

The Genera of Bethylinae (Hymenoptera: Bethylidae)

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Abstract. —The taxonomic status of the genera comprising the bethylid subfamily Bethylinae is reassessed using computerised phylogenetic analysis. From this analysis seven genera are considered valid, and the following are synonymised: *Trissomalus* Kieffer 1905 with *Odontepyrus* Kieffer 1904; and *Anoxus* Thomson 1862 with *Bethylus* Latreille 1802. Several species are transferred generically, and several new combinations are presented. The distribution and biology of the Bethylinae are summarised.

INTRODUCTION

The aculeate family Bethylidae (Chrysidoidea) is a moderately large family of about 1,900 described species with probably at least as many undescribed. Bethylids are mainly gregarious ectoparasitoids, the Bethylinae mostly developing on larval Lepidoptera, the remainder mostly on Coleoptera, although the hosts are known for only a small proportion of the family. Bethylids are frequently encountered as parasitoids of crop pests, especially in tropical areas, and several species have been used in attempted biological control (Gordh & Evans 1976; Hempel 1934). Successful identification of Bethylidae is therefore important for many economic entomologists, but has been extremely difficult because the most recent revision was published eighty years ago (Kieffer 1914) and contains many errors. Even at the generic level identification can be very difficult, particularly for the Palaeotropical species. For the Nearctic and Neotropical species this problem has largely been alleviated by the work of Evans (1964, 1978).

During our independent studies on African and Asian Bethylinae we have each discovered related undescribed species that do not fit Kieffer's (1914) concepts of the bethylid genera, but which we do not regard as meriting description in new

genera. Kieffer's and subsequent authors' concepts of the bethylid genera needed modification to accommodate the degree of morphological variation which we had discovered. Computerised phylogenetic analysis was selected as the most objective method of assessing character states within the bethylid genera, while providing a more stable classification of the subfamily. The following study was carried out primarily to set new limits to some of these genera, and to facilitate their identification.

Here we address the internal phylogeny of the Bethylinae. In comparison to the other bethylid subfamilies, the Bethylinae have been little affected at the generic level since Kieffer's (1914) revision. Only one genus, *Neoclystropsenella* Kurian (1955), was assigned to the Bethylinae since Kieffer's work. *Neoclystropsenella* was synonymised with *Tapinoma* (Formicidae) by Brown (1987), but mistakenly retained by Gordh & Moczar (1990) in the Bethylidae. Gordh & Moczar (1990) also mistakenly transferred *Odontepyrus* Kieffer to Epyrinae, thus assigning a total of eight genera to the Bethylinae (Table 1). When attempting to identify Bethylinae genera using Kieffer's (1914) key, the primary source of confusion is his treatment of the genera *Goniozus* Förster, *Parasierola* Cameron and *Perisierola* Kieffer. The latter two genera have since correctly been synonymised with *Goniozus* (Evans

1978), but from our studies it is clear that Kieffer intended something different from what he inadvertently achieved when he keyed and diagnosed these genera in his revision. *Goniozus* (*sensu* Evans 1978) contains species that either possess, or do not possess, a closed discoidal cell (areola, areolet) (Fig. 1). Kieffer assigned those species with a discoidal cell to *Perisierola*, and those without one to *Goniozus*. Kieffer (1907, 1911, 1914), Brues (1907a, 1907b) and Muesebeck (1940) all mistakenly selected *Parasierola* Cameron (1883) to accommodate species with both a closed discoidal cell and with one or more longitudinal carinae on the propodeum, this latter character being absent from Kieffer's concepts of the other two genera. Furthermore, Kieffer (1914) transposed his concepts of *Parasierola* and *Perisierola* when going from his key to genera (1914:238) to his generic diagnoses (1914:533, 542). Thus began 80 years of confusion surrounding these bethyline genera.

METHODS

Selection of taxa

To clarify the status of the genera of Bethylinae we analysed 11 taxa of Bethylinae for 22 morphological characters using the parsimony programme 'Hennig86' (Farris 1988). To polarise characters the genus *Lytopsenella* Kieffer was selected as the outgroup. *Lytopsenella* possesses all the characters common to all the remaining bethyline genera in their hypothetical plesiomorphic conditions (see character selection). Characters that are prone to reduction (e.g., number of antennal segments, maxillary and labial palp segments, and wing venation) are found at their maxima within *Lytopsenella*. *Lytopsenella* has previously been chosen as a basal group, not just for Bethylinae but for Bethylinidae as a whole (Evans 1964; Sorg 1988).

Representatives of each of the currently valid bethylid genera were included in the analysis. In cases of existing doubt or controversy surrounding the limits of some genera, type species of both current genera and formerly recognised genera were examined. Particular attention was paid to previous authors' concepts of *Goniozus*, *Odontepyrus*, *Parasierola*, *Perisierola* and *Trissomalus*. Three species of *Goniozus* (in the broad sense, i. e. that of Evans 1978) were selected to cover the range of known variation in propodeal and wing

venation characters which are important for deducing the phylogeny of the subfamily. Current interpretations of the genera *Anoxus* and *Bethylus* differ from each other only in whether the eyes are setose or not. This is a character that we have observed to vary intragenerically, so only one representative species of *Bethylus* was included in the analysis. The taxa selected are given in the data matrix below (Table 2) in the generic combinations which have resulted from this study. Former generic combinations can be found in the treatments of *Bethylus* and *Odontepyrus* (see below).

Selection of Characters

We consider the following to represent the ground plan characters of the subfamily Bethylinae. This character list is based partly on the work of Evans (1964) and of Sorg (1988) but largely on our own independent assessments.

Ground plan characters within Bethylinae

Antennae 13-segmented; clypeus with a well-developed keel, and frontal streak present; maxillary palps 6-segmented; labial palps 3-segmented; notauli and parapsidal lines present; scutellum flat, with two small grooves at its proximal corners (Fig. 2); propodeum without carinae (but see below); fore femora expanded; prostigma absent; discoidal cell (areolet) present, submarginal and marginal cells present; subdiscoidal cell absent (=discoidal cell of Evans 1964); sternum of petiole with a complete keel, sexual dimorphism limited to genital characters and head shape.

