

A new bethylid wasp from the Lowermost Eocene amber of France (Hymenoptera: Bethylidae: Bethylinae)

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ABSTRACT

Protobethylus eocenicus, new genus and species of Bethylidae: Bethylinae, is described from the Lowermost Eocene amber of the Paris Basin (France). A new phylogenetic analysis of the bethyline genera is proposed. Although having superficial similarities with the habitus of *Lytopsenella* and *Eupsenella*; *Protobethylus* is more derived than these basal genera.

KEYWORDS | Insecta. Hymenoptera. Bethylidae. gen. and sp. n. French amber. Phylogeny.

INTRODUCTION

Bethylid wasps are not very frequent in the fossil record, mainly known from the copal of Zanzibar (Krombein, 1992), the Lower Miocene Dominican amber, the Oligocene amber of Chiapas (Mexico) (Gordh and Moczar, 1990), and the lacustrine beds from Rubielos de Mora (Spain) (Peñalver, 1998), Rott (Germany) (Statz, 1938) and Florissant (USA), the Upper Eocene lacustrine beds of the Isle of Wight (UK) and Baltic amber (Brues, 1932; Polaszek and Krombein, 1994; Ohl, 1995), the probably Uppermost Cretaceous Burmese amber (Ross and York, 2000), the Upper Cretaceous ambers of Taimyr (Russia) (Evans, 1973) and New Jersey (USA) (Grimaldi et al., 2000), the Upper Cretaceous lacustrine Orapa deposit (Botswana) (Brothers and Rayner, 1993), the Cretaceous lacustrine outcrops of Transbaikalia (Rasnitsyn, 1990), the Lower Cretaceous amber of Álava (Spain) (Martínez-Delclòs et al., 1999), and the Lower Cretaceous Lebanese amber (Prentice, 1993, 1994). Nevertheless the present discovery in the Lowermost Eocene amber of a new genus of Bethylinae is the oldest representative of this subfamily. It is of great interest for the

evaluation of the past diversity of this small subfamily. We follow the wing venation and body terminology of Polaszek and Krombein (1994).

SYSTEMATIC PALEONTOLOGY

Order: Hymenoptera LINNAEUS, 1758

Family: Bethylidae HALIDAY, 1840

Subfamily: Bethylinae HALIDAY, 1840

GENUS *Protobethylus* n.gen.

Type species: *Protobethylus eocenicus* n. sp.

Diagnosis: General habitus superficially very similar to that of *Eupsenella*. The main differences from this genus are (for comparison see the generic diagnosis in Gordh and Harris, 1996): hind coxae simple; posterior transverse propodeal carina present but weak; median and discal longitudinal propodeal carinae and median propodeal pits absent. Other characters are: antenna 13-segmented; scutellar grooves not developed into foveae;

notauli present; wing venation very similar to that of *Eupsenella*, especially in the well developed pterostigma, small prostigma; short marginal cell, closed marginal, discoidal and submarginal cells.

Etymology: After Proto meaning 'before' and *Bethylus*.

***Protobethylus eocenicus* n. sp.**

Figure 1

Material: Holotype specimen PA 2436, (sex uncertain), in collection De Ploëg housed in the Muséum National d'Histoire Naturelle, Paris.

Locality deposit: Le Quesnoy, Chevreière, region of Creil, Oise department, France.

