Bull. Biogeogr. Soc. Japan
50 (1) : 1 - 9. Nov. 20, 1995

日本生物地理学会会報
第50巻第1号1995年11月20日

Phylogeny and Distribution of the Subfamily Bethylinae (Hymenoptera: Chrysidoidea: Bethylidae)

Mamoru Terayama

Abstract. The bethylid wasp subfamily Bethylinae is briefly revised : 7 genera are recognized and their distributions are treated, and possible phylogenetic relationships are discussed. The phylogenetic systerm here proposed is: 1) The cladogram has a polytomy involving *Eupsenella*, *Lytopsenella*, and remaining 5 genera ; 2) *Prosierola* and *Odontepyris* constitute a monophyletic assemblage. A key to the genera and distribution maps are also provided.

Introduction

The family Bethylidae, belonging to the Chrysidoidea, is widely distributed from the tropics to the subarctic regions of the world. They are represented by 1796 nominal species in 98 genera belonging to 4 to 6 subfamilies excluding fossile records as of 1992 (Gordh & Móczár, 1990; Strejček, 1990; Krombein, 1992; Argaman, 1990; Azevedo, 1992).

The subfamily Bethylinae was established by Kieffer (1914) as a tribe of the family Bethylidae. In 1928 Berland separated superfamily Bethyloidea from superfamily Proctotrupoidea. At the same time he raised this tribe to full subfamily rank. Evans (1978) established the tribes Bethylini and Sierolini in this subfamily. Recently, Polaszek & Krombein (1994) synonymized *Anoxus* and *Trissomalus* with *Bethylus* and *Odontepyris* respectively. Thus this subfamily contains 7 genera of 2 tribes up to the present.

The phylogenetic study has been made by Polaszek & Krombein (1994) using 11 species in 7 genera.

The present study aims to clarify the internal relationships of subfamily Bethylinae at genus level and to contribute to the biogeography.

Materials and Methods

Taxa included in the analysis

All the possible genera are examined. Six genera are examined with specimens. As for the remaining genus, *Lytopsenella*, I checked the character states based on the extensive literature (Evans, 1964; Kieffer, 1914). The specimens examined in this study are listed in the appendix of this part together with the institutions preserving the materials.

Methods of cladistic analysis

The cladistic analysis performed by PAUP Ver. 3. 1 drawn by Swofford (1993). All the search for the shortest tree(s) was made by the exact branch-and-bound algorithm which guarantees to find all optimal trees. The accelerated transformation (ACCTRAN) option, which minimizes the ratio of parallelism to reversal, was used. This minimizes the length of all subtrees in the multiple most parsimonious reconstructions (MPRs) (Minaka, 1993).

I made a character analysis determining the polarity of the characters used in this analysis, and the character state matrix for the taxa are given in the tables 1 and 2. The character state definitions and polarities largely followed prevailing theories of evolutionary change within the aculeate

Table 1. Characters and their states used in the analysis of subfamily Bethylinae. 0, plesiomorphic; 1, apomorphic.

1. Number of antennal segments. 13 [0]; 12 [1].
2. Number of segments of maxillary palpi. 6 [0]; 5 or less [1].
3. Number of segments of labial palpi. 3 [0]; 2 [1].
4. Head. Long, flat, and more or less lectangular [0]; broad and rounded [1].
5. Anterior border of clypeus. Angulate at middle [0]; rounded or truncated [1].
6. Mesopleura. Not expanded [0]; moderately to strongly expanded [1].
7. Posterior margin of pronotum.
   Almost straight [0]; slightly produced backward medially [1].
8. Notauli. Present, [0]; absent [1].
9. A pair of pits in basal inner portion of propodeum. Absent [0]; present [1].
10. A pair of pits in basal outer portion of propodeum. Absent [0]; present [1].
11. Median carina of propodeum. Present [0]; absent [1].
12. Transverse carina of propodeum. Present [0]; absent [1].
13. Length of rs-vein. Almost equal or shorter than m-vein [0]; longer than m-vein [1].
14. Pterostigma. Thin [0]; broad [1].
15. Prostigma.
   Not forming distinct large triangle [0]; large and forming a triangle [1].
16. Basal vein. Oblique [0]; forming a distinct angle with a short branch [1].
17. Anal and transverse median veins.
   Round, not forming an angle [0]; forming an angle [1].
18. Marginal cell. Present [0]; absent [1].
19. Submedian cell. Present [0]; absent [1].
20. Discoidal cell (=areolet). Present [0]; absent [1].
21. Hind coxae. Simple, without spine [0]; with a large blunt spine [1].
22. A strong notch on the anterior margin near the base of hind wings.
   Absent [0]; present [1].
23. Claws. Weakly to moderately curved [0]; strongly curved [1].