Characters Analysed

The following characters include all of those which have been used previously for the discrimination of genera within the Bethylinae (except eye setation, see above) as well as some which have not been used previously. We generally agree with Sorg (1988) concerning both the selection and polarization of characters. However, we disagree with Sorg's polarization of the scutellar foveae (character 6, below; Figs. 3, 4). Sorg considers that the occurrence of scutellar foveae in the Embolemidae (Sorg 1988: p 30) suggests plesiomorphy. The probability is that, at least in the Bethylinae, they are represented in their

Table 1: Genera of Bethylinae

Kieffer (1914)	Gordh & Moczar (1990)	This paper
(Bethylini)	(Bethylinae)	(Bethylinae)
<i>Anoxus</i>	<i>Anoxus</i>	<i>Bethylus</i>
<i>Bethylus</i>	<i>Bethylus</i>	<i>Bethylus</i>
<i>Clystopsenella</i>	not mentioned	Scolebythidae (Evans, 1963)
<i>Digoniozus</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Eupsenella</i>	<i>Eupsenella</i>	<i>Eupsenella</i>
<i>Goniozus</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Kathepyris</i>	Pristocerinae	Pristocerinae (Evans 1964)
<i>Lytopsenella</i>	<i>Lytopsenella</i>	<i>Lytopsenella</i>
	<i>Neoclystopsenella</i> (incertae sedis)	Formicidae (Brown 1987)
<i>Odontepyris</i> (Bethylini)	<i>Odontepyris</i> (Epyrinae)	<i>Odontepyris</i> (Bethylinae)
<i>Parasierola</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Perisierola</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Progoniozus</i>	<i>Goniozus</i>	<i>Goniozus</i>
<i>Prosierola</i>	<i>Prosierola</i>	<i>Prosierola</i>
<i>Sierola</i>	<i>Sierola</i>	<i>Sierola</i>
<i>Trissomalus</i>	<i>Trissomalus</i>	<i>Odontepyris</i>

plesiomorphic condition in *Lytopsenella*.

Assumed primitive (plesiomorphic) characters are coded '0' with '1', '2' representing assumed derived (apomorphic) states.

- Number of antennal segments:** The plesiomorphic condition in the Bethylinae is possession of 13-segmented antennae. In *Bethylus* (including *Anoxus*) a reduction to 12-segmented antennae has occurred. 0= antennae 13-segmented; 1= antennae 12-segmented.
- Number of labial palp segments:** The plesiomorphic condition is possession of 3-segmented labial palps. In *Bethylus* and *Sierola* the labial palps are 2-segmented. 0= labial palps 3-segmented; 1= labial palps 2-segmented.
- Number of maxillary palp segments:** The plesiomorphic condition is possession of 6-segmented maxillary palps, found in both *Eupsenella* and *Lytopsenella*. In the remaining taxa the number is reduced to five, except *Sierola* which has 4-segmented maxillary palps. 0= maxillary palps 6-segmented; 1= maxillary palps 5-segmented; 2= maxillary palps 4-segmented.
- Presence of an unsculptured streak frontally:** In many bethyline taxa a narrow impunctate, sometimes shiny, streak extends from the proximal end of the clypeal carina to the frontal ocellus (Fig. 12, see also Sorg 1988: 121, Fig. 33d, for its presence in Epyrinae: *Chilepyris*). In *Bethylus* (including *Anoxus*), *Goniozus* and *Sierola* the sculpturing of the head is reduced (i. e. smooth rather than strongly rugose) and this streak is absent. 0= frontal streak present; 1= absent.
- Presence of notauli:** The notauli, a pair of longitudinal furrows on the mesoscutum, occur throughout the Hymenoptera, and are often reduced. In the Bethylinae they are present only in the basal taxa, *Eupsenella* (Figs. 2, 3) and *Lytopsenella*. In all remaining Bethylinae the notauli are absent. The notauli should not be confused with the parapsidal lines, which are an additional pair of shallow grooves lateral to the position of the notauli (Menke 1993) (Fig. 2). 0= notauli present; 1= absent.
- Presence of scutellar grooves or pits:** In the basal taxa *Eupsenella* and *Lytopsenella* the scutellum has a pair of grooves at its anterior corners (Figs. 2, 3, 5). In several bethyline taxa

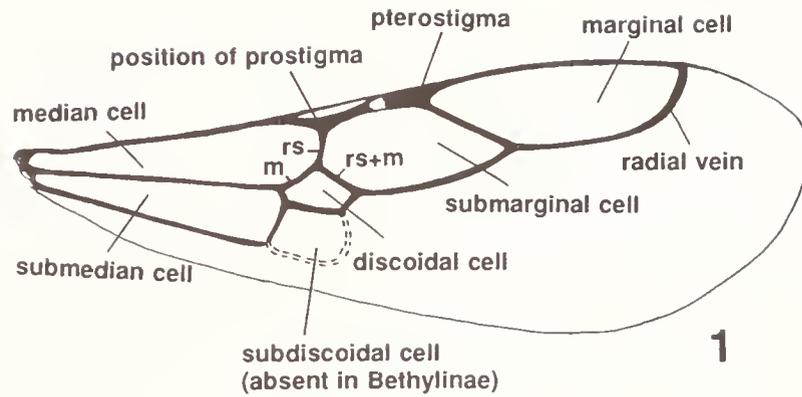


Fig. 1. Bethylinidae: terminology of wing venation

- these have apparently become enlarged to form pits, often connected by a broad transverse groove (Figs. 4, 6, 7). 0= scutellar pits or foveae present as grooves; 1= scutellar foveae enlarged.
7. **Expansion of mesopleuron:** Kieffer (1905) characterised his genus *Odontepyris* by the possession of dentate processes on the mesopleura (Figs. 6, 14). Although an apomorphic character in one lineage, it shows varying degrees of development in related taxa. 0= mesopleuron not expanded to form a dentate process; 1= mesopleuron moderately expanded; 2= mesopleura with dentate processes.
 8. **Presence of posterior transverse propodeal carina** (Figs. 2, 6, 7, 9, 10): 0= posterior transverse propodeal carina present; 1= posterior transverse propodeal carina absent.
 9. **Presence of median longitudinal propodeal carina** (Figs. 2, 5, 6, 8, 9): 0= median longitudinal propodeal carina present; 1= median longitudinal propodeal carina absent.
 10. **Presence of discal longitudinal propodeal carinae** (Figs. 2, 5, 6, 7, 8, 9, 10): 0= discal longitudinal propodeal carinae present; 1= discal longitudinal propodeal carinae absent.
 11. **Presence of median propodeal pits or foveae** (Figs. 4, 7, 10): The presence of these structures is characteristic of the genus *Prosierola*. 0= median propodeal pits absent; 1= median propodeal pits present.
 12. **Development of a smooth, triangular area on the dorsal propodeum:** In several bethyline taxa, particularly *Goniozus* and *Prosierola*, the proximal dorsum of the propodeum is characterised by a smooth, unsculptured triangular area which shows modifications in several taxa (Figs. 7, 10, 11). It is absent in the basal groups. The development of this character in some bethyline lineages should not be confused with the "propodeal triangle" in Apidae and Sphecidae (Brothers 1976). 0= smooth, triangular area absent from dorsal propodeum (Figs. 2, 5, 6, 8, 9); 1= smooth, triangular area present on dorsal propodeum (Figs. 7, 10, 11).
 13. **Petiole ventrally keeled:** To our knowledge, this character has not been used previously in defining the genera of Bethylinidae, but is important for separating *Goniozus* from superficially similar taxa in *Odontepyris* (see key to genera, below). In most Bethylinidae, a complete longitudinal keel is present on the ventral petiole (Fig. 13). This keel is reduced in several taxa (e. g. Fig. 15). 0= petiole with a complete ventral keel; 1= petiolar keel reduced; 2= petiolar keel absent.
 14. **Expansion of the fore femora:** Expansion of the fore femora for fossorial use is often encountered among the Bethylinidae, and also occurs in related chrysidoid taxa and other aculeates. Other modifications of the fore femora are frequent in the Aculeata. 0= fore femora strongly expanded; 1= fore femora less strongly expanded, half as wide as long.
 15. **Development of the pterostigma:** The expansion of the junction of the subcostal and basal veins into a secondary pterostigma is characteristic of the genus *Goniozus* (Figs. 20, 25), but also occurs elsewhere within the subfam-