Geological age: Lowermost Eocene, Sparnacian, level

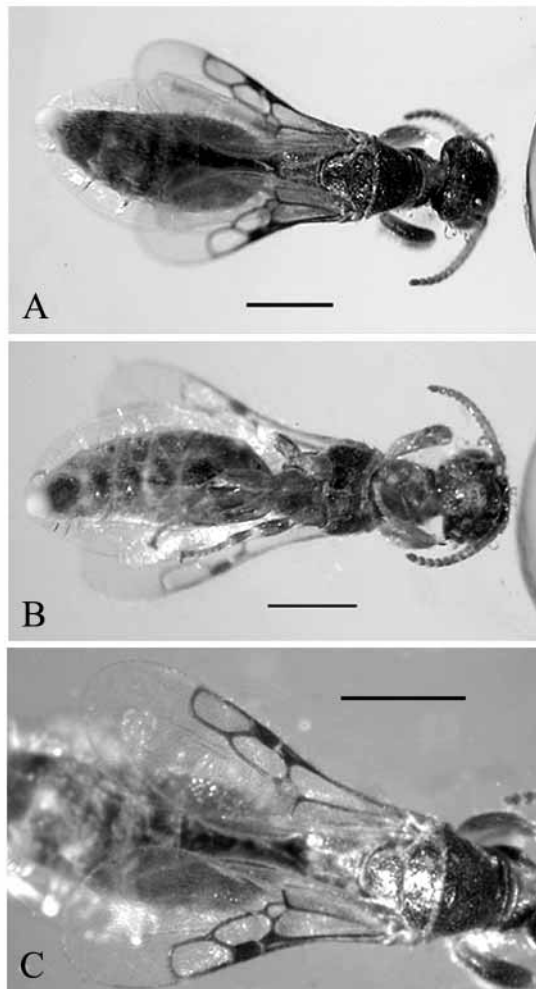


FIGURE 1 | *Protobethylus eocenicus* n. sp., holotype specimen PA 2436. A) Dorsal view. B) ventral view. C) Wing venation and thorax. Scale bar: 0.5 mm.

MP7 of the mammal fauna of Dormaal. We could demonstrate that the amber is autochthonous and very different from the Baltic amber in age, chemical composition and origin (Nel et al., 1999).

Etymology: After the Eocene period.

Diagnosis: That of the genus.

Description: Body 2.75 mm long. Head prognathous, long and flat, 0.38 mm long, 0.5 mm wide; eye 0.1 mm wide; distance between eyes 0.38 mm; frons with longitudinal median carina extending a short distance from clypeus; anterior border of clypeus angulate at middle; 13 antennal segments, scape 0.10 mm long, 0.05 mm wide; pedicel 0.04 mm long, 0.03 mm wide; 11 flagellomeres of nearly the same length and width; presence of frontal unsculptured streak between clypeal carina and ocellus; labial and maxillary palpi hidden by mandibles.

Pronotum 0.25 mm long, 0.5 mm wide, with anterior flange well developed; pronotum touching tegula; posterior margin of pronotum straight; propleuron not visible, concealed in dorsal view; prosternum 0.16 mm long, 0.21 mm wide, transverse, not diamond-shaped; notauli present, well developed; mesopleuron not expanded to form a dentate process; propodeum completely sculptured, 0.2 mm long, 0.2 mm wide; posterior transverse propodeal carina present but weak; median and discal longitudinal propodeal carinae and median propodeal pits absent; metapostnotum hidden; complete ventral keel on petiole.

Profemur moderately swollen, less than half as wide as long, 0.38 mm long, 0.11 mm wide; protibia not swollen, 0.3 mm long, 0.1 mm wide; protrochanter originating from posterior apex of procoxa; no large spine but two rather long setae on hind coxa; all claws strongly curved, with a broad basal smooth tooth; inner metatibial spur calcariform with dorsal blunt longitudinal setose carina.

Fully winged; fore wing 1.55 mm long, 0.6 mm wide; discoidal, submarginal and marginal cells present and closed; prostigma moderately expanded, but not forming a distinct large triangle and narrower than pterostigma, 0.02 mm long, 0.03 mm wide; pterostigma broad, 0.1 mm long, 0.05 mm wide; vein rs+m longer than rs; rs shorter than m; marginal cell 2.8 mm long, shorter than submarginal cell, 2.9 mm long; radial vein not sharply angled; anal and transverse median veins round, not forming an angle; cell 1Rs spectral but still visible, limited posteriorly and distally by spectral veins, as in *Lytopsenella* and *Eupsenella* (see Evans, 1964, fig. 125; Gordh and Harris, 1996, fig. 2).

