999). Structurally, it is very similar to some species of *Acrodactyla*, although it lacks a distinct mesoscutal crest (a vestige is discernible). It has a very strongly developed epomia, that reaches to the anterior margin of the pronotum, a feature found only in this genus, *Acrodactyla* s.str. and a few species of *Zatypota* (#26.1). Although *Longitibia* is well defined by six synapomorphies (#1.0, 3.3\*, 11.2, 42.1, 68.0, 92.1), it has several other features that combine characteristics of the different genera

that compose this genus-group. According to the relative importance we assigned to these characters at the time of the weighted analyses, the phylogenetic signal is not sufficiently structured at an intergeneric level to confer on *Longitibia* a stable position. In our analyses, *Longitibia* is associated with different genera, but always within the *Eruga*/*Acrodactyla*/*Zatypota* crown-group. It is the sister-group of *Acrodactyla* in two analyses (IW  $k = 1$  and  $k = 2$ ); it is grouped twice with *Zatypota bohemani* (unweighted analysis and IW  $k = 5$ ). In the remaining analyses (SW CI, RI, RC; IW  $k = 3$  and  $k = 4$ ), this genus is the sister-group of all the *Zatypota*. In most analyses, the position of *Longitibia* does not cast doubt over the integrity of the monophyly of its sister-group, except when it is grouped with *Z. bohemani*. However, this association is poorly supported by one or two highly homoplastic characters according to the analysis considered. On the other hand, the monophyly of *Zatypota* including *Z. bohemani* is supported by a diagnostic apomorphy (#40.2\*). Our dataset does not allow us to precisely investigate the monophyly or nonmonophyly of *Zatypota*, but clearly the position of *Longitibia* needs to be defined before a decision can be made about the validity of *Zatypota*.

Finally, the results of our analysis support the decision by Gauld (1984) to include *Millironia Baltazar* as a synonym of *Eriostethus*. Although accepted by many authors (e.g. Yu & Horstmann, 1997), without any explanation Gupta (1987) reverted to recognizing *Millironia* as distinct. Recognition of this genus (represented by *E. perkinsi* in our analysis) renders the restricted *Eriostethus* paraphyletic, and thus is not tenable.

### A reclassification of the *Polysphincta* genus-group

Following from the discussion, we recognize twenty-one genera. All, except the problematic *Polysphincta*, are demonstrably monophyletic. For each genus, we have endeavoured to list what is known about the possible host range of the various species. Some records are taken from museum specimens, but many are taken from the literature. Inevitably records in the literature will contain errors (see Shaw, 1994 for an excellent discussion of such errors), but repeated independent records warrant some credence. Throughout these accounts, the spider host classification and nomenclature follow Platnick (2004).

#### *Piogaster* Perkins

*Piogaster* Perkins, 1958: 263. Type-species: *Piogaster rugosa* Perkins (= *Polysphincta pilosata* Aubert), by original designation.

*Diagnosis.* Mandibles slender, not or weakly twisted, with upper tooth slightly the longer, the teeth of similar breadth; palp formula 5 : 4; clypeus strongly convex, separated from face by a strongly impressed clypeofacial

suture, transverse, with lateral margins more or less rounded; lower face strongly transverse, usually rugose; surface of eye more or less glabrous; ocelli always small and remote from eye margins; head posteriorly rounded, occipital carina mediodorsally complete. Pronotum in profile short, mediodorsally unspecialized, more or less without an epomia; mesoscutum short and convex, without impressed notauli, granulate to coarsely granulopunctate, hirsute; posterolateral flange of mesoscutum narrow; mesopleuron with epicnemial carina well developed, its upper end curved somewhat towards anterior margin of pleuron; mesopleural sulcus straight, not angled opposite mesepisternal scrobe; submetapleural carina more or less complete; propodeum short and rather strongly declivous posteriorly, without carinae or with vestigial lateromedian longitudinal carinae; hind coxal socket separated from metasomal foramen by a slender sclerotized bridge. Legs rather unspecialized, with only fourth tarsomeres more or less quadrate and fifth tarsomeres expanded; tarsal claws of female short with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* long; hind wing with basal abscissa of *M + Cu* strongly and evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner obtuse; distal abscissa of *Cu1* present, weak. Metasoma with tergite I short, subquadrate; tergites II–IV simply convex, generally coarsely and uniformly sculptured, without convexities or grooves; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor more or less straight, projecting beyond apex of metasoma by about length of hind tibia, robust and awl-like, without a basal ventral swelling.

*Comments.* *Piogaster*, a small Holarctic genus, comprises six described species (Yu & Horstmann, 1997). Structurally, it is very distinctive in having a rather granulate or granulopunctate mesoscutum that lacks deeply impressed notauli, the mesopleural suture straight and not slightly angled opposite the mesepisternal scrobe and the metasoma with tergites II and III more or less evenly convex, coarsely and punctate all over, without transverse impressions or convex lateromedian swellings. In these features, it also resembles *Inbioia* closely, but *Piogaster* has apomorphic features not shared by *Inbioia*: the epicnemial carina is somewhat curved towards the anterior margin of the pleuron, and the epomia is more or less completely absent.

There are no published host records for *Piogaster*, but we have seen a single North American specimen (in Canadian National Collection, Ottawa) that appears to have been reared from a species of *Habronattus* (Salticidae).

### ***Inbioia* Gauld & Ugalde Gomez**

*Inbioia* Gauld & Ugalde Gomez, 2002: 743. Type-species: *Inbioia pivai* Gauld & Ugalde Gomez, by original designation.

*Diagnosis.* Mandibles slender, weakly twisted, with upper tooth slightly the longer, the teeth of similar breadth; palp formula 5 : 4; clypeus strongly convex, separated from face by a strongly impressed clypeofacial suture, transverse, with lateral margins more or less rounded; lower face strongly transverse, usually rugose; surface of eye more or less glabrous; ocelli always small and remote from eye margins; head posteriorly rounded, occipital carina mediodorsally complete. Pronotum in profile short, mediodorsally unspecialized, epomia short, curved; mesoscutum short and convex, without impressed notauli, granulate to coarsely granulopunctate, hirsute; posterolateral flange of mesoscutum narrow; mesopleuron with epicnemial carina well developed, its upper end straight, not curved towards anterior margin of pleuron; mesopleural sulcus straight, not angled opposite mesepisternal scrobe; submetapleural carina weak but more or less complete; propodeum short and rather strongly declivous posteriorly, with lateromedian longitudinal carinae present anteriorly; hind coxal socket separated from metasomal foramen by a slender sclerotized bridge. Legs rather unspecialized, with only fourth tarsomeres more or less quadrate and fifth tarsomeres expanded; tarsal claws of female short with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* long; hind wing with basal abscissa of *M + Cu* strongly and evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner obtuse; distal abscissa of *Cu1* entirely absent. Metasoma with tergite I short, subquadrate; tergites II–IV simply convex, generally coarsely and uniformly sculptured, without convexities or grooves; laterotergites II–IV inconspicuous; tergite VII long, tergite VIII very long, quite strongly sclerotized, but laterally with a crescentic fenestra from which protrudes a three-branched hirsute appendage; apex of tergite VIII elongate, overhanging large, globose cerci; ovipositor more or less straight, projecting beyond apex of metasoma by about length of hind tibia, robust and awl-like, without a basal ventral swelling.

*Comments.* This genus includes a single described species from Costa Rica, known from a single specimen (Fig. 3). A second specimen (seen in INBio) may represent another species. Structurally *Inbioia* resembles *Piogaster*, in that both have a fairly evenly convex mesoscutum, the mesopleural sulcus straight, and tergites II–IV simply convex, granulate and without raised areas. However, *Inbioia* species have a well-developed epomia and, unlike *Piogaster*, entirely lack the distal abscissa of *Cu1* in the hind wing. However, the most striking autapomorphies of this genus are the extraordinary modifications of the posterior part of the metasoma. Tergites V+ are all unusually elongate, and tergite VIII is exceptionally long, and overhangs the large, globose cerci. Laterally in this tergite is a membranous fenestra, from within which arises a long three-branched, hirsute structure.

Nothing is known about the biology of these insects, except that both species were collected in wet areas – lake-side vegetation and highland bog. At present, we do not

understand what function this pair of appendages serves, as the dearth of material has prevented us from dissecting or sectioning specimens.

### *Schizopyga* Gravenhorst

*Schizopyga* Gravenhorst, 1829: 125. Type-species: *Schizopyga podagrica* Gravenhorst, by subsequent designation (Westwood, 1840).

[*Laufeia* Tosquinet, 1903: 381. Type-species: *Laufeia mira* Tosquinet, by monotypy. Junior homonym of *Laufeia* Simon, 1889.]

*Afrosphincta* Benoit, 1953: 140. Type-species *Afrosphincta congica* Benoit, by original designation. **Syn.n.**

*Dreisbachia* Townes, 1962: 38. Replacement name for *Laufeia* Tosquinet. **Syn.n.**

*Schizopyga* (*Schizopygoides*) Kasparayan, 1976: 71. Type-species: *Schizopyga* (*Schizopygoides*) *nitida* Kasparayan, by original designation.

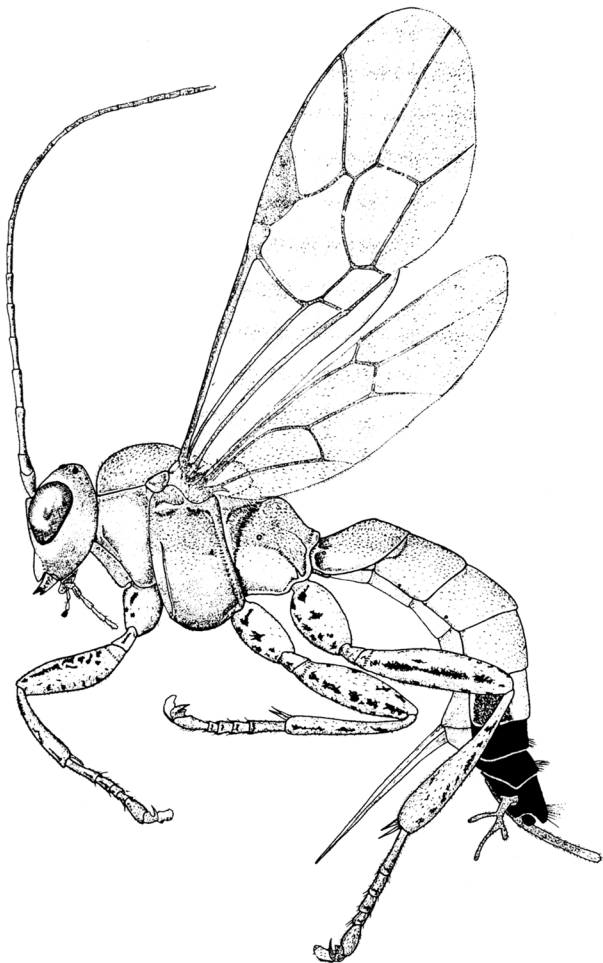


Fig. 3. *Inbioia pivai* female.

**Diagnosis.** Mandibles slender, from not twisted, with upper tooth distinctly the longer and the teeth of similar breadth, to twisted about 90° with lower internal tooth strongly broadened and bladelike; palp formula 5 : 4; clypeus always flat to very weakly convex, separated from face by a very weakly impressed clypeofacial suture, or confluent, the clypeus and face forming a single almost flat area, clypeus slightly transverse, with lateral margins more or less rounded; lower face subquadrate to slightly elongate, smooth and sparsely punctate; surface of eye with sparse pubescence; ocelli usually small and remote from eye margins; head posteriorly evenly to abruptly rounded, occipital carina mediodorsally complete. Pronotum in profile short, mediodorsally unspecialized, with upper part of epomia from strong and subvertical to weak; mesoscutum moderately long, convex or flattened, with impressed notauli, smooth to sparsely punctate, rather sparsely hirsute; posterolateral flange of mesoscutum narrow or discontinuous; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina more or less complete; propodeum moderately long, evenly declivous posteriorly, without carinae or with vestigial lateromedian longitudinal carinae; hind coxal socket separated from metasomal foramen by a slender sclerotized bridge. Legs from slightly specialized, with the third and fourth tarsomeres more or less quadrate and fifth tarsomere expanded, to highly specialized, with the femora incrassate and the second to fourth tarsomeres transverse; tarsal claws of female short with a high basal lobe. Fore wing with *3rs-m* from present to entirely absent, *2rs-m* long; hind wing with basal abscissa of *M + Cu* evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner obtuse; distal abscissa of *Cu1* generally present, strong. Metasoma with tergite I moderately short, slightly to distinctly elongate; tergite II with weak anterolateral oblique grooves, centrally weakly convex; tergite III with weak to moderately developed lateromedian convexities, tergite IV similar; all these tergites generally polished and sparsely punctate, rarely granulate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor distinctly up-curved towards apex, projecting beyond apex of metasoma by about length of hind tibia or less, sometimes very short and barely projecting, moderately slender, but awl-like, without a basal ventral swelling.

**Comments.** The species of three genera are treated as comprising a single genus. In the traditional sense (Townes, 1969), *Schizopyga* always has been restricted to a few species with the clypeus confluent with, and in the same plane as, the lower face and with the mandibles very strongly twisted with the lower (internal) tooth broadened into a flat blade. *Afrosphincta* species are similar but with the mandible less modified. Within *Dreisbachia*, a considerable range of form exists, but species can be arranged in a clear progression from those with weakly narrowed and barely twisted mandibles (such as *D. avivae* Gauld) through to species, such as *D. lutea* Gauld, that

closely approach the mandibular condition found in *Afrosphincta* (known only from a unique male). All species have the face and clypeus rather flat, but again one can trace a progressive loss of the clypeofacial suture from the plesiomorphic condition to the highly derived condition typical of taxa such as *S. frigida* Cresson. Traditionally (Townes, 1969), *Dreischbachia* has been defined by possession of an areolet in the fore wing, although a number of species (such as *D. aperta* Momoi) have been discovered that lack any trace of vein *3rs-m*, and some specimens of *D. lutea* Gauld may or may not have a trace of this vein (Gauld, 1984). Consequently, it seems best to include all these diverse species in a single genus, even though we concede *S. frigida* and its close relatives form a very derived group within this clade.