Table 2. Character matrix:

	Characters																					
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22
<i>Lytopsenella</i> sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eupsenella</i> sp.	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0
<i>Sierola</i> sp.	0	1	2	1	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	1
<i>Bethylus cephalotes</i>	1	1	1	1	1	0	0	0	0	0	0	0	2	0	0	0	0	0	1	1	1	1
<i>Odontepyrus flavivervis</i>	0	0	1	0	1	1	2	1	1	1	0	0	0	1	0	1	1	0	0	1	1	0
<i>Odontepyrus transvaalensis</i>	0	0	1	0	1	1	1	1	1	1	0	0	0	0	0	1	1	0	1	1	1	0
<i>Odontepyrus xanthoneurus</i>	0	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	1	1	0
<i>Prosierola</i> sp.	0	0	1	0	1	1	1	1	0	1	1	1	0	0	0	1	1	0	0	1	1	0
<i>Goniozus</i> sp.	0	0	1	1	1	0	0	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0
<i>Goniozus gallicus</i>	0	0	1	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0
<i>Goniozus indicus</i>	0	0	1	1	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0

- ily. Its presence outside *Goniozus* has previously led to the generic misplacement of certain species. 0= prostigma absent; 1= prostigma present.
16. **Length of rs+m:** In the basal taxa, fore wing vein rs+m forms the upper distal part of the discoidal cell (Fig. 1). In all *Goniozus* species it is present and well-developed, despite the fact that in *Goniozus (sensu stricto)* the discoidal cell is open. The genus *Odontepyrus* is here characterised partly by the reduction of this vein (Figs. 22-24). The absence of this vein in *Bethylus* is clearly convergent with its reduction in *Odontepyrus* (see below). 0= rs+m long; as long as, or longer than, rs (Figs. 16-18, 20, 25); 1= rs+m shorter than rs, or absent (Figs. 19, 22-24).
17. **Length of rs:** The length of rs relative to m (Fig. 1) characterises the *Prosierola* / *Odontepyrus* clade, in which rs has become elongated. 0= rs equal to or shorter than m (Figs. 16-20, 25); 1= rs clearly longer than m (Figs. 21-24).
18. **Length of marginal (radial) cell:** In *Eupsenella*, one of the basal taxa, the marginal cell is characteristically shortened (Fig. 17). In the remaining taxa which have a closed marginal cell (*Lytopsenella*, *Sierola*), the marginal cell is of normal dimensions. For those taxa in which the marginal cell is open, it is necessary to calculate the size of a hypothetical closed marginal cell by the length of the radial vein ($2r - rs$ of Sorg 1988; $r + Rs$ of Evans 1964). 0= marginal cell long (Fig. 16); 1= marginal cell shortened (Fig. 17).
19. **Presence of discoidal cell (areolet):** Within all Bethylinae the discoidal cell appears to be homologous, being plesiomorphically present. In *Goniozus* it is either clearly present or absent, whereas in *Odontepyrus* various intermediate degrees of reduction of the discoidal cell are apparent (c. f. Figs. 22, 23, 24). 0= discoidal cell present (Figs. 16, 17, 18, 21, 22, 23, 25); 1= discoidal cell absent (Figs. 19, 20, 24).
20. **Presence of submarginal cell.** In the Bethylinae, the submarginal cell is present and complete only in *Eupsenella* and *Lytopsenella*. It is absent in all remaining taxa. 0= submarginal cell present (Figs. 1, 16, 17); 1= submarginal cell absent (Figs. 18-25).
21. **Presence of closed marginal cell:** In the basal taxa, and in *Sierola*, the marginal cell is closed, the plesiomorphic condition for Bethylinae. 0= marginal cell closed (Figs. 1, 16-18); 1= marginal cell open (Figs. 19-25).
22. **Angle of radial vein:** The radial vein (Fig. 1; = vein $2r - rs$ of Sorg 1988; vein $r + Rs$ of Evans 1964) is distinctly angled in *Bethylus* and *Sierola* (Figs. 18, 19), genera respectively with an open and a closed marginal cell. The angle of the radial vein is thus independent of the closure of the marginal cell. 0= radial vein without a sharp angle; 1= radial vein sharply angled.