Hind wing 1.25 mm long, 0.3 mm wide, with no cell enclosed by tubular veins; a strong notch on anterior mar-

gin near base of hind wing; veins C and SC+R+S very short, at extreme wing base.

Metasoma 1.5 mm long, 0.55 mm wide; with 7 exposed terga; no visible sting.

Discussion: Following the key to families of Chrysoidea and that of subfamilies of Bethylidae proposed by Finnamore and Brothers (1993, pp. 131-134), *Protobethylus* n. gen. falls in the Bethylidae: Bethylinae because of the following characters: 11 flagellomeres, protibia slender, hind wing without cells, anterior flange of pronotum well developed, prosternum transverse, protrochanter originating from posterior apex of procoxa, metasoma with 7 exposed terga; pronotum touching tegula, fore wing discoidal cell closed. It also shares with this family the following further characters: inner metatibial spur calcariform with dorsal blunt longitudinal setose carina; metapostnotum hidden; hind wing veins C and SC+R+S very short; head prognathous. Carpenter (1999, p. 224) characterized the Bethylidae: Bethylinae by the three following synapomorphies present in *Protobethylus* n. gen.: clypeal carina extending onto frons, the antennal articulations lateral and the claws bifid. We prefer to use the character 'claws strongly curved' rather than the character 'claws bifid' as a synapomorphy of the Bethylinae, because the claws of *Cleptes* (Chrysididae) and *Pristocera* (Bethylidae: Pristocerinae) are also bidentate.

Polaszek and Krombein (1994) proposed the first phylogenetic analysis of the genera of Bethylinae. They used the bethyline genus *Lytopenella* as outgroup, thus, they could not establish the monophyly of the subfamily. Terayama (1995) proposed a second, slightly different analysis, based on a hypothetical ancestor (all-zero outgroup). Even if based on slightly different sets of characters, these analyses do not really conflict. That of Terayama (1995) is only less resolved than that of Polaszek and Krombein (1994), with an unresolved polytomy between *Bethylus*, *Sierola*, *Goniozus* and (*Odontepyris* + *Prosierola*). Carpenter (1999) gave a phylogenetic analysis of the chrysidoid families, based on a character matrix scored primarily from Sorg (1988), and confirmed the monophyly of the subfamily Bethylinae.

Both analyses of Polaszek and Krombein (1994) and Terayama (1995) are not based on primary polarisation of character states with reference to real outgroup(s), and both have some errors in character coding (see Appendix 1). Thus, we made a new analysis based on the combination of the characters of Polaszek and Krombein (1994) and Terayama (1995), polarized according to real outgroups. The chosen outgroups are *Pristocera gaullei* KIEFFER (a Bethylidae: Pristocerinae, which is the most basal lineage in the sister group of the Bethylinae), and *Cleptes pallipes* LEPelletier 1806 (a Chrysididae: Cleptinae,

which is the most basal lineage in this family) (Carpenter, 1999).

The analyses are based on the 22 characters proposed by Polaszek and Krombein (1994) + 7 characters extracted from the analysis of Terayama (1995). All were treated as unordered and equally weighted. We used the branch and bound option of the computer software Paup* 4.0b10 for PC and MacClade 3.08a for Macintosh, for the search of the most parsimonious trees.

The analyses with *Cleptes* or *Pristocera* alone or both taxa as outgroups give the same set of 11 most parsimonious cladograms, independently of the order of introduction of the outgroup(s) in the original matrix (see strict consensus tree T1 in Fig. 2), with the following characteristics: tree length = 51 steps, consistency index = 0.6275, consistency index excluding uninformative characters = 0.5870, retention index = 0.7206, RC = 0.4521. A research of decay index (*sensu* Bremer, 1994) gives: the clade Bethylinae has a decay index of 0, the clade [*Odontepyris* + *Prosierola*] has a decay index of 4; all other clades have decay indices of 1.