All host records for this genus are of species attacking Clubionidae and Miturgidae. The egg and developing larva are positioned on the cephalothorax, and the rather frail cocoon, which is usually spun in the host's retreat, lacks a definite orifice (Nielsen, 1935; Fitton *et al.*, 1988). Faecal material often adheres partly within the cocoon. Nielsen (1935) observed that *S. podagrica* used its mandibles to snip through the silken shroud of the nursery web, within which its host, *Cheiracanthium erraticum*, lived, then entered the retreat of the spider. This habit correlates with several morphological adaptations shown by the most specialized species in this genus – twisted mandible with a flattened, bladelike internal tooth; weakly convex, smooth clypeofacial region without an impressed clypeofacial suture; and very short ovipositor. A rather similar face is found in some metopiines which enter silken constructs to attack caterpillars, and we suspect that all *Schizopyga* species showing these adaptations attack spiders concealed in dense silken retreats or nests where the spider lays eggs. However, many other species do not have such specialized mandibles or such smooth clypeofacial profiles. All these species have longer ovipositors, and we suspect that these may attack more easily accessible hosts. A possible association with spiders in egg-nests (as shown by at least *S. podagrica*) is interesting, given the rather basal origin of this genus in the polysphinctine clade. *Zaglyptus* species attack hosts in similar situations (indeed the same species; see Nielsen, 1935), but these wasps apparently sting the spider through the wall of its retreat – behaviour which has not been observed in *Schizopyga*.

### ***Zabrachypus* Cushman**

*Zabrachypus* Cushman, 1920: 37. Type-species: *Zabrachypus primus* Cushman, by original designation.

**Diagnosis.** Mandibles weakly tapered, not twisted, with upper tooth slightly the longer and the teeth of similar breadth; palp formula 5 : 4; clypeus quite strongly convex basally, separated from face by an impressed clypeofacial suture, the clypeus transverse, lenticular, with lateral margins rounded; lower face subquadrate, smooth and

sparsely punctate; surface of eye with dense pubescence; ocelli small and remote from eye margins; head posteriorly fairly abruptly rounded, occipital carina mediodorsally complete. Pronotum in profile quite short, mediodorsally unspecialized, with upper part of epomia strong and subvertical; mesoscutum moderately long, convex, with impressed notauli, smooth to sparsely punctate, densely hirsute; posterolateral flange of mesoscutum moderately narrow to quite strongly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, with vestigial lateromedian longitudinal carinae; hind coxal socket separated from metasomal foramen by a slender sclerotized bridge. Legs specialized, with the fore femur incrassate, and second to fourth tarsomeres transverse, the fifth tarsomere exceptionally expanded; tarsal claws of female short, granulate with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* long; hind wing with basal abscissa of *M + Cu* evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu1* present, spectral. Metasoma with tergite I short, subquadrate; tergite II with weak anterolateral oblique grooves, centrally weakly biconvex; tergite III similar, but more weakly biconvex; tergite IV evenly convex; all these tergites uniformly closely and evenly punctate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight, projecting beyond apex of metasoma by about 0.8 of length of hind tibia or slightly less, stout, awl-like, without a basal ventral swelling, but with upper valve basally broadened, with a weak lateral triangular impression; ovipositor apex in dorsal perspective slightly flattened, expanded.

**Comments.** *Zabrachypus*, a small Holarctic genus, comprises two described species, *Z. primus* and *Z. moldavicus*. For reasons detailed in the discussion above, we here restrict this genus to this small group of species as all have weakly tapered, untwisted mandibles, a basally convex clypeus, densely hirsute eyes and a strongly basally broadened ovipositor. In addition, these species have a slightly flattened, expanded ovipositor apex (which is best seen from a dorsal perspective), and both have a rather small, externally granulate claw that is unlike any other found amongst the Pimplinae. Many of the other described (East Asian) species that have been placed in this genus (Yu & Horstmann, 1997) belong to the *tenuiabdominalis* complex, treated here as a separate new genus, *Brachyzapus*. Several species that have been placed under the name *Zabrachypus* in museum collections, such as *Z. curvicauda* (Seyrig) (in MNHN), belong to *Schizopyga/Dreischbachia* [*Schizopyga curvicauda* (Seyrig) **comb.n.**], but none seem to be very closely related to either of the aforementioned species-complexes and, in the collections that we have re-curved, we have placed them in more appropriate groups.

Nothing is known about the biology of any of the species in this genus.

### ***Brachyzapus* gen.n.**

Type-species: *Polysphincta tenuiabdionalis* Uchida.

**Diagnosis.** Mandibles moderately strongly tapered, twisted about 60–85°, with upper tooth slightly the longer; palp formula 5 : 4; clypeus very weakly convex, separated from face by a very weakly impressed clypeofacial suture, the clypeus rather long, often subquadrate, with lateral margins somewhat angulate; lower face elongate, smooth and very sparsely punctate; surface of eye with very sparse pubescence; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally complete. Pronotum in profile moderately long, mediodorsally with a weak median ridge extending forwards from hind margin, with upper part of epomia strong and subvertical; mesoscutum moderately long, convex, with impressed notauli, sparsely punctate, quite densely hirsute; posterolateral flange of mesoscutum strongly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, usually without carinae, but, in one species, the posterior transverse carina is strong; hind coxal socket separated from metasomal foramen by a broad sclerotized bridge. Legs from very slightly specialized, to with the fore femur distinctly incrassate, generally with third and fourth tarsomeres subquadrate or transverse, the fifth tarsomere is strongly expanded; tarsal claws of female moderately long, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* long; hind wing with basal abscissa of *M + Cu* evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu1* present, spectral. Metasoma with tergite I elongate; tergite II usually with weak anterolateral oblique grooves, and centrally weakly convex, although in one species a more strongly convex rhombic area is discernible; tergite III weakly biconvex, tergite IV almost evenly convex; all these tergites usually smooth with isolated fine punctures, in one species finely but more conspicuously punctate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight or slightly sinuous, projecting beyond apex of metasoma by about 0.8 of length of hind tibia or slightly less, moderately slender, awl-like, without either a basal ventral swelling, or with upper valve basally broadened.

**Comments.** *Brachyzapus* is a small eastern Palaearctic genus that includes *B. tenuiabdionalis* (Uchida) **comb.n.**, *B. nikkoensis* Uchida (Uchida) **comb.n.**, *B. unicarinatus* (Uchida & Momoi) **comb.n.** and at least one undescribed

species from Korea (in AEIC). This genus is characterized by twisted mandibles and a very weakly convex clypeus that is rather long and has a quite well-defined angulation laterally. The lower face is elongate and the pubescence on the eyes sparse. *Brachyzapus* species have a rather simple, awl-like ovipositor, like species in *Chablisea*, but, unlike *Chablisea*, the hind coxal cavities of *Brachyzapus* species are separated from the metasoma insertion by a very strong sclerotized bridge. A possible additional synapomorphy of the genus is the presence of a sharp tooth medially on the lower rim of the metasomal foramen, but it is difficult to ascertain that this is really absent in all other taxa.

Some *Brachyzapus* are physically rather large species with a fore wing length of up to 12 mm, suggesting that they attack quite large hosts. Little is known of their biology, but one Japanese species, *B. nikkoensis*, has been recorded as attacking *Tegenaria domestica* Clerck and *Agelena limbata* Thorell (Agelenidae) (Uchida, 1941; Iwata, 1942). The egg of the ichneumonid is attached to the dorsal surface of the cephalothorax near its hind margin (Iwata, 1942, 1976).

### ***Chablisea* gen.n.**

Type-species: *Chablisea imbiba* sp.n.

**Diagnosis.** Mandibles very strongly tapered, twisted about 10–20°, with upper tooth only slightly longer and broader than the lower tooth; palp formula 5 : 4; clypeus weakly convex, separated from face by shallow impressed clypeofacial suture, the clypeus clearly transverse, with lateral margins very obtuse; lower face slightly elongate, smooth and very sparsely punctate; surface of eye with very sparse pubescence; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally complete. Pronotum in profile moderately long, mediodorsally with a strong median bridge extending forwards from hind margin to anterior margin, with upper part of epomia strong and subvertical; mesoscutum moderately short, convex, with deeply impressed notauli, finely punctate, quite densely hirsute; posterolateral flange of mesoscutum quite strongly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, with lateromedian longitudinal carinae extending back 0.7 of its length, usually joining a transverse wrinkle posteriorly, which may be a vestige of the posterior transverse carina; hind coxal socket confluent with metasomal foramen. Legs very slightly specialized, with fourth tarsomeres subquadrate, the fifth tarsomere is expanded; tarsal claws of female very short, with a high, deep, basal lobe. Fore wing with vein *3rs-m* entirely absent, *2rs-m* less than 0.5 of length of abscissa of *M* between *2m-cu* and *2rs-m*; hind wing with basal abscissa of *M + Cu* evenly bowed;



subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu*1 present, spectral. Metasoma with tergite I subquadrate to slightly elongate; tergite II with anterolateral oblique grooves, and centrally with a convex almost rhombic area, which is generally slightly concave centrally; tergite III strongly biconvex, with a weak to strongly developed median rounded swelling immediately behind the lateromedian swellings; tergite IV similar, and generally even tergite V with a trace of such swelling; tergites II–V smooth and polished; generally with rather close punctures, but one species almost impunctate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight, projecting beyond apex of metasoma by about 0.7 of length of hind tibia or slightly less, moderately slender, awl-like, without either a basal ventral swelling, or with upper valve basally broadened, but with fine denticles or ridges on base of lower valve.

*Comments.* We have seen four species of *Chablisea* from Taiwan, West Malaysia and New Guinea (AEIC, BMNH) that were included in our analysis as ‘Wahl **gen.n.**’, ‘Genus A’ sp. 1, ‘*Dreisbachia*’ sp. 4 and ‘*Zabrachypus*’ sp. 1. Species of *Chablisea* have a series of very fine ridges on the base of the lower valve of the ovipositor, and all have the tarsal claws short, with a high narrow basal lobe. All have a distinct median longitudinal ridge on the pronotum extending from the front margin back to the collar, mandibles are strongly narrowed but less unequally bidentate than other genera with strongly narrowed mandibles. All species have tergite III bearing rounded lateromedian convexities and a more or less conspicuous median convex area behind these. Rather similar features are found in *Reclinervellus*, but *Reclinervellus* species differ from *Chablisea* species in having the base of the lower valve of the ovipositor strongly expanded, and having the subbasal cell of the hind wing broad and anteriorly acute.

Nothing is known of the biology of any species in this genus.

#### *Chablisea imbiba* sp.n.

*Female.* Fore wing length 4.8–5.2 mm; flagellum slender with twenty-four flagellomeres.

A blackish brown species with scape, pedicel and triangular marks on face below antennal sockets whitish; legs reddish with underside of fore and mid legs pallid; hind leg with basal 0.3 of basitarsus whitish. Wings blackish brown.

*Male.* Unknown.

*Remarks.* We have seen four species of this genus, and *imbiba* is the only species from New Guinea, and the only one to hand with strongly infumate wings. Named for an uncommonly good refreshment that has stimulated our ichneumonological discussions on many evenings.

*Material examined.* Holotype ♀, Papua New Guinea: Baiyer River, 1100 m, i–ii.1979 (*Sedlacek*) (AEIC). Paratypes, 6 ♀, Papua New Guinea: Baiyer River, 1100 m, i–ii.1979 (*Sedlacek*) (AEIC; BMNH).

#### *Acrodactyla* Haliday

[*Barypus* Haliday in Curtis, 1837: 37. Type-species: *Barypus degener* Haliday, by subsequent designation (Westwood, 1840). Junior homonym of *Barypus* Laporte 1835.]

*Acrodactyla* Haliday, 1838: 117. Replacement name for *Barypus* Haliday.

*Colpomeria* Holmgren, 1859: 126. Type-species: *Colpomeria laevigata* Holmgren (= *Ichneumon quadrisculptus* Gravenhorst), by monotypy.

[*Symphylus* Foerster, 1871: 105. Type-species: *Symphylus hadrodactylus* Foerster (= *Barypus degener* Haliday), by original designation. Junior homonym of *Symphylus* Dallas 1851.]

*Polemophthorus* Schulz, 1911: replacement name for *Symphylus* Foerster.

*Pantomima* Van Rossem (1990): 314. Type-species: *Pantomima festata* Van Rossem (= *Acrodactyla degener* (Haliday)), by original designation. Synonymized by Broad, 2004.

*Diagnosis.* Mandibles moderately strongly tapered, not twisted or twisted about 15–25°, with upper tooth longer than the small lower tooth; palp formula 5 : 4; clypeus from weakly convex basally to almost flat, separated from face by a weakly impressed clypeofacial suture, the clypeus of moderate length, slightly transverse, with lateral margins somewhat rounded; lower face slightly transverse to elongate, smooth and very sparsely punctate; surface of eye glabrous; ocelli usually small and remote from eye margins, or larger in one Australian species (*A. zekhem* Gauld); head posteriorly evenly rounded, occipital carina mediodorsally complete, strong. Pronotum in profile moderately long, mediodorsally flat or slightly concave, sometimes with weak oblique ridges extending from upper end of epomia to meet on midline behind reflexed marginal tooth, with upper part of epomia strong and subvertical, its lower end very sharp and extended forwards to slightly project beyond the anterior margin of the pronotum; mesoscutum moderately long, convex, with impressed notauli, and with a very sharp vertical crestlike carina in front of each notaulus; mesoscutum sparsely punctate, more or less glabrous with posterolateral flange moderately broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum quite long, dorsally usually very weakly declivous posteriorly, usually with posterior transverse carina and lateromedian longitudinal carinae, sometimes also with lateral longitudinal carinae, and often rather rugose; hind coxal socket separated from metasomal

foramen by a sclerotized bridge. Legs generally rather slender, with only fourth tarsomeres subquadrate, the fifth tarsomere strongly expanded, with femora slender or with fore and mid femora swollen, with a ventral toothlike prominence, and fore tibia with a sharp longitudinal ridge on inner surface; tarsal claws of female moderately short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* < 0.3 times as long as abscissa of *M* between *2rs-m* and *2 m-cu*; hind wing with basal abscissa of *M + Cu* strongly bowed in distal 0.3; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cul* usually present, spectral, or entirely absent. Metasoma with tergite I elongate; tergite II usually with weak anterolateral and posterolateral oblique grooves, centrally with a weakly and evenly convex, more or less rhombic area; tergite III weakly and fairly uniformly convex, with weak grooves posterolaterally, tergite IV almost evenly convex; all these tergites usually smooth with very isolated fine pubescence; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike, or slightly flattened; ovipositor straight with apex very slightly up-curved, projecting beyond apex of metasoma by about 0.4–0.5 of length of hind tibia, slender, with a conspicuous basal ventral swelling.