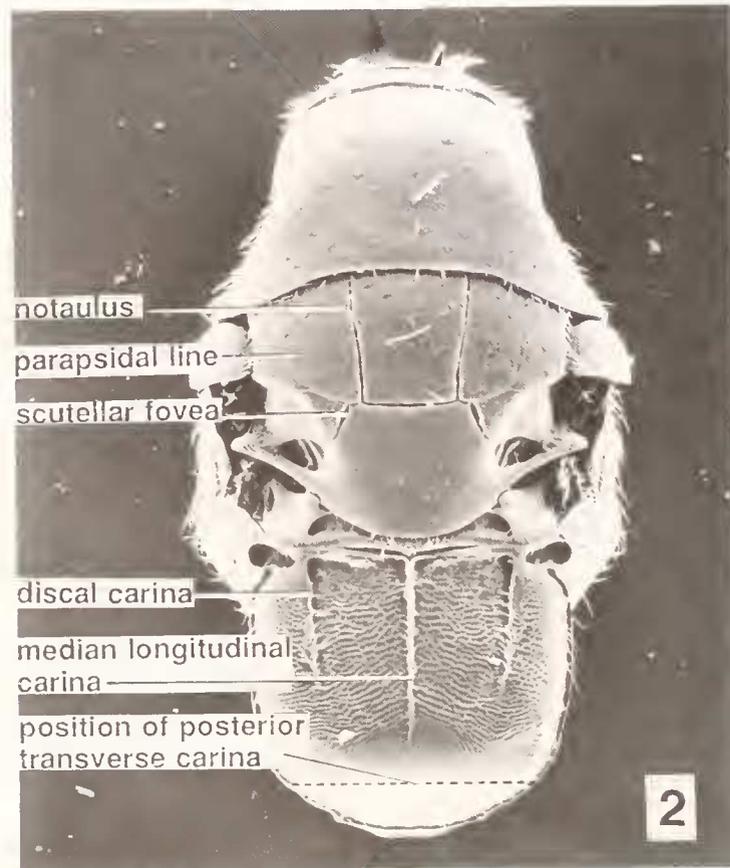


Fig. 2. Bethyline: terminology of mesosoma.

The character matrix was analysed using the 'implicit enumeration' option of Hennig86, the procedure which computes the maximum possible number of cladograms, or 'trees'. Multistate characters (3: number of maxillary palps; 5: presence of notauli; 7: expansion of the mesopleuron; 13: reduction of the petiolar keel) were treated both as unordered (non-additive) and ordered (additive).

RESULTS

A single cladogram (tree) resulted from the analysis, having the following characteristics: length 35 steps, consistency index 71 and retention index 80 (Fig. 26). Ordering the data had no effect on the topology of the tree, only increasing its length by one step, and reducing the consistency index by two.

Characters Supporting Monophyly of Bethyline Genera / Clades

1. (node A, Fig. 26): ((*Prosierola* + *Odontepyris*) + ((*Sierola* + *Bethylus*) + *Goniozus*)).
Monophyly of this clade is supported by the following synapomorphies: 3: reduction of number of maxillary palp segments from six to five; 5: loss of notauli; 20: loss of submarginal cell; 21: marginal cell open (reversed in *Sierola*).
2. (node B, Fig. 26): (*Prosierola* + *Odontepyris*)
Monophyly of this clade is supported by the following synapomorphies: 6: expansion of the scutellar pits; 7: expansion of the mesopleura; 8: presence of a posterior transverse propodeal carina; 10: presence of discal carinae; 16: rs+m shorter than rs; 17: rs longer than m.
3. (node C, Fig. 26): *Odontepyris*



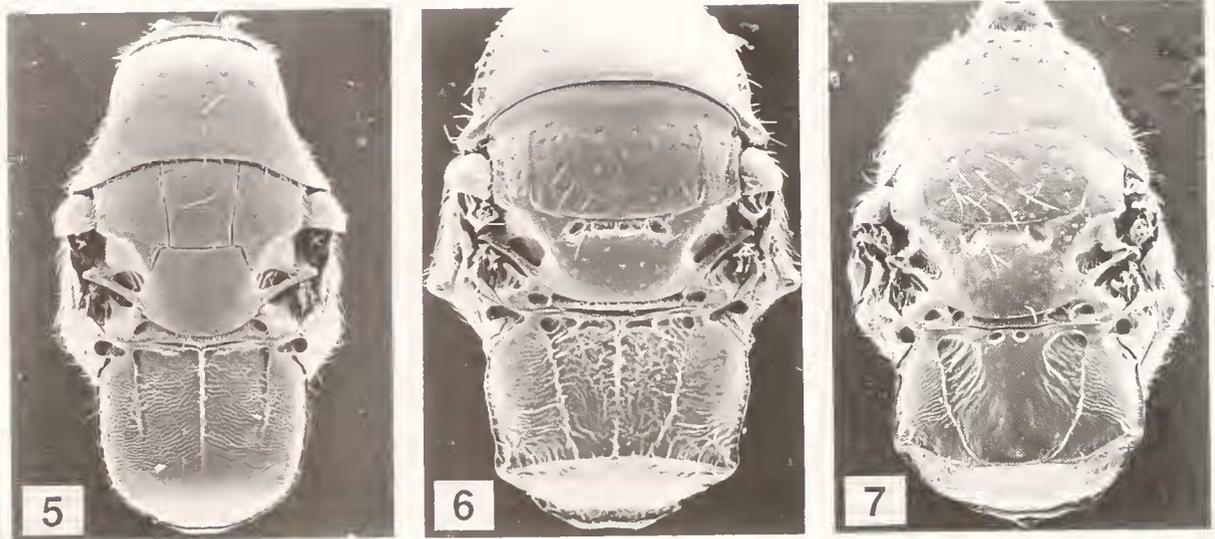
Figs. 3-4. 3, *Eupsenella* sp.: detail of mesosoma 4, *Prosierola* sp.: scutellum and propodeum.

- Monophyly of *Odontepyris* is supported by the following synapomorphy: 9: presence of a median propodeal carina.
4. (node D, Fig. 26): *Prosierola*
Monophyly of *Prosierola* is supported mostly by convergent characters, except for the autapomorphic character (11) presence of propodeal pits.
5. (node E, Fig. 26): ((*Sierola* + *Bethylus*) + *Goniozus*)
Monophyly of this clade is supported by a single synapomorphy: 4: loss of the frontal streak.
6. (node F, Fig. 26): *Goniozus*
Monophyly of *Goniozus* is supported by a single synapomorphy: 13: reduction of the petiolar keel. Character 12, presence of a smooth triangular area on the propodeum is a synapomorphy for *Goniozus* which occurs as a homoplasy in *Prosierola*.
7. (node G, Fig. 26): (*Sierola* + *Bethylus*)
Monophyly of this clade is supported by the following synapomorphies: 2: reduction of the number of labial palp segments from three to two; 22: radial vein sharply angled.
8. (node H, Fig. 26): *Sierola*
Monophyly of *Sierola* is supported by 3: maxillary palps 4-segmented, as well as by the closed marginal cell (21) which is here a reversal.
9. (node I, Fig. 26): *Bethylus*
Monophyly of *Bethylus* is supported by the following synapomorphies: 1: reduction of the number of antennal segments from 13 to 12; 13: petiolar keel absent.

DISCUSSION

The analysis supports monophyly of our modified concept of *Odontepyris*, including *Trissomalus* Kieffer, and *Parasierola* Cameron *sensu* Kieffer (1914), not Cameron (1883). The currently accepted definitions of most of the remaining genera are also supported by the analysis.