An analysis made with the computer software Nona version 2, options 'starting trees' and 'Heuristic Mult TBR + TBR (searches for trees using tree bisection-reconnection method of branch-swapping)', with 1000 iterations, gave only 4 cladograms of Length 52 steps, thus longer than those obtained using Paup, but with the same strict consensus cladogram.

The Bethylinae appear monophyletic, the clade being supported by the character states '28, state 1' (a strong notch on anterior margin near base of hind wings present) and '29, state 1' (claws strongly curved). *Lytopenella*, *Eupsenella* and *Protobethylus* n. gen. fall in an unresolved basal quadrotomy with a clade that comprises all the other genera. The character '5, state 1' (notauli absent) supports this last clade. The clade ((*Odontepyris* + *Prosierola*) + [*Goniozus* + (*Sierola* + *Bethylus*)]) is supported by the characters '20, state 1' (closed submarginal cell absent) and maybe '3, states 1-2' (4-5 maxillary palp segments), but this character is unknown in *Protobethylus* n. gen.

Protobethylus n. gen. shares with *Eupsenella* the character '18, state 1' (marginal cell shortened) but it shares the character '27, state 0' (hind coxae simple, without spine) with the more advanced Bethylinae. Because of this conflict, its position remains uncertain.

The clade [*Odontepyris* + *Prosierola*] is supported by the characters '6, state 1' (scutellar grooves or pits present as enlarged foveae), '7, state 1' (mesopleuron moderately expanded), '16, state 1' (vein rs+m shorter than rs) and