*Comments.* This moderately large genus currently includes about twenty-six described species in the Holarctic and the Indo-Australian regions (Yu & Horstmann, 1997). We have seen several undescribed species from eastern Asia, including the Philippines and Fiji, but none have been found either in the Afrotropical or Neotropical realms.

*Acrodactyla* is recognizable immediately by the presence of sharp vertical carina at the anterior end of the notauli, and by the sharply projecting end of the epomia. Our conservative interpretation of this genus includes the *quadriscuplta* complex of species (which often are accorded status as *Colpomeria*) together with the *degener* species-complex (*Acrodactyla* s.str.). Both seem monophyletic (Fig. 2), but the former is a very derived species-group, with a slightly flatter clypeus and more twisted mandibles than the latter, and with rather coarsely rugose sculpture on the meta-pleuron. Most species of the *quadriscuplta* species-complex also have the fore and mid femora enlarged, with a more or less developed ventral toothlike swelling, and a sharp longitudinal ridge on the inner surface of the fore tibia.

The host range of *Acrodactyla* seems to focus around two families, apparently further characterizing the two species-complexes the genus seems to be divided into. Members of the *degener* species-complex (which also includes *A. ocellata* Townes) are parasitoids of Linyphiidae (Nielsen, 1923; Townes & Townes, 1960; Fitton *et al.*, 1988), whilst members of the *quadriscuplta* species-complex are known primarily to attack Tetragnathidae (Nielsen, 1937; Capener, 1938; Howell & Pienkowski, 1972). Some Japanese species in this complex (*A. takewakii* Uchida; *A. varicarinata* Uchida & Momoi) are recorded as parasitoids of *Meta* species (Tetragnathidae) (Uchida, 1928; Hashimoto,

1963). All *Acrodactyla* species apparently attach their eggs to the abdomen of the host. The cocoon is parchmentlike, and quadrate in cross-section, with a small caudal orifice.

### *Megaetaira* gen.nov.

Type-species: *Pimpla (Acrodactyla) madida* Haliday.

*Diagnosis.* Mandibles moderately strongly tapered, not twisted, with upper tooth very slightly longer than the lower tooth; palp formula 5 : 4; clypeus weakly convex basally, separated from face by an impressed clypeofacial suture, the clypeus transverse, with lateral margins somewhat rounded; lower face slightly transverse, smooth and very sparsely punctate; surface of eye glabrous; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally complete, strong. Pronotum in profile moderately long, mediodorsally more or less flat, with upper part of epomia strong and subvertical, its lower weak and curved to run downwards, parallel to anterior margin of pronotum; mesoscutum moderately long, convex, with broad, deeply impressed notauli, without a crestlike carina in front of each notaulus; mesoscutum sparsely punctate, more or less glabrous with posterolateral flange moderately broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum of moderate length, dorsally evenly and quite steeply declivous posteriorly, with weak vestiges of carinae; hind coxal socket separated from metasomal foramen by a weakly sclerotized bridge. Legs quite slender, with fourth tarsomeres slightly elongate, the fifth tarsomere strongly expanded, with femora slender, and with hind tibia with a weak groove on inner surface; tarsal claws of female moderately short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* < 0.3 times as long as abscissa of *M* between *2rs-m* and *2 m-cu*; hind wing with basal abscissa of *M + Cu* strongly bowed in distal 0.3; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cul* absent. Metasoma with tergite I elongate; tergite II with very weak anterolateral and posterolateral oblique grooves, centrally with a weakly and evenly convex area; tergites III+ more or less uniformly convex, without grooves, all these tergites smooth with very isolated fine pubescence; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus slightly flattened; ovipositor straight with apex very slightly up-curved, projecting beyond apex of metasoma by about 0.5 of length of hind tibia, apically very slender, with a conspicuous basal ventral swelling.

*Comments.* This genus is dedicated to an underground comic strip antiheroine from the 1980s by Spain Rodriguez, and is from the Greek *Mega* meaning big and *etaira* meaning a courtesan, and the gender is most definitely feminine.

*Megaetaira* presently comprises a single species, the Western Palaearctic *M. madida* (Haliday) **comb.n.** In overall general appearance, this species resembles *A. degener* quite closely, but lacks the autapomorphies that define *Acrodactyla* – the epomial tooth and the mesoscutal crest. The general resemblance between the two species probably is due to symplesiomorphies. The mandibles of *M. madida* differ from those of *Acrodactyla* species in being more evenly tapered, with the teeth only slightly unequal, and the hind tibia has a weak groove on the inner surface. These two apomorphic features characterize the genus.

Most host records for this species are from species of *Metellina* (Tetragnathidae) (Nielsen, 1923 – as *P. clypeata*; Fitton *et al.*, 1988). However, there is one questionable rearing from a linyphiid (Fitton *et al.*, 1988), but we suspect this may be incorrect. Unlike species of *Acrodactyla*, *M. madida* spins a more or less fusiform, densely woven cocoon that is more or less circular in cross-section.

### ***Pterinopus* Townes**

*Pterinopus* Townes, 1969: 102. Type-species: *Pterinopus scambus* Townes, by original designation.

**Diagnosis.** Mandibles moderately strongly tapered, not twisted, with upper tooth distinctly the longer and broader than the small lower tooth; palp formula 5 : 4; clypeus moderately convex, separated from face by a weakly impressed clypeofacial suture, the clypeus almost as long as broad, apically simply arcuate, with lateral margins rounded; lower face elongate, smooth and very sparsely punctate; surface of eye apparently glabrous; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally strong, complete. Pronotum in profile moderately long, with upper part of epomia strong, continuing dorsally to more or less meet counterpart at anterior margin mediodorsally; mesoscutum quite long, weakly convex, with weakly impressed notauli, very sparsely punctate, not obviously hirsute; posterolateral flange of mesoscutum weakly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, with lateromedian longitudinal carinae present anteriorly, and with a vestige of a transverse carina present between them; hind coxal socket separated from metasomal foramen by a narrow sclerotized bridge. Legs with fore and mid femora swollen, with a large blunt flattened tooth on underside, with tibiae curved to fit round the tooth with a sharp ridge along underside, with third tarsomere elongate, fourth tarsomere subquadrate, the fifth tarsomere strongly expanded; hind tarsal claws of female moderately long, with a short but high basal lobe, the proximal side of which bears a fringe of long hairlike projections. Fore wing with *3rs-m* entirely absent, *2rs-m* about 0.4 times as

long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M* + *Cu* strongly bowed towards distal end; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu1* present, spectral. Metasoma with tergite I elongate, slender; tergite II usually with weak anterolateral oblique grooves, and centrally weakly convex; tergites III and IV almost evenly convex; all these tergites smooth with isolated fine punctures; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight, projecting beyond apex of metasoma by about 0.6 of length of hind tibia or slightly less, moderately slender, with a distinct basal ventral swelling, without upper valve basally broadened.

**Comments.** This small genus includes a single described species, *P. scambus* from Madagascar (Yu & Horstmann, 1997), and is distinguished from all other polysphinctine genera by the basally fringed tarsal claws. The form of the fore and mid femora closely resembles that of the *Acrodactyla quadrisculpta* species-complex, but the epomia is of quite a different form, curving forwards to meet its counterpart mediodorsally, suggesting that the two are not exceptionally closely related.

Nothing is known about the biology of any of the species in this genus.

### ***Eruga* Townes**

*Eruga* Townes in Townes & Townes, 1960: 258. Type-species: *Eruga lineata* Townes, by original designation.

**Diagnosis.** Mandibles strongly tapered, not twisted or twisted about as much as 15°, with upper tooth distinctly longer and broader than the small lower tooth; palp formula 5 : 4, the maxillary palp very long and extending backwards beyond epomia; clypeus weakly convex basally, separated from face by an impressed clypeofacial suture, the clypeus transverse, with lateral margins somewhat rounded; lower face slightly transverse, smooth and very sparsely punctate; surface of eye glabrous; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally complete, strong. Pronotum in profile moderately long, mediodorsally with a rather strong transverse furrow, with epomia almost always absent or vestigial, rarely (in *E. telljohanni* Gauld) present but weak; mesoscutum moderately long, convex, with broad, weakly impressed notauli, without a crestlike carina in front of each notaulus; mesoscutum smooth and impunctate, glabrous with posterolateral flange moderately broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum of moderate length, evenly declivous posteriorly, dorsally without carinae or with weak vestiges of anterior transverse lateromedian longitudinal carinae; hind coxal socket separated from metasomal foramen by a weakly

sclerotized bridge. Legs quite slender, with fourth tarsomeres usually slightly elongate, rarely subquadrate, the fifth tarsomere strongly expanded, with femora slender, and with hind tibia with no trace of a groove on inner surface; tarsal claws of female moderately short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* < 0.3 times as long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M + Cu* strongly bowed in distal 0.3; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cul* very weak, spectral, but its position always indicated by an angulation of *Cul* and *cu-a*. Metasoma with tergite I elongate; tergite II with very weak anterolateral and posterolateral oblique grooves, centrally with a weakly and evenly convex area; tergites III+ more or less uniformly convex, without grooves, all these tergites smooth with very isolated fine pubescence; laterotergites II–IV weakly sclerotized, quite broad and usually conspicuous; hind end of metasoma unspecialized, cercus slightly flattened; ovipositor straight, usually very slightly up-curved, projecting beyond apex of metasoma by 0.3–0.5 of length of hind tibia, with apex very slender, with a conspicuous basal ventral swelling.

*Comments.* *Eruga*, a moderately small genus, comprises fourteen described species (Yu & Horstmann, 1997). Most occur in the Afrotropical and Neotropical regions, but three are present in the Nearctic (Townes & Townes, 1960). *Eruga* species closely resemble species of *Acrodactyla*, but are readily discernible by the complete absence of either a mesoscutal crest or a strong epomia. In our analysis, *Eruga* species seem to be more closely related to *M. madida* and *Pterinopus*, but their mandibles are far more like typical *Acrodactyla* in having the teeth very unequal. Unlike *M. madida*, they have shallow notauli and no furrow on the hind tibia.

One of the Nearctic species, *E. rufa* Townes, has been reared from a cocoon found in the web of *Frontinella communis* (Hentz) (Linyphiidae). The cocoon is parchmentlike and quadrate in cross-section, like that of *Acrodactyla*. One specimen seen of an unidentified Cuban species (in the collection of H. Grillo) was reared from an unidentified spider. Its cocoon is also quadrate in cross-section. No other biological information is available about the genus.

### **Longitibia He & Ye**

*Longitibia* He & Ye, 1999: 8. Type-species: *Longitibia sinica* He & Ye, by original designation.

*Diagnosis.* Mandibles moderately tapered, not twisted, with upper tooth slightly longer and much broader than the small lower tooth; palp formula 5 : 4; clypeus weakly convex, basally separated from face by a weakly impressed clypeofacial suture, the clypeus of moderate length, with lateral margins angular and protuberant; lower face elongate, smooth and very sparsely punctate; surface of

eye glabrous; ocelli small and remote from eye margins. Pronotum in profile moderately long, mediadorsally flat or slightly concave, with upper part of epomia strong and subvertical, its lower end very sharp and extended forwards to slightly project beyond the anterior margin of the pronotum; mesoscutum moderately long, convex, with impressed notauli, and with very weak trace of a vertical crestlike carina in front of each notaulus; mesoscutum sparsely punctate, more or less glabrous with posterolateral flange moderately broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum quite long, dorsally usually very weakly declivous posteriorly, dorsally granulate, without carinae; hind coxal socket separated from metasomal foramen by a sclerotized bridge. Legs rather slender, with only fourth tarsomeres elongate, the fifth tarsomere strongly expanded, with femora slender or with fore and mid femora swollen, without a ventral toothlike prominence, and fore tibia without a longitudinal ridge on inner surface; tarsal claws of female moderately short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* < 0.3 times as long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M + Cu* strongly bowed in distal 0.3; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cul* usually present, spectral. Metasoma with tergite I elongate; tergite II usually with weak anterolateral and posterolateral oblique grooves, centrally with a weakly and evenly convex, more or less rhombic area; tergite III weakly and fairly uniformly convex, with weak grooves posterolaterally, tergite IV almost evenly convex; all these tergites usually smooth with very isolated fine pubescence; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike, or slightly flattened; ovipositor straight with apex very slightly up-curved, projecting beyond apex of metasoma by about 0.5 of length of hind tibia, slender, with a conspicuous basal ventral swelling.

*Comments.* This small genus currently includes a single described species, *L. sinica*, in the Eastern Palaearctic region (He & Ye, 1999). Structurally, this species is closely related to *Acrodactyla*, which it resembles in its slender build and strong epomia reaching to the anterior margin of the pronotum. It is recognized most readily by the characteristic mandible with a broad, blunt upper tooth, and the clypeus with the lateral angles protuberant. Nothing is known of the biology of this species.

### **Sinarachna Townes**

*Sinarachna* Townes in Townes & Townes, 1960: 258. Type-species: *Polysphincta pallipes* Holmgren, by original designation.