Trissomalus (Kieffer 1905) was characterised in a key, but not formally diagnosed until Kieffer's (1914) generic revision. *Odontepyris* (Kieffer 1904) was characterised mainly by the possession of dentate processes on the enlarged mesopleura



Figs. 5-7. 5. *Eupsenella* sp.: mesosoma. 6. *Odontepyris* sp.: mesosoma. 7. *Prosierola* sp.: mesosoma.

(Fig. 14). We have examined many described and undescribed species belonging to the *Odontepyris* / *Trissomalus* group, and conclude that the degree of variation in the development of the mesopleural processes, coupled with a successive reduction in the size of the discoidal cell (Figs. 22-24) suggests the group should be treated as a single genus, for which *Odontepyris* Kieffer is the oldest available name. The alternative would be to treat as new genera all intermediate species or species-groups.

Examination of *Anoxus* specimens shows that the genus differs from *Bethylus* only in the extent of setation of the eyes, other characters are identical in the two genera. Furthermore in some *Bethylus* species some setation can be found on the eyes (e. g. *B. amoenus* Fouts). Since we know that the degree of eye setation is a character that clearly varies interspecifically within other bethyline genera, we do not see how retaining *Anoxus* as a distinct genus can be justified, and it is therefore synonymised below.

GENERIC SYNONYMY

ODONTEPYRIS Kieffer

Odontepyris Kieffer 1904: 378. Type species *Odontepyris flavinervis* Kieffer 1904 by original designation. Holotype female: SUMATRA: Pangherang-Pisang x. 90 e iii. 91 (E. Modigliani) (MCSN) [examined].

Trissomalus Kieffer 1905: 105. Type species *Goniozus transvaalensis* Du Buysson, 1888: 354 by subsequent designation. Holotype female: [SOUTH AFRICA:] Transvaal, Hamman's Kraal 1893 (E. Simon) (MNHN) [examined] syn. n.

Diagnosis.—Antennae 13-segmented. Palpal formula 5:3. Frontal streak present. Notauli absent. Scutellar foveae well developed. Mesopleuron expanded, sometimes developed into a dentate prominence (Fig. 14). Median, discal and posterior transverse carinae present on propodeum, the longitudinal carinae occasionally reduced. Petiole with a complete ventral keel. Prostigma present or absent. *rs* + *m* reduced, *rs* elongate. Discoidal cell present, reduced or absent. Marginal and submarginal cells absent. Radial vein smoothly curved.

Included species.—*Odontepyris argyriae* Kurian; *O. batrae* Kurian; *O. cameroni* (Kieffer) (**comb. n.** from *Trissomalus*, holotype examined); *O. cirphi* Kurian; *O. erucarum* (Szelenyi) (**comb. n.** from *Parasierola*); *O. flavinervis* (Kieffer) (holotype examined); *O. fuscicrus* (Kieffer) (**comb. n.** from *Trissomalus*, holotype examined); *O. hypsipylae* (Kurian) (**comb. n.** from *Goniozus*); *O. indicus* Kurian (**comb. n.** from *Trissomalus*); *O. moldavicus* (Nagy) (**comb. n.** from *Prosierola*); *O. peringueyi* (Kieffer) (**comb. n.** from *Trissomalus*); *O. quadrifoveatus* (Muesebeck) (**comb. n.** from *Parasierola*, holotype examined); *O. ruficeps* Kieffer;

KEY TO GENERA OF BETHYLINAE

- 1 Closed submarginal cell present (Figs. 1, 16, 17) 2
 — Closed submarginal cell absent (Figs. 18-25) 3
 2 Marginal cell elongate, larger than submarginal (Figs. 1, 16) *Lytopsenella*
 — Marginal cell short, smaller than submarginal (Fig. 17) *Eupsenella*
 3 Marginal cell closed (Figs. 1, 16-18) *Sierola*
 — Marginal cell open (Figs. 19-25) 4
 4 Antennae 12-segmented. Wing venation as in Fig. 19; radial vein at apex turned abruptly upward, but not reaching wing margin. Fore wing with rs+m always absent *Bethylus*
 — Antennae 13-segmented. Wing venation different; radial vein shorter and evenly curved towards wing apex (Figs. 20-25). Fore wing with rs+m present or absent 5
 5 Propodeum without well-developed lateral carinae (fig 11). Scutellum without large foveae, with small grooves (as in Fig. 3). Petiole ventrally with a reduced, forked keel (Fig. 15) *Goniozus*
 — Propodeum with well-developed lateral carinae (Figs. 9, 10). Scutellum with large foveae (Figs. 6, 7). Petiole ventrally with a complete keel (Fig. 13) 6
 6 Median longitudinal propodeal carina present (Fig. 9). Propodeum without median foveae *Odontepyris*
 — Median longitudinal propodeal carina absent (Fig. 10). Propodeum with median foveae (Fig. 10) *Prosierola*

O. transvaalensis (De Buysson) (comb. n. from *Goniozus*, holotype examined); *O. waterhousei* (Kieffer) (comb. n. from *Parasierola*, holotype examined); *O. xanthoneurus* (Kieffer) (comb. n. from *Parasierola*, holotype examined).

Comments.—Tryapitsin (1978) and Terayama (1990) mistakenly included the Neotropical bethylid genus *Prosierola* in their respective keys to Russian and Japanese bethylid genera. In each case the error was due to misidentification of an *Odontepyris* species.

BETHYLUS Latreille

Bethylus Latreille, 1802: 315. Type species *Omalus fuscicornis* Jurine 1807: 301 by subsequent designation (International Commission on Zoological Nomenclature, opinion 153). Holotype ?female [not examined, ?lost].

Anoxus Thomson 1862: 451. Type species *Anoxus boops* Thomson 1862: 452. Monotypic. Lectotype female (Naturhistoriska Riksmuseet, Stockholm) [not examined] syn. n.

For full synonymy see Gordh & Moczar 1990.

Diagnosis.—Antennae 12-segmented. Palpal formula 5:2. Frontal streak absent. Eyes with or without long hairs. Notauli absent. Scutellar foveae narrow, groove-like. Mesopleuron not expanded. Propodeum without carinae. Petiole with the ventral keel absent. Prostigma and discoidal cells absent. Marginal and submarginal cells absent. Radial vein usually sharply angled.