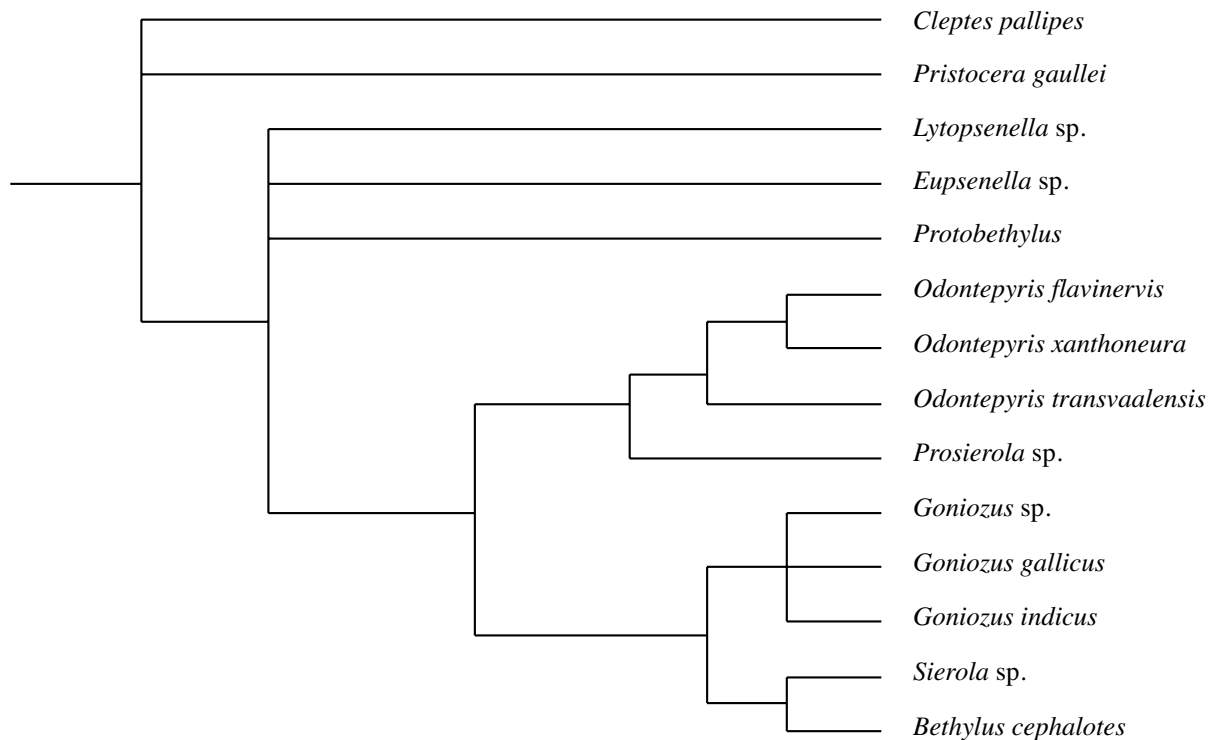


FIGURE 2 | Strict consensus cladogram T1 of 11 minimal trees.

'17, state 1' (rs clearly longer than m). The clade *Goniozus* + (*Sierola* + *Bethylus*) is supported by the character state '4, state 1' (no unsculptured streak frontally). The clade *Sierola* + *Bethylus* is supported by the characters '2, state 1' (two labial palp segments) and '22, state 1' (radial vein with a sharp angle). The wing venation characters are rather homoplastic, especially the presence versus absence of a discoidal cell and closure of the discoidal cell.

In conclusion, the present analysis (tree T1) is congruent with the topology of the consensus tree proposed by Polaszek and Krombein (1994), but we could correct and specify the character states that support the various clades. We confirm the monophyly of the subfamily, as proposed by Carpenter (1999). *Protobethylus* n. gen. shares with *Eupsenella* (as defined by Polaszek and Krombein or Terayama) the reduction of the marginal cell, but this character alone is not sufficient for its inclusion in this genus, even if it is currently used in the key to genera of Bethylinae (Polaszek and Krombein, 1994; Terayama, 1995).

Brues (1923) described three species of Bethylinae from Baltic amber that he attributed in 1932 to the genus *Eupsenella*. Later, Evans (1964, p. 183) transferred them to *Lytopsenella* without explanation. These species are *L. setigera* (BRUES 1923), *L. simplex* (BRUES 1923) and *L.*

crastina (BRUES 1923). Brues (1923) indicated nothing concerning the structures (hind leg and propodeum) that allow separation between *Eupsenella* and *Protobethylus* n. gen., for *L. simplex*, but this species is distinctly larger than *Protobethylus eocenicus* n. gen., n. sp., *L. setigera* and *L. crastina* differ from *Protobethylus* n. gen. in the presence of a median propodeal carina (Brues, 1932, pp. 126 and 128). Ohl (1995) described a new species, *Lytopsenella kerneggeri*, from the Baltic amber. He indicated nothing about the notauli but he added that it has median and discal longitudinal propodeal carinae. Thus *L. kerneggeri* cannot be attributed to *Protobethylus* n. gen. Lastly, the presence of the median (and discal) propodeal carinae would suggest closer affinities of *L. kerneggeri*, *L. setigera* and *L. crastina* with *Eupsenella* rather than with the recent *Lytopsenella* (see Evans, 1964, p. 181). A revision of these fossil species attributed to *Lytopsenella* would be welcome, in order to determine if they really belong to the genus *Lytopsenella* rather than *Eupsenella*.

Lytopsenella is Neotropical, *Eupsenella* is known from Australia and New Zealand. The other recent genera are rather widespread, except for the Nearctic and Neotropical genus *Prosierola*, which is not in a very basal phylogenetic position. Therefore, no clear biogeographic implications can be made after the present discovery of *Protobethylus* n. gen.

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Appendix. List of characters, combined after Polaszek and Krombein (1994) (indicated with a 'P&K') and Terayama (1995) (indicated with a 'T'). Characters used by both authors are indicated with a 'P&K-T'

TABLE 1 | List of characters and species studied.