*Diagnosis.* Mandibles strongly tapered, not distinctly twisted, with upper tooth slender, much longer than the small lower tooth; palp formula 5 : 4; clypeus weakly convex basally, separated from face by a weak impressed clypeofacial suture, the clypeus transverse, with lateral margins somewhat rounded; lower face slightly transverse to slightly elongate, smooth and sparsely punctate; surface of eye glabrous; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally narrowly interrupted. Pronotum in profile moderately short, mediodorsally with a strong transverse furrow, with epomia very sharply raised, subvertical, but with lower end not reaching pronotal margin; mesoscutum moderately long, convex, with broad, anteriorly strongly impressed notauli, without a crestlike carina in front of each notaulus; mesoscutum sparsely punctate, finely and sparsely hirsute all over, with posterolateral flange moderately broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum of moderate length, evenly declivous posteriorly, dorsally with lateromedian longitudinal carinae quite strong, anteriorly parallel, posteriorly curving outwards to seamlessly join the lateral parts of the posterior transverse carina, this latter carina absent medially; hind coxal socket confluent with metasomal foramen. Legs moderately slender, with fourth tarsomeres subquadrate to slightly transverse, the fifth tarsomere strongly expanded, with femora slender, and with hind tibia with no trace of a groove on inner surface; tarsal claws of female short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* about 0.3 times as long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M + Cu* fairly evenly but strongly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu1* absent, its position generally not even indicated by any angulation of *Cu1* and *cu-a* (we have seen one individual with one wing showing a trace of angulation and a vestige of the distal abscissa of *Cu1*). Metasoma with tergite I elongate; tergite II with distinct anterolateral and posterolateral oblique grooves, centrally with a weakly and evenly convex, raised rhombic area; tergite III with weak lateromedian convexities, with weakly impressed grooves anterolaterally and posteriorly; tergite IV similar but with convex areas and groove very weak; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus slightly flattened; ovipositor straight, projecting beyond apex of metasoma by about 0.8 of length of hind tibia, with apex very slender, with a conspicuous basal ventral swelling.

*Comments.* *Sinarachna*, a small genus, comprises three described species from the Holarctic region (Yu & Horstmann, 1997). Attributed tropical species probably belong to *Zatypota*, as does the Holarctic species *S. anomala*. As mentioned above, previously *Sinarachna*

has been defined rather tenuously – ‘lacks distal abscissa of *Cu1* in the hind wing and has the mesoscutum hirsute all over’ (Townes, 1969), and, as such, has had species attributed to it that are better placed elsewhere. The most striking autapomorphy of *Sinarachna* s.str. is the presence of a very narrow median discontinuity in an otherwise very sharply raised occipital carina.

Species of *Sinarachna* primarily are parasitoids of species of Araneidae and Linyphiidae. Records of this genus attacking Dictynidae concern *S. anomala*, that we have concluded is better placed in *Zatypota*, although there is one questionable record of a *Sinarachna* from Theridiidae. The larva is attached to the host’s abdomen, and the cocoon is narrowly fusiform and densely woven with a tight outer cover of coarse fibres. It is spun in the host’s web (Fitton *et al.*, 1988).

### ***Reclinervellus* He & Ye**

*Reclinervellus* He & Ye, 1998: 166. Type-species: *Reclinervellus dorsiconcavus* He & Ye, by original designation.

*Diagnosis.* Mandibles long and strongly tapered, twisted about 40–85°, with upper tooth very much longer than the lower, curved slightly upwards and greatly overlapping its opposite number at rest; palp formula 5 : 4; clypeus weakly to moderately convex, separated from face by an impressed clypeofacial suture, the clypeus strongly transverse lenticular, with lateral margins rounded; lower face subquadrate to transverse, smooth and very sparsely punctate; surface of eye more or less glabrous; ocelli moderately small, separated from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally complete. Pronotum in profile moderately long, mediodorsally with a strong median bridge extending forwards from hind margin to anterior margin, with upper part of epomia strong and subvertical; mesoscutum moderately short, convex, with deeply impressed notauli, finely and sparsely punctate, quite densely hirsute; posterolateral flange of mesoscutum weakly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, usually without carinae, but in a few species the vestiges of the lateromedian longitudinal carinae present anteriorly; hind coxal socket confluent with metasomal foramen. Legs very slightly specialized, with fourth tarsomeres subquadrate, the fifth tarsomere strongly expanded; tarsal claws of female short, with a short, high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* shorter than 0.5 of length of abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M + Cu* evenly bowed; subbasal cell broad, with anterodistal corner strongly acute, the combined *Cu1* and *cu-a* oblique, often almost straight; distal abscissa of *Cu1* at most discernible as a weak mark in wing membrane.

Metasoma with tergite I subquadrate to slightly elongate; tergite II with anterolateral oblique grooves, and with well-developed lateromedian convex areas, with a slight swelling medially behind these; tergite III strongly biconvex, with a strongly developed median rounded swelling immediately behind the lateromedian swellings; tergite IV similar, and generally even tergites V and VI with traces of such swellings; tergites II–VI smooth and polished, rather closely punctate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight, projecting beyond apex of metasoma by about 0.7 of length of hind tibia or slightly less, slender, with a very conspicuous basal ventral swelling, and centrally slightly broadened.

*Comments.* This moderately small Old World genus has two described Palaearctic species: *R. dorsiconcavus* from China and *R. nielseni* (Roman) **comb.n.** widely distributed from Western Europe to Japan. We have seen several undescribed species from the Oriental region (Sri Lanka, Sumatra and Sulawesi) (in BMNH) and one from West Malaysia (included in our analysis and labelled as '*Oxyrrhexis*' sp. 1 (in AEIC)) which also belong in this genus, suggesting that the greatest species-richness may occur in the latter region. *Reclinervellus* may be recognized by the fact that all species have the subbasal cell in the hind wing rather broad, with *Cu1* and *cu-a* strongly oblique so that the anterodistal corner of the subbasal cell is acute. All also have a more or less well-developed posteromedian swelling on tergite II, a very strongly basally broadened ovipositor, a median longitudinal crest on the pronotum, and slender mandibles with an elongate, up-curved, upper tooth.

The Palaearctic species, *R. nielseni*, has been reared several times as a parasitoid of *Cyclosa conica* (Pallas) (Araneidae) (Nielsen, 1923; Fitton *et al.*, 1988; Shaw, 1994). The larva develops attached to the spider's abdomen, and pupates in a fusiform, densely woven cocoon that has a loose outer cover of coarser threads, that is suspended in the web of the spider host. The final web of the spider is often rather small and relatively robust (Nielsen, 1923), but a detailed study of whether this is host manipulation by the parasitoid, or simply the result of reduced activity by a weakened spider, has yet to be performed.

### *Flacopimpla* Gauld

*Flacopimpla* Gauld, 1991: 360. Type-species: *Flacopimpla varelae* Gauld, by original designation.

*Diagnosis.* Mandibles very strongly tapered, not appreciably twisted, with upper tooth far longer than the lower; palp formula 5 : 4; clypeus very weakly convex but flaring slightly outwards to apex, separated from face by an impressed clypeofacial suture, the clypeus rather long, but transverse, with lateral margins very slightly angulate and slightly concave laterally; lower face slightly transverse, smooth and very sparsely punctate; surface of eye glabrous; ocelli quite small and separated from eye

margins; head posteriorly evenly rounded, occipital carina mediadorsally complete. Pronotum in profile moderately long, mediadorsally simple, with upper part of epomia quite strong and subvertical, then curved and continued shortly downwards; mesoscutum moderately long, convex, with weakly impressed notauli, polished and impunctate, almost glabrous; posterolateral flange of mesoscutum weakly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina from complete to completely absent; propodeum moderately long, evenly declivous posteriorly, without carinae; hind coxal socket confluent with metasomal foramen. Legs slightly specialized, with a longitudinal, granulate, furrow on the inner surface of hind tibia, mid trochanter of female generally with a weak to conspicuous ventral swelling and with fourth tarsomere subquadrate, the fifth tarsomere strongly expanded; tarsal claws of female quite short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* very short, <0.3 times as long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M + Cu* strongly and evenly bowed; subbasal cell broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu1* present, spectral. Metasoma with tergite I slightly elongate; tergite II with strong anterolateral and posterolateral oblique grooves, centrally defining a raised, weakly convex, granulate, rhombic area; tergite III similar, though with defined area tending to be more transversely oval; tergite IV similar, but with anterolateral grooves weak, the posterolateral ones very strong; tergites III–V centrally granulate, peripherally smooth with isolated fine punctures, tergites VI+ smooth; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight, projecting beyond apex of metasoma by about 0.3–0.4 times length of hind tibia, apically elongately tapered to a very fine point, with a basal ventral swelling, and a weak median swelling.

*Comments.* This small New World group of species comprises *F. varelae* Gauld and *F. gerardoi* (Gauld, Ugalde & Hanson) **comb.n.**, both from Costa Rica (Gauld *et al.*, 1998), *F. sulina* Brazil (Graf & Kumagai, 1997) and *F. nigriceps* (Walsh) **comb.n.** and *F. parva* (Cresson) **comb.n.**, both from the U.S.A. *F. gerardoi*, *parva* and *nigriceps* were placed previously in *Zatypota*, as no-one noticed the weakly impressed tibial groove. Unlike *F. varelae*, *F. gerardoi* totally lacks the submetapleural carina. Re-examination clearly shows that this species is best placed in *Flacopimpla*, as it has a definite trace of a tibial groove, and a more extensive granulate area in the position this groove occupies in other species. The genus is characterized by the granulate sculpture of the metasoma and, to a lesser extent, of the propodeum, and a slight ventral swelling on the mid trochanter of the female. It is closely related to *Eriostethus*, as both genera have similar mandibles and an impressed groove on the inner side of the hind tibia. *Eriostethus* species are, however, far more

derived, with a 4 : 3 palp formula and no trace of an epomia. The cocoon of the North American *F. nigriceps* is described as being 'subcylindric with a little taper towards the end, loose enough to be transparent and composed of coarse straw-coloured silk, in a loose looped weave. Erect loops stand out all over the surface giving it a somewhat fuzzy appearance, and there is the usual hole in the hind end' (Townes & Townes, 1960: 274).

Cushman (1926) reported that the Nearctic species *F. parva* has been reared from *Theridion punctipes* Emerton (Theridiidae).

### *Eriostethus* Morley

*Eriostethus* Morley, 1914: 34. Type-species: *Eriostethus pulcherrimus* Morley, by monotypy.

*Millironia* Baltazar, 1964: 394. Type-species: *Millironia trifasciata* Baltazar, by original designation.

**Diagnosis.** Mandibles very strongly tapered, not or only weakly twisted up to 20°, with upper tooth far longer than the lower; palp formula 4 : 3; clypeus very weakly convex, weakly separated from face by a vestigial clypeofacial suture, the clypeus rather long, but transverse, with lateral margins rounded; lower face elongate, smooth and very sparsely punctate; surface of eye glabrous; ocelli from quite small and separated from eye margins to very large and more or less contiguous with eyes; head posteriorly from evenly to abruptly rounded, occipital carina from mediodorsally complete to entirely absent. Pronotum in profile from moderately long to very long, mediodorsally simple, with epomia more or less entirely absent; mesoscutum moderately long to very long, convex, with weakly impressed notauli, polished and impunctate, more or less glabrous; posterolateral flange of mesoscutum weakly broadened; mesopleuron with epicnemial carina usually quite well developed, its upper end remote from anterior margin of pleuron, but, in some species, with the carina laterally reduced, and in one only present as a ventral vestige; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, without carinae; hind coxal socket usually more or less confluent with metasomal foramen, sometimes separated by a narrow slightly sclerotized region. Legs rather slender, hind tibia with a longitudinal, granulate, furrow on the inner surface; fourth tarsomere rather slender, slightly longer than broad, the fifth tarsomere strongly expanded; tarsal claws of female quite short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* < 0.5 times as long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M* + *Cu* weakly bowed; subbasal cell usually not broad, with anterodistal corner acute or right angled; distal abscissa of *Cu* usually discernible, represented by a slight angulation in *Cu*1 and *cu-a*. Metasoma with tergite I slightly elongate; tergite II with anterolateral and posterolateral oblique grooves, centrally

defining a raised, weakly biconvex, smooth or sparsely punctate central area; tergite III similar; tergite IV similar, but with a slight tendency towards biconvexities being present; tergites III–V smooth and highly polished, sparsely punctate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus rather long and fingerlike; ovipositor straight, rapierlike, projecting beyond apex of metasoma by about 1.0 or more times length of hind tibia, apically elongately tapered to a very fine point, with a basal ventral swelling, and a weak median swelling.

**Comments.** This moderately large Indo-Australian genus comprises eighteen described species (Yu & Horstmann, 1997), mostly quite large insects (fore wing length 3.9–9.2 mm). Gauld (1984) saw an undescribed New Guinea specimen associated with the remains of a jewel spider (Araneidae) on which was observed ichneumonid larval remains (Gauld, 1984: fig. 97).

### *Zatypota* Foerster

*Zatypota* Foerster, 1869: 166. Type-species: *Ichneumon percontatorius* Müller, by subsequent designation (Viereck, 1914).

*Polysphinctopsis* Habermehl, 1917: 167. Type-species: *Polysphincta eximia* Schmiedeknecht (= *Glypta albicoxa* Walker), by monotypy.

*Lycorinopsis* Haupt, 1954: 110. Type-species: *Lycorinopsis rhombifer* Haupt (= *Ichneumon percontatorius* Müller), by original designation.