Species transferred from *Anoxus*

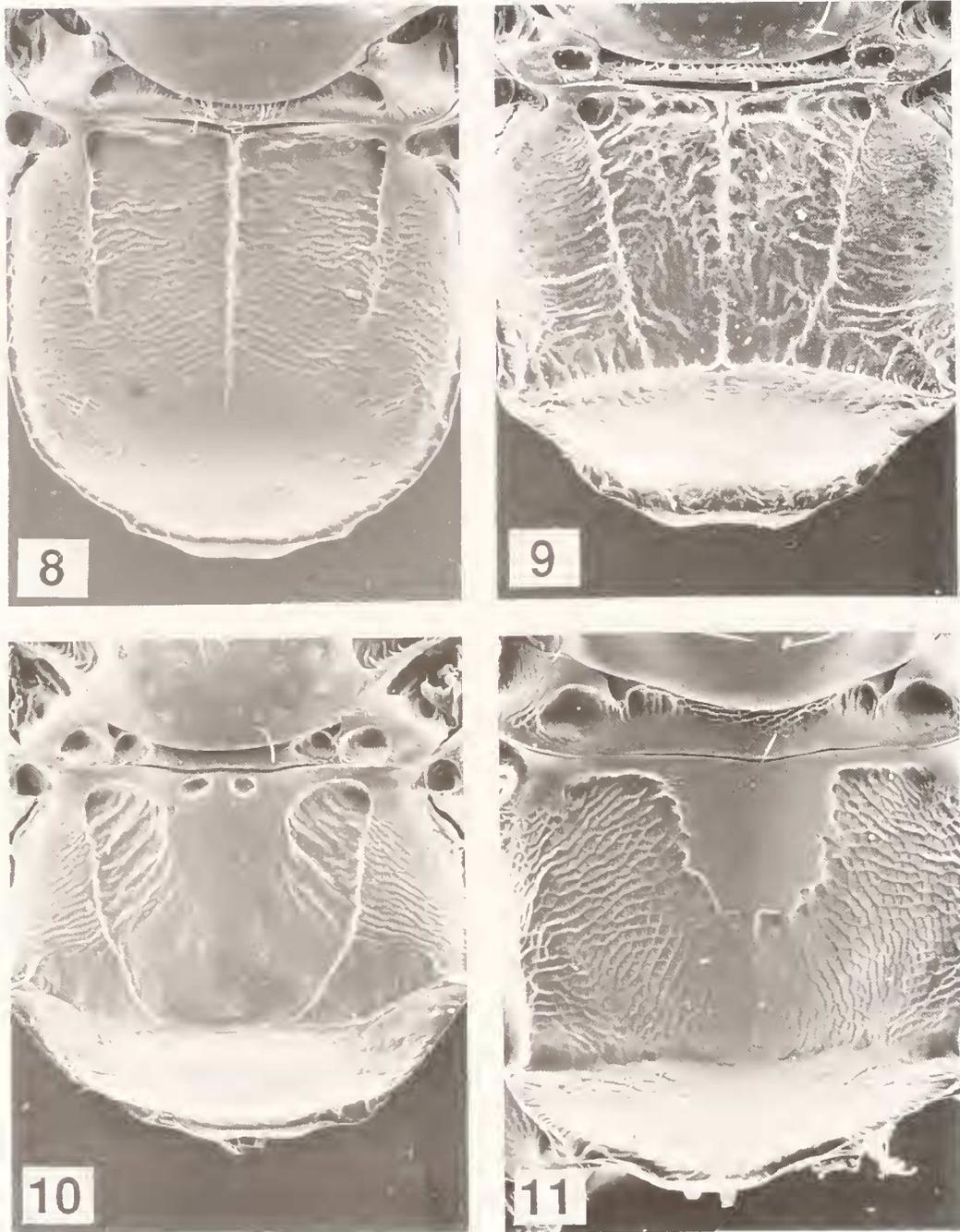
B. boops (Thomson) comb. n.; *B. coniceps* (Kieffer) comb. n.;
B. pilosus (Kieffer) comb. n.

Comments.—It might appear questionable to synonymise *Anoxus* with *Bethylus* without having examined the type species of either genus. However, there has not been any controversy surrounding these genera since Kieffer's (1914) generic revision, and we have examined sufficient material conforming to the original descriptions and Kieffer's interpretations of *Anoxus* and *Bethylus*.

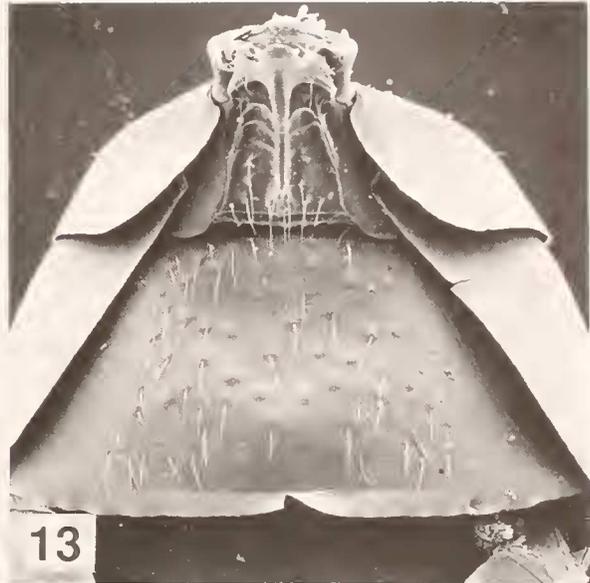
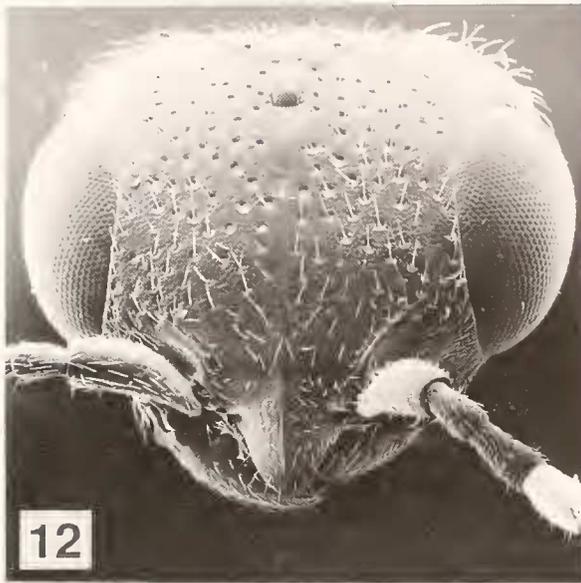
DISTRIBUTION OF BETHYLINAE

The most primitive bethylid, *Lytopsenella*, is known only from two extant species, both from Chile. Three fossil species are known from Baltic amber (Evans 1964). *Eupsenella* is known so far only from Australia.