Taxa/Characters	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	
<i>Lytopsenella</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	?	1	1
<i>Eupsenella</i>	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	1	1	1
<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	0	0	0	1	0	1	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	1	0	0	1	0	1	1	
<i>Odontepyris flavinervis</i>	0	0	1	0	1	1	2	1	1	1	0	0	0	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	1	
<i>Odontepyris transvaalensis</i>	0	0	1	0	1	1	1	1	1	1	0	0	0	0	1	1	0	1	1	1	0	0	0	0	1	1	0	1	1	
<i>Odontepyris xanthonurus</i>	0	0	1	0	1	1	1	1	1	1	0	0	0	1	1	1	1	0	0	1	1	0	0	0	1	1	0	1	1	
<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	0	1	0	1	0	1	1	
<i>Goniozus</i> sp.	0	0	1	1	1	1	0	1	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	1	
<i>Goniozus gallicus</i>	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	1	0	1	1	
<i>Goniozus indicus</i>	0	0	1	1	1	1	0	0	0	0	0	1	1	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1	1	
<i>Protobethylus eocenicus</i> n. sp.	0	?	?	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0	1	1	
<i>Cleptes pallipes</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0/1	0	0	0	0	0	1	1	0	0	
<i>Pristocera gaullei</i>	0	0	0	0	0	0	0	1	1	0	0	0	0	1	0	?	?	0	1	0	1	0	0	0	1	1	1	0	0	

0: primitive character; 1 and 2: derivate character; and ?: not observed.

- 1. Number of antennal segments (P&K-T) ...
13-segmented. 0.
12-segmented. 1.
- 2. Number of labial palp segments (P&K-T) ...
Three. 0.
Two. 1.
- 3. Number of maxillary palp segments (P&K) ...
Six. 0.
Five. 1.
Four. 2.
- [Note. Terayama (1995) divided this character into six (state 0) and five or less (state 1)].
- 4. Presence of an unsculptured streak frontally (P&K) ...
Present. 0.
Absent. 1.
- [After Polaszek and Krombein (1994), the absence of this streak is related to the reduction of the head sculpturing.]
- 5. Notauli (P&K-T) ...
Present. 0.

- Absent. 1.
- 6. Presence of scutellar grooves or pits (P&K) ...
Present as grooves. 0.
Present as enlarged foveae. 1.
- 7. Mesopleuron (P&K) ...
Not expanded to form a dentate process. 0.
Moderately expanded. 1.
With dentate process. 2.
- [Terayama (1995) only divided this character into 'not expanded' versus 'moderately to strongly expanded'].
- 8. Posterior transverse propodeal carina (P&K-T) ...
Present. 0.
Absent. 1.
- 9. Median longitudinal propodeal carina (P&K-T) ...
Absent. 0.
Present. 1.
- [Note. Polaszek and Krombein (1994: 94) and Terayama (1995) made an inversion between 'presence' and 'absence' for this structure. This carina is clearly present in *Eupsenella* and absent in *Prosierola* (see Polaszek and Krombein, 1994, figs. 2, 5, and 7)].