**Diagnosis.** Mandibles strongly tapered, from not distinctly twisted to twisted about 20°, with upper longer than the small lower tooth, but never exceptionally slender and up-curved; palp formula most usually 4 : 3, sometimes 5 : 3, but then with a tendency for reduction/fusion of the most distal two maxillary palpomeres; clypeus weakly convex basally, separated from face by a weak impressed clypeofacial suture, the clypeus transverse, with lateral margins somewhat rounded, sometimes with the entire apical margin of the clypeus rounded; lower face from slightly transverse to slightly elongate, most usually smooth and sparsely punctate; surface of eye glabrous; ocelli generally moderately small and widely separated from eye margins; head posteriorly evenly rounded, occipital carina almost always complete, or, in a few Neotropical species, broadly absent dorsally, never mediodorsally narrowly interrupted. Pronotum in profile moderately short, usually with a strong transverse furrow mediodorsally, sometimes with this furrow occluded, usually with epomia very sharply raised and subvertical, but sometimes shorter and weaker or vestigial, or, in a few taxa, with lower end more or less reaching pronotal margin; mesoscutum moderately short, convex, with broad, and generally rather weakly impressed notauli, without a crestlike carina in front of each notaulus; mesoscutum most usually smooth, polished and glabrous, sometimes slightly

granulate and occasionally finely and sparsely hirsute all over; posterolateral flange of mesoscutum moderately broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum of moderately short length, evenly declivous posteriorly, dorsally almost always with lateromedian longitudinal carinae quite strong, anteriorly parallel, posteriorly joining the complete posterior transverse carina, rarely with carinae vestigial or absent; hind coxal socket confluent with metasomal foramen. Legs moderately slender, with fourth tarsomere from subquadrate to slightly transverse, the fifth tarsomere strongly expanded, with femora slender, and with hind tibia with no trace of a groove on inner surface; tarsal claws of female short, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* < 0.3 times as long as abscissa of *M* between *2rs-m* and *2m-cu*, sometimes occluded by fusion of *Rs* and *M*; hind wing with basal abscissa of *M* + *Cu* fairly evenly but strongly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu* usually absent, occasionally present. Metasoma with tergite I subquadrate to elongate; tergite II with distinct and generally very sharply impressed anterolateral and posterolateral oblique grooves, defining a central evenly convex, raised rhombic area; tergite III generally similar, but with central area more strongly transverse and sometimes not clearly delineated anteriorly; tergite IV similar, but with generally only a weak transverse impression posteriorly; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike or slightly flattened; ovipositor straight or sometimes very short and up-curved, projecting beyond apex of metasoma by < 0.5 of length of hind tibia, generally very slender apically and always with conspicuous basal ventral and median swellings.

*Comments.* This large cosmopolitan genus comprises thirty-eight described species (Yu & Horstmann, 1997), but many undescribed species exist in museum collections, and *Zatypota* probably includes as many species as there are in all the other genera in the *Polysphincta* genus-group combined. *Zatypota* is characterized by the sculpture of tergites II–IV, all of which have the central area flat or very weakly convex, and bordered posteriorly by sharp transverse grooves. When anterolateral oblique grooves are present on tergites II and III, the central areas are rhombic or transversely rhombic. All species have a short ovipositor which is centrally swollen and tapered to a long fine point apically. Almost all species have the posterior transverse carina of the propodeum complete and horseshoe-shaped, and most have the lateromedian longitudinal carinae reaching back to this carina. A very few species have reduced carinae and a few, such as the Australian species *Z. velata*, have no propodeal carinae at all. Most species of *Zatypota* also have an epomia, a polished and almost glabrous mesoscutum and lack the distal abscissa of *Cu* in

the hind wing, but there are exceptions to all these. The European *Z. bohemani* has the mesoscutum closely hirsute and has the distal abscissa of *Cu* present in the hind wing, and several undescribed Afrotropical species (in BMNH) virtually lack an epomia. A few species (such as *Z. petronae*) have the upper part of the epomia very strong and continued almost to the front margin of the pronotum, rather similar to species of *Acrodactyla*.

*Zatypota* has not been differentiated clearly from *Sinarachna* in the past, and at least one Palaearctic species attributed to the latter genus, *S. anomala*, is better placed in *Zatypota* (*Zatypota anomala* Holmgren, **comb.n.**). True *Sinarachna* species all have a broad shallow transverse groove on tergite III with the area before this slightly concave centrally, an ovipositor that projects beyond the apex of the metasoma by more than the length of tergite II, and, most characteristically, have a narrow gap medio-dorsally in the occipital carina. This carina is generally always complete in *Zatypota* species, although in some Neotropical species, such as the *Z. morsei* species-group (Gauld, 1991), it is entirely absent dorsally.

*Zatypota* species are reared most commonly as ectoparasitoids on species of Theridiidae (Nielsen, 1923; Jiménez, 1987; Fitton *et al.*, 1988). The ichneumonid's egg is attached to the abdomen of the host, often close to the petiole. The cocoon of some species, such as *Z. albicoxa* and *Z. dandiensis*, is rather dense and subcylindrical, with whorls of looser silk on its outer surface. Some other species, such as *Z. bohemani*, have a rather open cocoon of loose whorls, rather like that of hemerobiids, which may account for records of some having been reared from such hosts (e.g. Maneval, 1935). A few records concern some *Zatypota* species parasitizing other hosts and require confirmation, but others, such as *Z. anomala* and *Z. pulchrator* attacking various species of Dictynidae (Howard, 1888; Lichtenstein & Rabaud, 1922; but see note in Aubert, 1969), almost certainly are correct. Whether or not the dictynid parasitoids form a clade within *Zatypota* is unknown, but more information about host ranges would be interesting. Some more questionable records exist on Araneidae (Aubert, 1969; Constantineanu & Pisica, 1977), Agelenidae (Uchida, 1927 in Aubert, 1969) and Tetragnathidae (Bignell, 1898; Morley, 1908; Schmiedeknecht, 1934; Aubert, 1969).

### *Oxyrrhexis* Foerster

*Oxyrrhexis* Foerster, 1869: 166. Type-species: *Cryptus carbonator* Gravenhorst, by subsequent designation (Schmiedeknecht, 1888).

*Diagnosis.* Mandibles moderately strongly tapered, twisted about 20–40°, with upper tooth slightly the longer; palp formula 5 : 4; clypeus very flat, separated from face by a very weakly impressed clypeofacial suture, the clypeus transverse, with lateral margins somewhat angulate, centrally truncate; lower face elongate, smooth and very sparsely punctate; surface of



eye with very sparse inconspicuous pubescence; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally complete. Pronotum in profile moderately long, mediodorsally without a median ridge extending forwards from hind margin, with upper part of epomia strong and subvertical; mesoscutum moderately long, convex, with deeply impressed notauli, uniformly punctate, quite densely hirsute; posterolateral flange of mesoscutum strongly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, usually without carinae, but, in one species, lateral longitudinal carinae quite strong, reaching back to and joining posterior transverse carina; hind coxal socket confluent with metasomal foramen. Legs very slightly specialized, to with the fore femur distinctly incrassate, generally with third and fourth tarsomeres subquadrate or transverse, the fifth tarsomere is strongly expanded; tarsal claws of female moderately short, with a high basal lobe. Fore wing with  $3rs-m < 0.5$  of length of  $M$  between  $3rs-m$  and  $2m-cu$ ; hind wing with basal abscissa of  $M + Cu$  fairly evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of  $Cu1$  present, spectral. Metasoma with tergite I not elongate, posteriorly more or less as wide as long; tergite II usually with broad shallow anterolateral oblique grooves, and centrally strongly biconvex; tergite III biconvex, tergite IV almost biconvex; all these tergites usually smooth with close coarse punctures in grooves, more sparsely and shallowly punctate on convexities; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight or slightly sinuous, projecting beyond apex of metasoma by about 0.25 of length of hind tibia or slightly less, moderately stout, awl-like, with a basal ventral swelling, and without upper valve basally broadened.

*Comments.* This small Palaearctic genus comprises two described species: *Oxyrrhexis carbonator* and *O. eurus* Kasparyan (Yu & Horstmann, 1997). The literature includes a wide range of purported hosts for *O. carbonator* including species of Theridiidae, Linyphiidae, Araneidae, Tetragnathidae and Thomisidae, but all require verification. However, there are records in both Europe and North America of this wasp attacking species of *Steatoda* (Theridiidae) (Aubert, 1969; Carlson, 1979; Shaw, 1994).

### ***Polysphincta* Gravenhorst**

*Polysphincta* Gravenhorst, 1829: 112. Type-species: *Polysphincta tuberosa* Gravenhorst, by subsequent designation (Schmiedeknecht, 1888).

*Diagnosis.* Mandibles moderately strongly tapered, twisted about 0–5°, with upper tooth usually distinctly the longer; palp formula 5 : 4; clypeus flat, separated from face by a very weakly impressed clypeofacial suture, the clypeus transverse, apically centrally truncate, with lateral margins straight; lower face usually slightly elongate, smooth and very sparsely punctate; surface of eye glabrous; ocelli usually rather small, in a few tropical taxa quite large and fairly close to eye margins; head posteriorly abruptly tapered, occipital carina mediodorsally complete, generally not raised to form a flange. Pronotum in profile moderately long, mediodorsally flat, or with hind margin slightly forming a shelflike promontory; with a sharp vertical epomia; mesoscutum moderately long, convex, with weakly impressed notauli, sparsely punctate, from quite densely and uniformly hirsute in Holarctic species to smooth and glabrous in tropical taxa; posterolateral flange of mesoscutum quite strongly broadened; mesopleuron with epicnemial carina present, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, usually without carinae; hind coxal socket not separated from metasomal foramen by a sclerotized bridge. Legs very slightly specialized, to with the fore femur slightly incrassate, with the fourth tarsomere subquadrate or transverse, the fifth tarsomere is strongly expanded; tarsal claws of female moderately long, with a high subbasal lobe. Fore wing with  $3rs-m$  entirely absent,  $2rs-m < 0.5$  times as long as abscissa of  $M$  between  $2rs-m$  and  $2m-cu$ ; hind wing with basal abscissa of  $M + Cu$  evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner almost right angled; distal abscissa of  $Cu1$  present, spectral. Metasoma with tergite I slightly elongate; tergite II with weak anterolateral oblique grooves, and centrally weakly convex; tergite III weakly biconvex, tergite IV almost evenly convex; all these tergites usually smooth with isolated fine punctures; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight or slightly sinuous, projecting beyond apex of metasoma by about 0.65 or more of length of hind tibia or slightly less, moderately slender, rapierlike, with a distinct basal ventral swelling, without upper valve basally broadened.

*Comments.* *Polysphincta* is a large Holarctic/Neotropical genus with twenty-five described species (Yu & Horstmann, 1997). At various times, most pimelines associated with spiders have been placed in this genus. This is never recovered as a monophyletic group; it is paraphyletic with respect to *Acrotaphus/Hymenoepimecis*, and these genera, together with *Ticapimpla*, form a monophyletic group.

Rather more is known about the biology of these species than other polysphinctines (Fitton *et al.*, 1988). The genus is associated primarily with Araneidae, although two doubtful records report *Polysphincta* species on Theridiidae and Miturgidae (Aubert, 1969). The larva is positioned towards the anterior end of the abdomen. The

cocoon is parchmentlike or loosely woven, fusiform and with a caudal orifice. In Costa Rica, *P. gutfreundi* Gauld parasitizes *Allocyclosa bifurca* (Araneidae) (W. Eberhard, pers. com.), and we have seen six specimens of *P. janzeni* reared from *Cyclosa fililineata* (Araneidae) in Brazil.

### *Ticapimpla* Gauld

*Ticapimpla* Gauld, 1991: 342. Type-species: *Ticapimpla vilmae* Gauld, by original designation.

**Diagnosis.** Mandibles moderately strongly tapered, twisted about 0–15°, with upper tooth distinctly the longer; palp formula 5 : 4; clypeus flat, separated from face by a very weakly impressed clypeofacial suture, the clypeus transverse, apically centrally truncate, with lateral margins straight; lower face slightly elongate, smooth and very sparsely punctate; surface of eye glabrous; ocelli quite large and fairly close to eye margins; head posteriorly abruptly tapered, occipital carina mediodorsally complete, raised to form a flange. Pronotum in profile moderately long, mediodorsally flat without a discernible epomia; mesoscutum moderately long, convex, with weakly impressed notauli, sparsely punctate, quite densely and uniformly hirsute; posterolateral flange of mesoscutum quite strongly broadened; mesopleuron with epicnemial carina absent, only discernible medioventrally as a tubercle; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, without carinae; hind coxal socket separated from metasomal foramen by a narrow sclerotized bridge. Legs very slightly specialized, to with the fore femur slightly incrassate, with the fourth tarsomere subquadrate or transverse, the fifth tarsomere is strongly expanded; tarsal claws of female moderately long, with a high subbasal lobe or in one species with a lobelike tooth. Fore wing with *3rs-m* entirely < 0.5 times as long as abscissa of *M* between *2rs-m* and *2m-cu*; hind wing with basal abscissa of *M + Cu* evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly acute to almost right angled; distal abscissa of *Cu1* present, spectral. Metasoma with tergite I slightly elongate; tergite II with weak anterolateral oblique grooves, and centrally weakly convex; tergite III weakly biconvex, tergite IV almost evenly convex; all these tergites usually smooth with isolated fine punctures; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight or slightly sinuous, projecting beyond apex of metasoma by about 0.65 of length of hind tibia or slightly less, moderately slender, rapierlike, with a distinct basal ventral swelling, without upper valve basally broadened.

**Comments.** *Ticapimpla*, a small tropical American genus, includes a single described species from Costa

Rica (Gauld, 1991) and several other undescribed species from South America (I. Sääksjärvi, pers. comm.). The head is modified in a similar way to *Acrotaphus/Hymenoepimecis*, with the occipital carina flangelike and extending backwards over the anterior rim of the pronotum, but it differs from either in having the mesoscutum uniformly hirsute and the submetapleural carina strong. The biology of this species is unknown, but pale colour and large ocelli suggest nocturnal activity. Previously (Gauld, 1991), the characteristic form of the claw, with a lobelike tooth, but no real lobe, is now seen as pertaining only to the type-species, with others (in ZMTU) having a more normal claw with a large basal lobe.

Nothing is known about the biology of any of the species in this genus.

### *Acrotaphus* Townes

*Acrotaphus* Townes in Townes & Townes, 1960: 256. Type-species: *Epimecis wiltii* Cresson, by original designation.