Odontepyris is predominantly Palaeotropical, but its distribution spans southeastern Europe to South Africa and northern Queensland. The small genus *Prosierola* is primarily Neotropical although one species ranges into the extreme southern United States; a fossil species from Baltic Amber is certainly incorrectly assigned to *Prosierola* (Brues 1933). *Goniozus*, with about 150 described species,



Figs. 8-11. 8, *Eupsenella* sp.: propodeum. 9, *Odontepyris* sp.: propodeum. 10, *Prosterola* sp.: propodeum. 11, *Gomozus* sp.: propodeum.

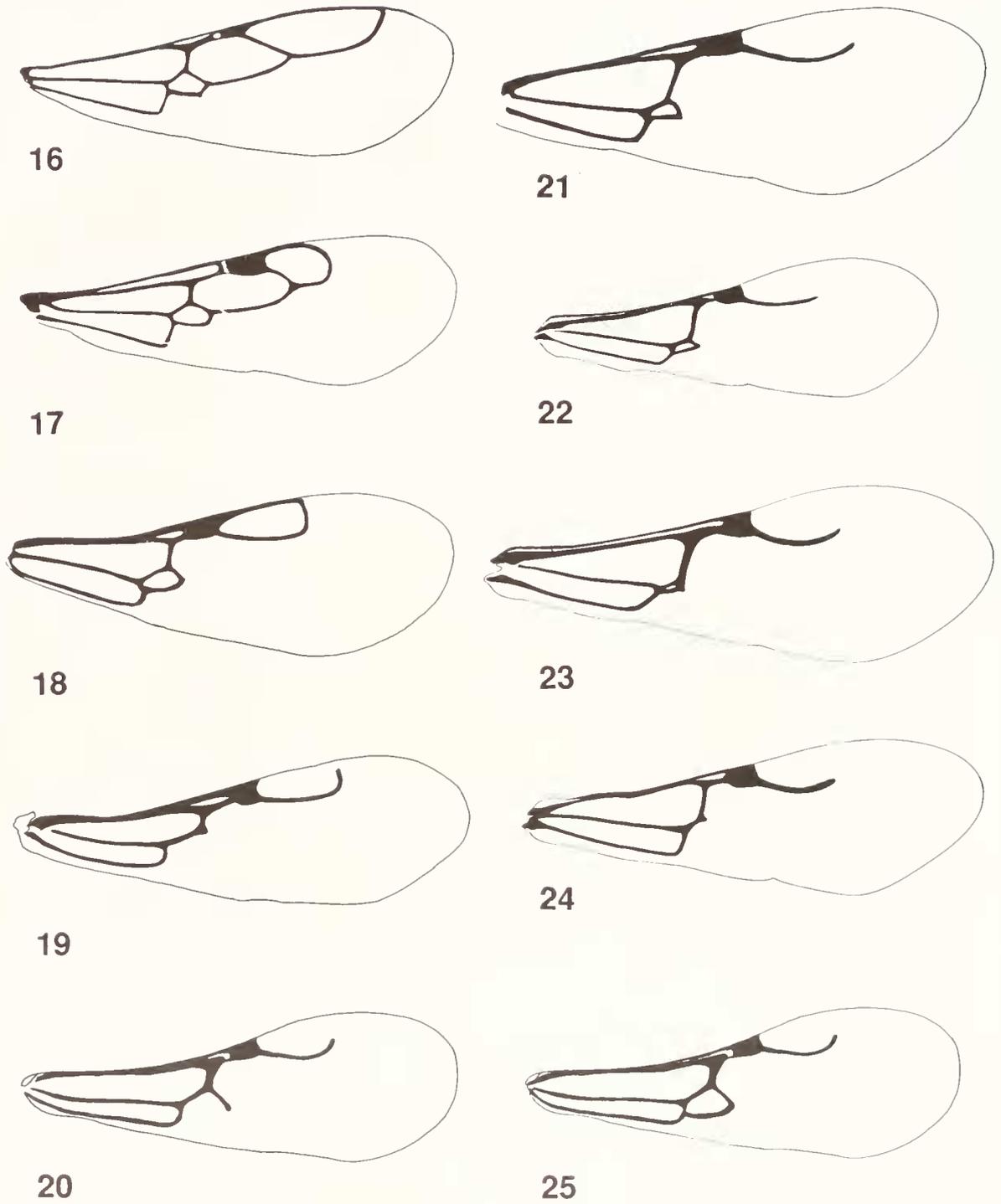


Figs. 12-15. 12, *Odontepyris* sp.: head. 13, *Odontepyris* sp.: ventral petiole and sternite 2. 14, *Odontepyris* sp.: side of mesopleuron showing dentate process. 15, *Goniozus* sp.: ventral petiole and sternite 2.

is cosmopolitan although only one species is known from the Pacific Islands. Approximately three dozen species each were described from the Oriental, Nearctic and Neotropical regions, and about a dozen each from the Palaeartic, Ethiopian and Australian regions. A number of species have been introduced into other countries as biological control agents. A few fossil species have been

described from Baltic and Dominican amber.

Sierola contains almost 200 described species, mostly from Hawaii, with three endemic species in Australia. The genus underwent tremendous speciation in Hawaii, and a secondary small speciation in the Marquesas Islands. Evans (1978) suggested that the single Californian species might be introduced, and this is possibly also true of the



Figs. 16-25. Fore wings of various Bethyloidea: 16, *Lytopsenella* sp. 17, *Eupsenella* sp.; 18, *Sierola* sp. 19, *Bethylus* sp. 20, *Goniozus* (*sensu stricto*) 21, *Prosierola* sp. 22-24, *Odontepyris* spp. 25, *Goniozus* ("*Parasierola*") sp.