10. Discal longitudinal propodeal carina (P&K) ...
Absent. 0.
Present. 1.
[Note. Polaszek and Krombein (1994, p. 94) made an inversion between 'presence' and 'absence' for this structure. These carinae are clearly present in *Eupsenella* and *Prosierola* (see Polaszek and Krombein, 1994, figs. 2, 5, and 7)].
11. Basal inner propodeal pits or foveae (P&K-T) ...
Absent. 0.
Present. 1.
[Note. This character is an autapomorphy of *Prosierola*, thus of little use in the present analysis].
12. A dorsal smooth, triangular area on propodeum (P&K) ...
Absent. 0.
Present. 1.
13. Petiole ventrally keeled (P&K) ...
Complete. 0.
Reduced. 1.
Absent. 2.
14. Expansion of fore femora (P&K) ...
Strongly expanded. 0.
Less expanded. 1.
15. Prostigma (P&K) ...
Absent. 0.
Present. 1.
[Note. Terayama (1995) established a different character after this structure, i.e. prostigma forming a large triangle, as an autapomorphy of *Goniozus*, which is useless for our phylogenetic analysis. Nevertheless, the 'absence' versus 'presence' proposed by Polaszek and Krombein (1994) are not easy to establish (compare the situations in *Lytopsenella* (supposed to be in the state 0) and *Sierola* (supposed to be in the state 1). Thus, this character is ambiguous and rather poorly defined].
16. Length of rs+m (P&K-T) ...
As long as, or longer than, rs. 0.
Shorter than rs. 1.
17. Length of rs (P&K-T) ...
rs equal of shorter than m. 0.
rs clearly longer than m. 1.
18. Marginal (radial) cell (P&K) ...
Long. 0.
Shortened. 1.
[Polaszek and Krombein (1994) considered the state 1 as an autapomorphy of *Eupsenella*. But this character is problematic because the marginal cell is open in all taxa except *Lytopsenella* and *Eupsenella*. These authors proposed to calculate its hypothetical length in other taxa after the length of radial vein. Terayama (1995) rejected this character.]
19. Discoidal cell (areolet) (P&K-T) ...
Present. 0.
Absent. 1.
20. Closed submarginal cell (P&K) ...
Present. 0.
Absent. 1.
21. Marginal cell (P&K-T) ...
closed. 0.
open. 1.
[Terayama (1995) coded this character as follows: marginal cell present versus absent. He erroneously indicated the character state 'marginal cell absent' in *Sierola*. This cell is present and closed in this taxon.]
22. Angle of radial vein (P&K) ...
Without a sharp angle. 0.
With a sharp angle. 1.
[This character is ambiguous because the radial vein has a strong curve in *Eupsenella*, rather similar to those of *Sierola* and *Bethylus*, with a strong angle.]
23. Anterior border of clypeus (T) ...
Angulate at middle. 0.
Rounded or truncate. 1.
[The character state '1' is uniquely present in *Bethylus*, thus of little use in the present analysis.]
24. Posterior margin of pronotum (T) ...
Almost straight. 0.
Slightly produced backward medially. 1.
[The character state '1' is uniquely present in *Prosierola*, thus of little use in the present analysis.]
25. A pair of pits in basal outer portion of propodeum (T) ...
Absent. 0.
Present. 1.
[The character state '1' is present in *Odontepyris* and *Pristocera*.]
26. Pterostigma (T) ...
Thin. 0.
Broad. 1.
27. Hind coxae (T) ...
Simple. 0.
With a large blunt spine. 1.
[In Bethylinae except *Eupsenella*, this spine is replaced by 2 long setae, unfortunately, this character is unknown in *Lytopsenella*. Terayama (1995) considered the presence of this spine as a derived character state of *Eupsenella*, but it is also present in *Cleptes* and *Pristocera*. Thus it is probably plesiomorphic.]
28. A strong notch on the anterior margin near the base of hind wings. (T) ...
Absent. 0.
Present. 1.
[This character is present in all Bethylinae.]
29. Claws (T) ...
Weakly to moderately curved. 0.
Strongly curved. 1.
[This character is present in all Bethylinae. We prefer to use it rather than the character 'claws bifid' proposed

by Carpenter (1999, p. 224) as a synapomorphy of the Bethylinae. The claws of *Cleptes* (Chrysididae) and of *Pristocera* (Bethylidae: Pristocerinae) are also bidentate.]

Note. Terayama (1995) proposed some characters that we exclude from the present analysis because they are weakly defined. Also, they are of rather little

importance because their supposed derived states are monogeneric. This concerns the characters 'Head long, flat, and more or less rectangular (state 0) versus broad and rounded (state 1)'; 'Basal vein oblique (state 0) versus forming a distinct angle with a short branch (state 1)'; 'Anal and transverse median veins round, not forming an angle (state 0) versus forming an angle (state 1)'.