**Diagnosis.** Mandibles moderately strongly tapered, twisted about 40–85°, with upper tooth slightly the longer; palp formula 5 : 4; clypeus very weakly convex, separated from face by a very weakly impressed clypeofacial suture, the clypeus rather long, often subquadrate, with lateral margins somewhat angulate; lower face elongate, smooth and very sparsely punctate; surface of eye with very sparse pubescence; ocelli small and remote from eye margins; head posteriorly evenly rounded, occipital carina mediodorsally complete. Pronotum in profile moderately long, mediodorsally with a weak median ridge extending forwards from hind margin, with upper part of epomia strong and subvertical; mesoscutum moderately long, convex, with impressed notauli, sparsely punctate, quite densely hirsute; posterolateral flange of mesoscutum strongly broadened; mesopleuron with epicnemial carina well developed, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled opposite mesepisternal scrobe; submetapleural carina complete; propodeum moderately long, evenly declivous posteriorly, usually without carinae, but, in one species, the posterior transverse carina is strong; hind coxal socket separated from metasomal foramen by a broad sclerotized bridge. Legs from very slightly specialized, to with the fore femur distinctly incrassate, generally with the third and fourth tarsomeres subquadrate or transverse, the fifth tarsomere is strongly expanded; tarsal claws of female moderately long, with a high basal lobe. Fore wing with *3rs-m* entirely absent, *2rs-m* long; hind wing with basal abscissa of *M + Cu* evenly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu1* present, spectral. Metasoma with tergite I elongate; tergite II usually with weak anterolateral oblique grooves, and centrally weakly convex, although in one species a more strongly convex rhombic area is

discernible; tergite III weakly biconvex, tergite IV almost evenly convex; all of these tergites usually smooth with isolated fine punctures, in one species finely but more conspicuously punctate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight or slightly sinuous, projecting beyond apex of metasoma by about 0.8 of length of hind tibia or slightly less, moderately slender, awl-like, with a basal ventral swelling, without upper valve basally broadened.

*Comments.* *Acrotaphus* is a large genus of physically large polysphinctines (fore wing length 7.5–18.0 mm). Ten species have been described (Yu & Horstmann, 1997), mostly from the Neotropics, but with one, *A. wiltii* (Cresson), from North America. However, several apparently undescribed species are present in large museum collections. Most *Acrotaphus* species are yellowish brown with large ocelli and are nocturnally active. They are parasitoids of orb-web spinning spiders of the families Araneidae and Tetragnathidae (Gauld, 1991; Eberhard, 2000b), and the spider is generally attacked whilst sitting in the web. The cocoon is fusiform, golden and loosely spun of coarse silk, covered externally with loops of silk. It is spun in the host spider's web. Unlike many other derived polysphinctines, the cocoons of *Acrotaphus* species lack a distinct caudal orifice (although some species do have a small hole that probably results from the wasp larvae poking its hind end through the cocoon to defecate).

#### *Hymenoepimecis* Viereck

[*Epimecis* Brullé in Lepelletier, 1846: 112. Type-species: *Epimecis bicolor* Brullé, by subsequent designation (Ashmead, 1900: 54). Junior homonym of *Epimecis* Huebner 1825.]

*Hymenoepimecis* Viereck, 1912: 149. [Replacement name for *Epimecis* Brullé.]

*Diagnosis.* Mandibles moderately strongly tapered, twisted about 10–85°, with upper tooth slightly the longer; palp formula 5 : 4; clypeus almost flat, separated from face by a very weakly impressed clypeofacial suture, the clypeus transverse, often subquadrate, with lateral margins somewhat straight, centrally truncate; lower face elongate, smooth and very sparsely punctate; surface of eye with very sparse pubescence; ocelli often large and contiguous with eye margins; head posteriorly evenly constricted with occipital carina broadened and flangelike, occipital carina mediodorsally complete. Pronotum in profile often very long, mediodorsally with a distinct forwardly directed pocketlike structure, with epomia absent; mesoscutum moderately long, convex, with impressed notauli, sparsely punctate, glabrous; posterolateral flange of mesoscutum quite strongly broadened; mesopleuron with epicnemial carina vestigial or absent, its upper end remote from anterior margin of pleuron; mesopleural sulcus angled

opposite mesepisternal scrobe; submetapleural carina from complete to entirely absent; propodeum moderately long, evenly declivous posteriorly, usually without carinae; hind coxal socket separated from metasomal foramen by a broad sclerotized bridge. Legs from very slightly specialized, to with the fore femur distinctly incrassate, generally with the third and fourth tarsomeres subquadrate or transverse, the fifth tarsomere is strongly expanded; tarsal claws of female moderately long, with a high basal lobe that, in some species, is reduced to a lamellate toothlike structure. Fore wing with  $3rs-m < 0.5$  times as long as abscissa of *M* between  $2rs-m$  and  $2m-cu$ ; hind wing with basal abscissa of *M* + *Cu* evenly and uniformly bowed; subbasal cell not exceptionally broad, with anterodistal corner slightly obtuse; distal abscissa of *Cu*1 usually present. Metasoma with tergite I elongate; tergite II usually with weak anterolateral oblique grooves, and centrally weakly convex, although, in one species, a more strongly convex rhombic area is discernible; tergite III weakly biconvex, tergite IV almost evenly convex; all of these tergites usually smooth with isolated fine punctures, in one species finely but more conspicuously punctate; laterotergites II–IV inconspicuous; hind end of metasoma unspecialized, cercus fingerlike; ovipositor straight, projecting beyond apex of metasoma by about 1.2 times the length of hind tibia or slightly less, slender, rapierlike, with a distinct basal ventral swelling, with upper valve basally broadened.

*Comments.* *Hymenoepimecis* is a large Neotropical genus of large-sized polysphinctines (fore wing length 6.5–14.0 mm). Most species are yellowish brown with large ocelli and are nocturnally active. They are parasitoids of orb-web spinning spiders of the families Araneidae and Tetragnathidae (Gauld, 1991; Eberhard, 2000b), and the spider generally is attacked whilst sitting in the web. The cocoon is fusiform, golden and tightly spun of coarse silk. It is spun in the spider's web. Unlike the cocoon of *Acrotaphus* species, the cocoon of *Hymenoepimecis* species has a distinct caudal orifice.

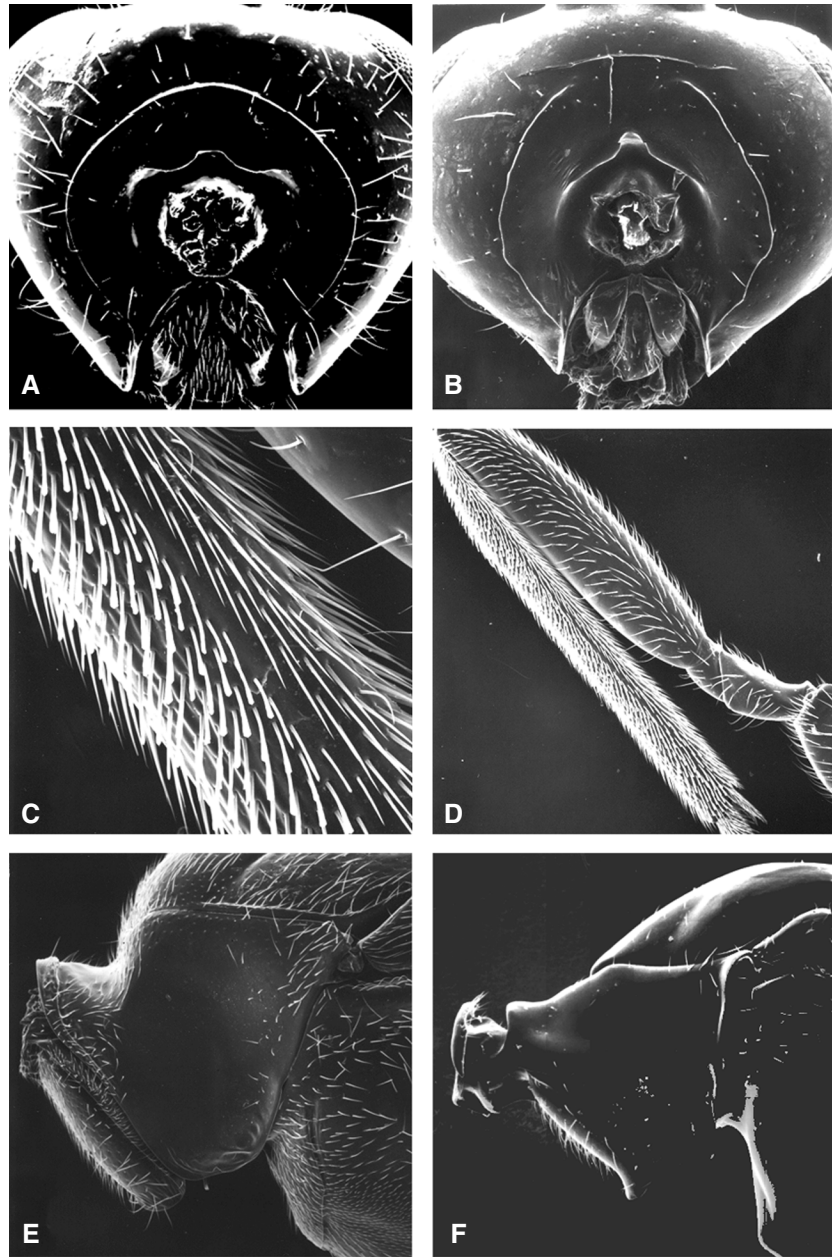
#### Key to females<sup>1</sup> of the genera of the *Polysphincta* genus-group

1. Proximal end of lower valve of ovipositor not expanded, at most slightly membranous laterally close to base (Fig. 6A–C) . . . . . 2
- Proximal end of lower valve of ovipositor expanded to form a lobe which may be low and rounded or strong and somewhat angulate distally (Fig. 5A) . . . . . 7
2. Ovipositor weakly to strongly up-curved towards the apex (Fig. 6A); *either* with clypeus and lower face

<sup>1</sup>Males are morphologically too generalized to be keyed easily (although some can be recognized by comparison with females) and, for some genera (*Pterinopus*, *Inbioia*, *Ticapimpla*), males are as yet unknown.

- forming a more or less flat, continuous surface, without a distinctly impressed clypeofacial suture *or* with fore wing with an enclosed areolet, thus vein *3rs-m* present . . . . . *Schizopyga*  
Ovipositor straight or very slightly sinuous (Fig. 6B, C); clypeus weakly convex or ridged basally, not forming a continuous flat surface with lower face, with a distinctly impressed clypeofacial suture; fore wing with vein *3rs-m* entirely absent . . . . . 3
3. Mesoscutum evenly convex, without deeply impressed notauli, centrally granulate to coarsely and closely punctate; mesopleural suture straight, not slightly angled opposite mesepisternal scrobe; metasoma with tergites II and III more or less evenly convex, coarsely and punctate, without transverse impressions or convex lateromedian swellings (Fig. 3) . . . . . 4
4. Mesoscutum trilobed, with deeply impressed notauli, centrally smooth to finely and sparsely punctate; mesopleural suture slightly angled opposite mesepisternal scrobe; metasoma with tergites II and III usually with transverse impressions or convex lateromedian swellings, if rather evenly convex, then more or less smooth and very sparsely punctate . . . . . 5
4. Metasoma with tergite VIII very long, laterally with a crescentic lateral fenestra from which protrudes a three-branched hirsute appendage; apex of tergite VIII elongate, overhanging large, globose cerci (Fig. 3); hind wing with distal abscissa of *Cu1* entirely absent . . . . . *Inbioia*  
Metasoma with tergite VIII shorter than tergite VII, without a lateral fenestra and without branched appendages; apex of tergite VIII short, not overhanging slender, fingerlike cerci; hind wing usually with distal abscissa of *Cu1* present though weak. . . . . *Piogaster*
5. Proximal end of upper valve of ovipositor broadened, laterally with a triangular scabrous area (Fig. 6B); mandibles weakly and evenly tapered, not twisted; clypeus rather strongly convex, usually swollen near base, so there is a strong clypeofacial suture; fore leg very stout, with tarsomere 2 subquadrate and tarsomere 3 transverse . . . . . *Zabrachypus*  
Proximal end of upper valve of ovipositor not unusually broadened, laterally without a triangular scabrous area (Fig. 6C); mandibles strongly tapered, often twisted; clypeus weakly and evenly convex, with a weakly impressed clypeofacial suture; fore leg not exceptionally stout, with tarsomere 2 elongate, and often with tarsomere 3 subquadrate . . . . . 6
6. Foramen where metasoma inserts into propodeum confluent with hind coxal cavity (Fig. 6G); tergite III with conspicuous anterolateral rounded swellings, and with a median rounded swelling behind these; lower valve of ovipositor with very weak ridges on proximal 0.3 . . . . . *Chablisea* **gen.n.**  
Foramen where metasoma inserts into propodeum separated from hind coxal cavity by a sclerotized bridge (Fig. 6H); tergite III from weakly and evenly convex to with low indistinct lateromedian swellings, never with a median rounded swelling behind these; lower valve of ovipositor smooth, without any trace of ridges on proximal 0.3 . . . . . *Brachyzapus* **gen.n.**
7. Hind tibia with an impressed longitudinal groove on inner surface, this groove often slightly granulate and sculpturally differentiated from the remainder of the tibial surface (Figs 4C, D; 5B), or sometimes rather faint<sup>2</sup> . . . . . 8  
Hind tibia without any trace of a longitudinal groove on inner surface. . . . . 10
8. Pronotum quite long, with epomia more or less entirely absent; ovipositor long, projecting beyond apex of metasoma by about 1.0 or more times length of hind tibia . . . . . *Eriostethus*  
Pronotum short, with upper part of epomia strongly raised; ovipositor short, projecting beyond apex of metasoma by 0.5 or less times length of hind tibia . . . . . 9
9. Metasoma with tergites II–III with oblique grooves defining a more or less rhombic raised central area, this area finely granulate, matt. . . . . *Flacopimpla*  
Metasoma with tergites II–III without distinct oblique grooves defining a central raised area, the entire surface of the tergites more or less smooth and somewhat polished . . . . . *Megaetaira* **gen.n.**
10. Mandible with upper tooth very broad and blunt (Fig. 6I) . . . . . *Longitibia*  
Mandible with upper tooth slender and very acutely pointed . . . . . 11
11. Head posteriorly with occipital carina raised on a flangelike protuberance which, in profile, is almost horizontal or even slightly up-curved; pronotum moderately to very conspicuously lengthened, the horizontal part tending to extend slightly into a concavity on the back of the head . . . . . 12  
Head posteriorly more or less evenly rounded, occipital carina not flangelike; pronotum generally not conspicuously lengthened . . . . . 14
12. Mesoscutum uniformly closely hirsute; submetapleural carina very strong and complete . . . . . *Ticapimpla*  
Mesoscutum glabrous or with isolated sparse hairs; submetapleural carina more or less absent, or incomplete and weak (Fig. 5D) . . . . . 13
13. Neck region of propodeum with a mediodorsal pocketlike structure (Fig. 4F); epicnemial carina usually absent, sometimes present but weak . *Hymenoepimecis*  
Neck region of propodeum simple, without a mediodorsal pocketlike structure; epicnemial carina always very strongly raised ventrally . . . . . *Acrotaphus*
14. Mesoscutum with a strong vertical sharp crest at end of notaulus; pronotum with upper part of epomia very strong, extended forwards and down to reach and slightly protrude beyond margin of pronotum very high up (Fig. 6D). . . . . *Acrodactyla*  
Mesoscutum without a distinct vertical sharp crest at end of notaulus; pronotum with epomia variously