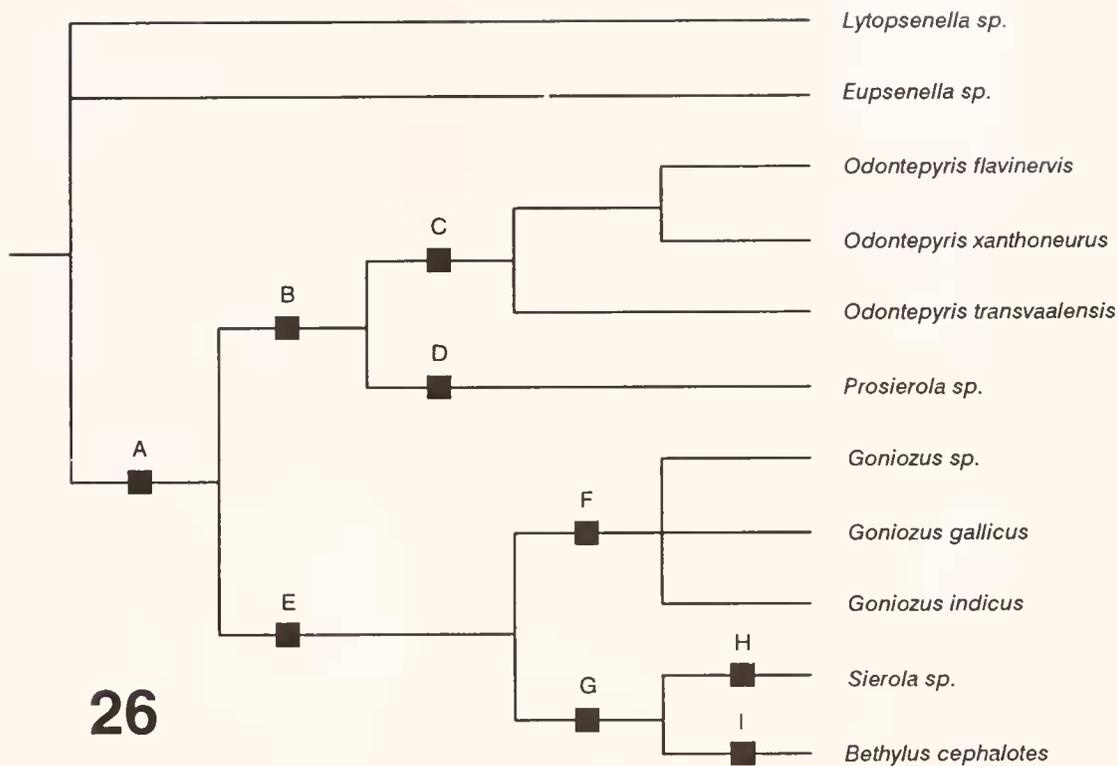


Fig. 26. Cladogram of the Bethylinae.

single Chinese species. A fossil species has been described from Baltic amber (Sorg 1988).

Bethylus, containing some 30 described species, was previously considered as Holarctic, and predominantly Palaearctic, only two species being definitely known from the Nearctic. Recently, the first author examined several specimens of *Bethylus* from South Africa. *Homalus ?amplipennis* Motschulsky was erroneously placed by Gordh & Moczar (1990) in *Bethylus*; Krombein (1987) transferred it to *Holepyris*.

BIOLOGY OF BETHYLINAE

Bethylinae are characterized in part by parasitizing lepidopterous larvae, whereas members of the other subfamilies attack primarily coleopterous larvae. A few exceptions to these host preferences are documented in Bethylinae, Epyrinae and Pristocerinae, but the few known hosts of Mesitiinae are case-bearing coleopterous larvae.

The preferred hosts within the Bethylinae are mostly microlepidopterous as listed by Evans (1978) and Gordh & Moczar (1990). However,

there are a few anomalous or questionable host records. It should be noted that, under experimental conditions, females of the epyrine *Sclerodermus immigrans* Bridwell (1920) will successfully parasitize a variety of insect larvae other than their normal coleopterous host. These include other Hawaiian beetles, bees, wasps, ants, and even braconid and chalcidoid parasites of the normal host larva. Bridwell also reared *S. immigrans* from normal workers, dealate adults, and nymphs of the termite *Neotermes castaneus* (Burmeister), although not from the soldiers. Perhaps some of the questionable records below may reflect this capability in other bethylids.

Evans (1964) reported that a specimen of *Lytopsenella herbsti* (Kieffer) was labelled as attacking an adult cantharid beetle. This record is dubious, inasmuch as hosts of all other bethylids are larvae. The only other records of bethylines attacking a host stage other than the larva are those of Nagy (1976). He reported *Odontepyris moldavicus* (Nagy) (as *Prosierola moldavica*) as reared from "pupae of a noctuid moth" and *Goniozus plugarui* Nagy attacking a lepidopterous pupa. These

records of bethylids reared from pupae are dubious, and the most probable explanation is that "pupal parasites" were reared from larvae which had spun cocoons but had not yet pupated.

Evans (1962) reported that *Bethylus amoemus* Fouts was reared from an olethreutid moth and a nitidulid beetle. The latter record was later omitted from Evans' (1978) list of host records, and to us seems doubtful. A species tentatively identified as *Goniozus gestroi* (Kieffer) was reported by Richards (1955) as being reared from larvae of the anobiid beetle, *Lasioderma*. The rearing was not questioned, only the specific identity of the *Goniozus*, and we therefore accept this record as authentic. *Goniozus morindae* Kurian (1952), described from a single male, was reared from the gall of a cecidomyiid fly, *Asphondylia morindae* Mani in flowers of *Morinda tinctoria*. The record is anomalous, and is the first for a dipteran as a host of a bethylid. The most recent authentic record of a hymenopterous host for a bethyline is that of Melo and Evans (1992) who reported *Goniozus microstigni* Evans as being reared from a brood cell of the sphecid wasp *Microstigmus xylicola* Melo, a predator of nymphal Thysanoptera. The nests were in abandoned beetle galleries in beams of an exposed roof, and a dozen *G. microstigni* females were collected while walking near and entering nests of *M. xylicola* and *M. similis* Melo.

So far as is known, all Bethylinae are gregarious parasitoids, laying a clutch of eggs on each host larva. The host is stung, sometimes repeatedly, behind the gula. Paralysis of the host larva may be temporary or permanent, depending upon the species of wasp. The number of eggs per clutch varies according to the size of the host, as well as interspecifically (Gordh & Evans 1976), ranging from one or two to as many as 40. Placement of the eggs depends upon the species, eggs being deposited either intersegmentally or longitudinally, and either dorsally, ventrally or laterally. Eggs hatch about two days after oviposition, and the larvae complete feeding in 2 to 5 days. Each larva spins a cocoon on the substrate near the host remains. The pupal period varies from 8-14 days, depending upon the species and ambient temperature. Males emerge a day or two before females are ready to eclose; they have been observed chewing into a cocoon containing a female and mating with her while she is still teneral. The progeny from a clutch usually consists of a single male and a number of

females, and sibling mating is common (Hardy 1992). Maternal care of the larvae has been observed in *Bethylus* and *Prosierola*, and the mother may subsequently mate again with one of her male offspring. Maternal care has also been observed in *Goniozus* (Hardy & Blackburn 1991). Adults of both sexes feed on honey in culture, and females have been observed feeding on haemolymph exuding from the paralysed host.

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