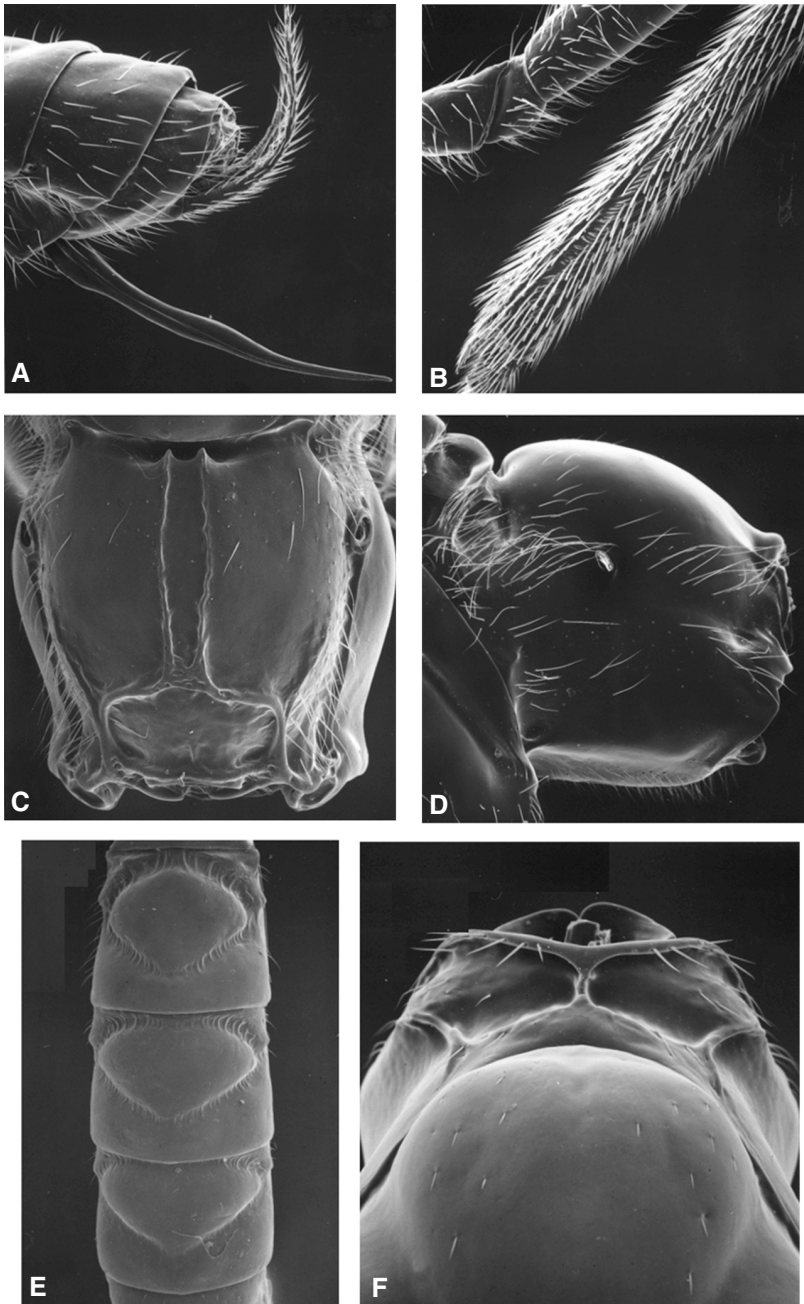
<sup>2</sup>In *Megaetaira*, this groove is rather faint and could be overlooked; thus, to facilitate reliable identification, we have taken this genus out both sides of this couplet.



**Fig. 4.** Scanning electron micrographs of polysphinctines. A, B, head, posterior; A, *Zatyptota alborhombata*; B, *Sinarachna pallipes*. C, D, hind tibia *Eriostethus* sp., C showing detail. E, F, pronotum, lateral; E, *Eruga* sp.; F, *Hymenoepimecis* sp.

- developed, if strong then not extended forwards to reach and slightly protrude beyond margin of pronotum very high up, but often angled downwards (Fig. 6E) . . . . . 15
15. Fore and mid femora with a median toothlike promontory ventrally; tarsal claws with distinct basal fringes (Fig. 6H) . . . . . *Pterinopus*  
Fore and mid femora without a median toothlike promontory ventrally; tarsal claws basally without fringes. . . . . 16
16. Metasoma with tergite III with a strongly and sharply impressed transverse groove about 0.7 of its

length, the area in front of this groove flat or very weakly and evenly convex (Fig. 5E), sometimes with oblique grooves anterolaterally making this area rhombic; propodeum usually with posterior transverse carina complete, horseshoe-shaped, and often with lateromedian longitudinal carinae reaching back to it (Fig. 5C) . . . . . *Zatyptota*  
Metasoma with tergite III without a sharply impressed transverse groove about 0.7 of its length, at most with a broad, shallow groove in this position, and then usually with the area in front of this groove biconvex or centrally depressed;



**Fig. 5.** Scanning electron micrographs of polysphinctines. A, ovipositor, *Zatypota alborhombata*; B, hind tibia, *Megaetaira madida*; C, propodeum dorsal, *Zatypota alborhombata*; D, propodeum lateral, *Acrotaphus* sp.; E, tergites II–IV, *Zatypota alborhombata*; F, metasoma, *Reclinervellus* sp.

propodeum with posterior transverse carina absent or incomplete centrally. . . . . 17

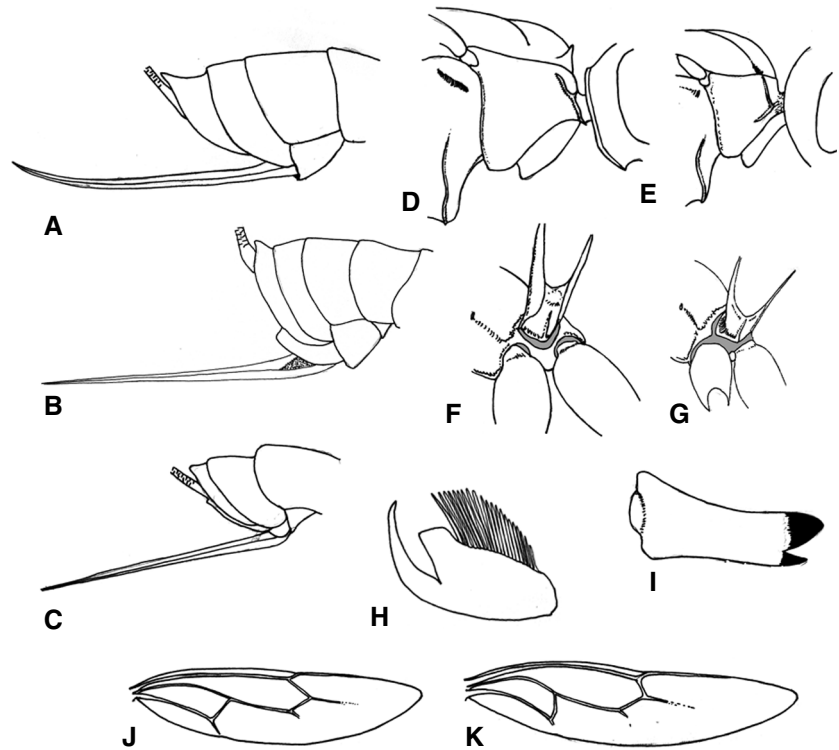
17. Pronotum mediodorsally with a longitudinal flange from fore margin to collar (Fig. 5F); hind wing with subbasal cell broad, somewhat acutely pointed anterodistally with vein *Cu* and *cu-a* (the nervellus) almost straight and oblique (Fig. 6J); metasoma with tergite III with prominent lateromedian convexities, and with a single posteromedian convex area behind these. . . . . *Reclinervellus*

Pronotum mediodorsally without a longitudinal flange from fore margin to collar; hind wing with subbasal cell

not unusually broad, somewhat right angled or obtusely pointed anterodistally (Fig. 6K); metasoma with tergite III various, *if* with prominent lateromedian convexities, *then* never with a single posteromedian convex area behind these . . . . . 18

18. Tergite III more or less evenly convex, with very weak impressions posterolaterally; tergite IV simply evenly convex; foramen where metasoma inserts into propodeum separated from hind coxal cavity by a sclerotized bridge . . . . . 19

Tergite III with moderate to strong posterolateral impressions, and most usually with the area in front



**Fig. 6.** Polysphinctinae. A–C, ovipositor, lateral; A, *Schizopyga avivae*; B, *Zabrachypus primus*; C, *Chabisea* sp. (Malaysia). D, E, pronotum lateral; D, *Acrodactyla* sp.; E, *Megaetaira madida*. F, G, hind end of propodeum, tergite I, posteroventral (membranous area is shaded); F, *Brachyzapus tenuiabdominalis*; G, *Chablisea imbiba*. H, hind tarsal claw, *Pterinopus scambus*. I, mandible, *Longitibia sinica*. J, K, hind wing; J, *Reclinervellus nielsenii*; K, *Eruga yehi*.

- of this biconvex; tergite IV always weakly biconvex or laterally swollen; foramen where metasoma inserts into propodeum confluent with hind coxal cavity . . . . . 20
19. Pronotum with epomia dorsally strong, its lower end short, curved down and parallel to anterior margin of pronotum (Fig. 6E); mesoscutum with scattered sparse pubescence . . . . . *Megaetaira* **gen.n.**  
Pronotum with epomia more or less entirely absent (Fig. 4E); mesoscutum centrally more or less entirely glabrous . . . . . *Eruga*
20. Occipital carina with a narrow mediodorsal discontinuity (Fig. 4B); hind wing with distal abscissa of *Cul* entirely absent, and mesoscutum with sparse pubescence all over. . . . . *Sinarachna*  
Occipital carina dorsally complete (cf. Fig. 4A); either with hind wing with distal abscissa of *Cul* discernible, or, if it is absent, then mesoscutum is entirely glabrous . . . . . 21
21. Ovipositor short, 0.8 or less times as long as hind tibia; metasoma with tergites II and III with close fairly coarse punctures . . . . . *Oxyrrhexis*  
Ovipositor long, 1.0 or more times as long as hind tibia; metasoma with tergites II and III generally smooth and almost impunctate centrally, at most with sparse, scattered punctures . . . . . *Polysphincta*

### Supplementary material

The data matrix is available at: <http://www.blackwell-synergy.com> under the DOI reference doi: 10.1111/j.1365-3113.2006.00334.x

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## Appendix 1. The taxa used in the analysis, and the geographical area in which they occur

The polysphinctines are arranged in the groups recognized from this study, but we have used their original generic placements to show where confusion has occurred in the past. These incorrect placements are shown by enclosing the generic name in quotation marks and, for each, a new generic assignment has been made in the reclassification section. The six-letter code given after each taxon refers to the code used for brevity in the data matrix.

### Outgroups

*Delomerista diprionis* Cushman (Nearctic) [DEL DIP]  
*Acropimpla alboricta* (Cresson) (Nearctic) [ACP ALB]  
*Gregopimpla inquisitor* (Scopoli) (Palearctic) [GRE INQ]  
*Iseropus stercorator* (Fabricius) (Palearctic) [ISO STE]  
*Tromatobia blancoi* Gauld (C. America) [TRO BLA]  
*Tromatobia oculatoria* (Fabricius) (Palearctic) [TRO OCU]  
*Zaglyptus simonis* (Marshall) (Neotropic) [ZAG SIM]  
*Zaglyptus varipes* (Gravenhorst) (Palearctic) [ZAG VAR]  
*Clistopyga calixtoi* Gauld (C. America) [CLI CAL]  
*Clistopyga henryi* Gauld (C. America) [CLI HEN]  
*Clistopyga incitator* (Fabricius) (Palearctic) [CLI INC]  
*Clistopyga mami* Cushman (Nearctic) [CLI MAN]

### The *Piogaster* clade

*Inbioia pivai* Gauld & Ugalde (C. America) [INB PIV]  
*Piogaster pilosator* (Aubert) (W. Palearctic) [PIO PIL]  
*Piogaster* sp. 1 (in AEIC) (Nearctic) [PIO SP1]

### The *Schizopyga* clade

*Dreischbachia avivae* Gauld (C. America) [DRE AVI]  
*Dreischbachia lutea* Gauld (Australia) [DRE LUT]  
*Dreischbachia mira* (Tosquinet) (S.E. Asia) [DRE MIR]  
*Dreischbachia pictifrons* (Thomson) (W. Palearctic) [DRE PIC]  
*Dreischbachia slossonae* (Davis) (Nearctic) [DRE SLO]  
*Dreischbachia* sp. 3 (in AEIC) (Taiwan) [DRE SP3]  
‘*Zabrachypus*’ *curvicauda* (Seyrig) (Kenya) [ZAB CUR]  
*Schizopyga frigida* Cresson (Holarctic) [SCH FRI]  
*Schizopyga* sp. 1 (in AEIC) (Afrotropical) [SCH SP1]  
*Zabrachypus primus* Cushman (Nearctic) [ZAB PRI]  
*Zabrachypus moldavicus* Constantineanu<sup>2</sup> (W. Palearctic) [ZAB MOL]  
‘*Zabrachypus*’ *nikkoensis* (Uchida) (E. Palearctic) [ZAB NIK]  
‘*Zabrachypus*’ *tenuiabdominalis* (Uchida) (E. Palearctic) [ZAB TEN]

‘*Zabrachypus*’ *unicarinatus* (Uchida & Momi) (E. Palearctic) [ZAB UNI]  
‘*Dreischbachia*’ sp. 4 (in AEIC) (Taiwan) [DRE SP4]  
‘*Zabrachypus*’ sp. 1 (in AEIC) (Taiwan) [ZAB SP1]  
WAHL **gen.n.** (in AEIC) (New Guinea) [WAH GEN]  
Genus A sp. 1 (in BMNH) (W. Malaysia) [GEN A01]

### The *Polysphincta* clade

*Reclinervellus* sp. 1 (in BMNH) (Sri Lanka) [REC SP1]  
*Reclinervellus* sp. 2 (in BMNH) (Sumatra) [REC SP2]  
‘*Oxyrrhexis*’ sp. 1 (in AEIC) (W. Malaysia) [OXY SP1]  
‘*Polysphincta*’ *nielseni* Roman (W. Palearctic) [POL NIE]  
*Sinarachna nigricornis* (Holmgren) (Palearctic) [SIN NIG]  
*Sinarachna pallipes* (Holmgren) (Palearctic) [SIN PAL]  
*Acrodactyla cursor* Gauld (Australia) [ACR CUR]  
*Acrodactyla degener* (Haliday) (Holarctic) [ACR DEG]  
*Acrodactyla micans* Gauld (Australia) [ACR MIC]  
*Acrodactyla quadrisculpta* (Gravenhorst) (Palearctic) [ACR QUA]  
*Acrodactyla* sp. 1 (in BMNH) (India) [ACR SP1]  
*Pterinopos scambus* Townes (Madagascar) [PTE SCA]  
‘*Acrodactyla*’ *madida* (Haliday) [ACR MAD]  
*Eruga rufa* Townes (Nearctic) [ERU RUF]  
*Eruga yehi* Gauld (C. America) [ERU YEH]  
*Eruga* sp. 1 (in BMNH) (Cameroon) [ERU SP1]  
*Flacopimpla varelae* Gauld (C. America) [FLA VAR]  
‘*Zatypota*’ *gerardoi* Gauld, Ugalde & Hanson (C. America) [ZAT GER]  
‘*Zatypota*’ *parva* (Cresson) (Nearctic) [ZAT PAR]  
*Eriostethus maximus* Gauld (Australo-Papuan) [ERI MAX]  
*Eriostethus perkinsi* (Baltazar) (Australia) [ERI PER]  
*Eriostethus pulcherrimus* Morley (Australia) [ERI PUL]  
*Eriostethus* sp. A (in BMNH) (Fiji) [ERI SPA]  
*Longitibia sinica* (He & Ye) (China) [LON SIN]  
*Zatypota bohemani* (Holmgren) (Holarctic) [ZAT BOH]  
*Zatypota kauros* Gauld (Australia) [ZAT KAU]  
*Zatypota percontatoria* (Müller) (Holarctic) [ZAT PER]  
*Zatypota petronae* Gauld (C. America) [ZAT PET]  
*Zatypota riverai* Gauld (C. America) [ZAT RIV]  
‘*Sinarachna*’ *anomala* (Holmgren) (Holarctic) [SIN ANO]  
*Oxyrrhexis carbonator* (Gravenhorst) (Holarctic) [OXY CAR]  
*Oxyrrhexis eurus* Kasparyan (Palearctic) [OXY EUR]  
‘*Zabrachypus*’ sp. 2 (in AEIC) (Nearctic) [ZAB SP2]  
*Acrotaphus tibialis* (Cameron) (Neotropic) [ATP TIB]  
*Acrotaphus wiltii* (Cresson) (Nearctic) [ATP WIL]  
*Hymenoepimecis bicolor* (Brullé) (Neotropic) [HYM BIC]  
*Hymenoepimecis argyraphaga* Gauld (C. America) [HYM ARG]  
*Polysphincta gutfreundi* Gauld (C. America) [POL GUT]  
*Polysphincta koebeli* Howard (Nearctic) [POL KOE]  
*Polysphincta purcelli* Gauld (C. America) [POL PUR]  
*Polysphincta shabui* Gauld (C. America) [POL SHA]  
*Polysphincta tuberosa* Gravenhorst (W. Palearctic) [POL TUB]  
*Ticapimpla vilmae* Gauld (C. America) [TIC VIL]  
*Ticapimpla* sp. 1. (*Ilari Sääksjärvi*) (Peru) [TIC SP1]

Appendix 2. Data matrix (Nexus files available as Supplementary Material).

000000000	111111111	222222222	333333333	444444444	555555555	666666666	777777777	888888888	9999999
123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
DEL DIP	000000000	000000000	000000000	000000000	000010000	000000010	100000000	000000000	0000100
ACP ALB	000000000	000010010	010000001	100001001	001001000	000001101	000010000	000001000	0000000
GRE INQ	000000000	000010010	010000001	100001000	101000000	000001101	000010000	010001000	0000000
ISE STE	000000000	000010010	010000001	100000000	101000001	000001101	000010000	010001000	0000000
TRO BLA	000000000	000020300	010000101	110001000	101000000	000001010	000010000	010001100	0002000
TRO OCU	000000000	000010000	010000001	110001000	101000000	000010011	000010000	010001100	0002000
ZAG SIM	110010000	000010010	000002011	110001000	101000011	000001111	010010000	100001100	0000001
ZAG VAR	110010000	000010010	000000011	110001000	101000010	000001111	010010000	100001100	0000001
CLI CAL	110011000	000110010	000000101	110001000	101001000	000000102	010010000	000101100	1011000
CLI HEN	110011000	000010010	100000001	110001000	101000010	000000111	210010000	000101000	1010000
CLI INC	110110000	000010100	000000001	110001000	101001000	000000111	010010000	000101100	1011000
CLI MAN	110110100	000010100	000000200	110001000	101001001	000001111	010010000	000101100	1010000
INB PIV	210000110	020100010	000010010	110000000	111000011	010201001	301000200	010000100	1010000
Pio PIL	210000110	001010030	000310010	110000000	111000011	000010010	301000200	010000100	1010000
Pio SP1	210100010	0?1010030	000310010	11?0000??	11?0000110	010001001	301000200	?10?0?0?	?1?1?1?
DRE AVI	210100010	010100010	010000001	100010001	111000011	000000211	210010000	010001100	1010000
DRE LUT	211100210	010100010	010000001	110010001	111000110	010100011	21?010000	010001100	1010000
DRE MIR	211100210	010100010	010000001	110010001	111000110	000000111	210010000	010001100	1010000
DRE PIC	211100010	010100010	001000001	100010001	111000110	000000111	210010000	010001100	1010000
DRE SLO	211100210	010100010	001000001	100010001	111000110	000000011	210010000	010001100	1010000
DRE SP3	211200010	010100010	000000001	110010011	111000110	000000011	010010000	010000100	1010000
ZAB CUR	211100010	010100010	010000001	110010001	111000110	000000111	010010000	0?0000110	1010000
SCH FRI	212200010	011100010	000000001	000010011	111000111	000000111	310000000	010000220	1010000
SCH SP1	212200010	011100010	000000001	000010011	111000112	010100011	310000000	0?0000220	1010000
ZAB PRI	100000010	030100010	001000001	100010001	111000011	000010110	011000000	0?0000101	1110000
ZAB MOL	100000010	030100010	000000001	100010001	111000011	000010110	011000000	0?0000101	1110000
ZAB NIK	210200010	010100010	001000001	110010001	111000110	000010110	010010000	0?0000100	1010010
ZAB TEN	210200010	010100010	001000001	110010001	111000111	000000110	200000200	010000100	1010010
ZAB UNI	210200010	010100010	001000001	110010001	111000110	000000111	210010200	010000100	1010010
DRE SP4	210100210	010100010	011000001	100011000	111000010	000000112	010010010	0?0000100	1010010
ZAB SP1	210100210	010100010	001000001	100011000	111000010	000000112	210010010	0?0000100	1010010
WAH GEN	210100010	010100010	001000001	100011000	111000010	000000112	010010010	0?0000100	1010010
GEN A01	210100010	010100010	001000001	100011000	111000010	000000112	010010010	0?0000100	1010010
REC SP1	220000010	010100100	000000001	100011000	111000010	011001111	010010010	0?00001002	1020010
REC SP2	220000010	010100100	000000001	100011000	111000010	011001111	010010010	0?00001002	1020010
OXY SP1	220000010	010100010	000000001	100011000	111000010	011001111	010010010	0?00001002	1020010
POL NIE	220000010	010100010	000000001	100011000	111000010	011001111	010010010	0?00001002	1020010
SIN NIG	210000010	010100110	000000001	100011000	111000010	010000110	210010000	0100001002	1010010
SIN PAL	210000010	010100110	000000001	100011000	111000010	010000110	210010000	0100001002	1010010
ACR CUR	210000010	000100010	100000001	000110000	111000012	110000011	210010000	010000001	1010010
ACR DEG	210000010	000100010	100000001	000110000	111000012	110000011	210010000	010000001	1010010
ACR MIC	210100010	001000010	100000001	000110000	111100012	100000011	210010000	0100001001	1020000
ACR QUA	210100010	001000010	100000001	000110000	111000012	100000011	210010000	0100001001	1020000
ACR SP1	210100010	001000010	100000001	000110000	111000012	100000011	210010000	0?00001001	1020000
PTE SCA	210000010	001000010	100000001	000010000	111000012	100000010	210000000	0?00001001	1020000
ACR MAD	210000010	000100010	000000001	100010000	111010012	110000011	210000000	0100001001	1020000
ERU RUF	210000110	010100010	100000001	110010000	111000012	100000010	2101010001	0100002001	1020000
ERU YEH	210000010	010100010	100000001	110010000	111000012	100000011	2101010001	0100002001	1020000

## Appendix 2. Continued.

00000000	1111111111	2222222222	3333333333	4444444444	5555555555	6666666666	7777777777	8888888888	99999999
123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456789	0123456
ERU SP1	010100010	0010200300	1000000001	1100100000	1110000112	1000000111	2101010001	0100002001	1020000
FLA VAR	110100010	0010100000	1000000101	1110110000	1110100112	1000001111	3100200000	0?00002001	1020000
ZAT GER	110100010	0010100000	1000002101	1110110000	1110100112	1000001111	3100200000	0?00002001	1020000
ZAT PAR	110100010	0010100000	1000000101	1110110000	1110100112	1000001111	3100200000	0100002001	1020000
ERI MAX	010100020	0112100301	1000000001	1100110000	1110100110	2100001101	2100200000	0100000001	1020000
ERI PER	010100020	0112100301	1000000001	1100110000	1110100110	2100001101	2100200000	0100000001	1020000
ERI PUL	010100210	0010100301	1000000001	1100110000	1110100110	2100001111	2100200000	0100000001	1020000
ERI SPA	010100210	0111100301	1000000001	1100110000	1110100110	2100001101	2100200000	0?00000001	1020000
LON SIN	020100010	0010101200	0000000001	1111110000	1110000112	1000001101	2100200000	0?00000001	1010010
ZAT BOH	010100010	0010100202	0000000001	2100110000	1110000112	1000001111	3100200000	0100002001	1020010
ZAT KAU	010100010	0010100200	1000000001	2000110001	1110000112	1100001111	2100200000	0100002001	1020010
ZAT PER	010100010	0010100200	1000000001	2000110001	1110000112	1100001111	3100200000	0100002001	1020010
ZAT PET	010101010	0010101200	1000000001	2000110001	1110000112	1100001111	2100200000	0100002001	1020010
ZAT RIV	010101010	0010101200	1000000001	2000110001	1110000112	1100001111	2100200000	0100002001	1020010
SIN ANO	010100010	0010100200	0000000001	2000110001	1110000112	1100001111	2100200000	0100002001	1020010
OXY CAR	010100010	1010100200	0000000001	0000110000	1110000110	0000010111	0100100000	0100012001	1020000
OXY EUR	010100010	1010100200	0000000001	0000110000	1110000110	0000010111	0100100000	0100012001	1020000
ZAB SP2	010100010	1010100100	0000000001	1000110000	1110000110	0000010011	0100100000	0?00012001	1020000
ATP TIB	0101103211	0102200300	1000012101	1100100000	1110000110	0001000111	2100101000	0100001001	1020000
ATP WIL	0101103211	0002200300	1000012101	1100100000	1110000110	0001000112	2100101000	0100001001	1020000
HYM BIC	010100210	0002230300	1002002101	1100110000	1110000110	0001000102	2100101000	0100001001	1020000
HYM ARG	0101003211	0002230300	1001001101	1100110000	1110000110	0001000102	2100101000	0100001101	1020000
POL GUT	010100010	0010120200	1000000101	1100110000	1110000110	0100010111	2100100000	0100011001	1020000
POL KOE	010100010	0010100200	1000002101	1100100000	1110000110	0000000111	2100100000	0100011001	1020000
POL PUR	010100010	0010100200	1000002101	1100110000	1110000110	0100000101	2100101000	0100011001	1020000
POL SHA	010100010	0001220300	1001002101	1100110000	1110000110	0000000102	2100101000	0100011001	1020000
POL TUB	010100010	0010100200	0000001101	1000110000	1110000110	0000010111	2100100000	0100011001	1020000
TIC VIL	0101003210	0002200300	0001000101	1100100000	1110000110	0011000001	2000101000	0?00001001	1010000
TIC SP1	0101003210	0002200301	0001000101	1100100000	1110000110	0011000001	2000101000	0?00001001	1010000