Hymenoptera (Carpenter, 1986, 1991; Brothers, 1975; Brothers & Carpenter, 1993; Königsmann, 1978). Since the phylogenetic relationships between the bethylids and other wasps have not been fully resolved, I used hypothetical ancestor which had the plesiomorphic state in every character.

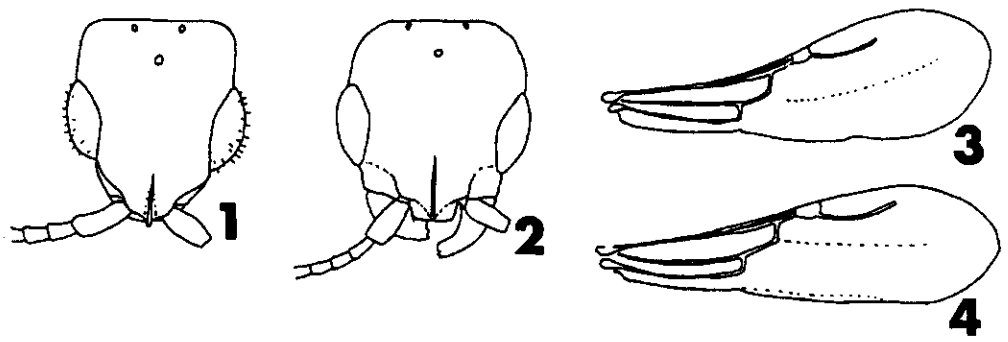
Results and Discussion

Cladistic analysis

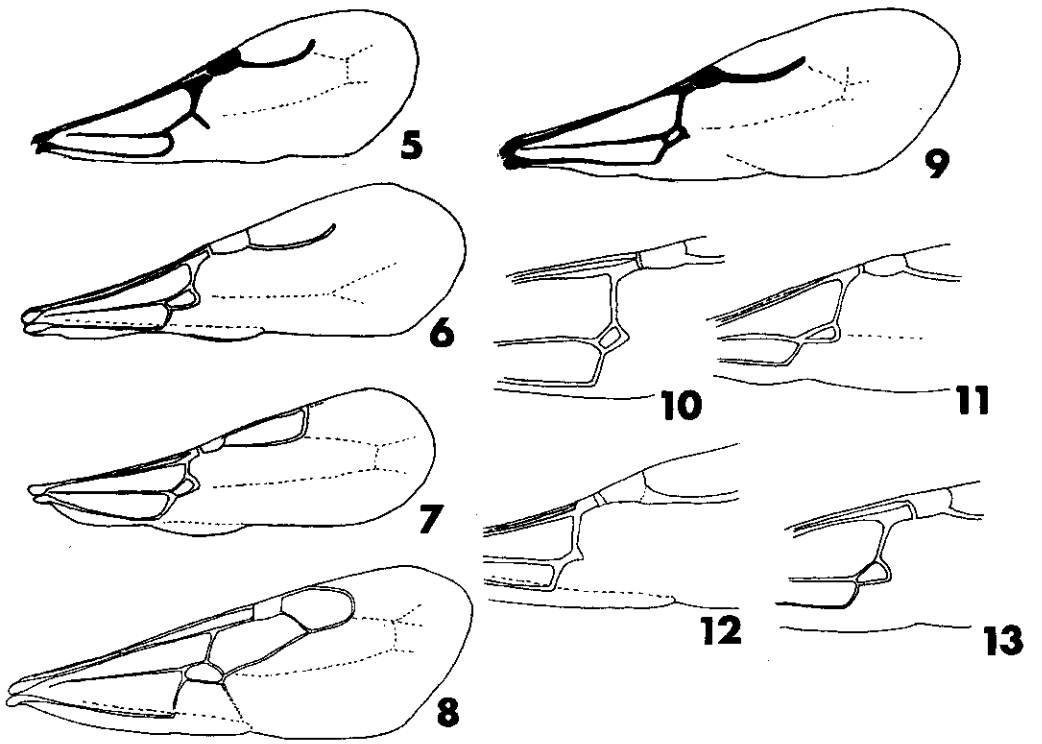
The analysis yielded 12 equally most parsimonious trees, of length 31, consistency index 0. 871, and retention index 0.756. Figure 14 gave the strict consensus of all 12 trees. The tree has a basal polytomy involving *Eupsenella*, *Lytopsenella*, and the remaining 5 genera, *Bethylus*, *Sierola*, *Goniozus*, *Prosierola*, and *Odontepyris*. The latter 5 genera were found to possess 3 synapomorphies: maxillary palpi

Table 2. Character coding for the analysis of the generic relationships in the subfamily Bethylinae. "P " indicates polymorphic.

Taxon	000000000 123456789	1111111111 0123456789	2222 0123
Bethylus	111110010	0110101111	1011
Sierola	011000010	01P0100010	0011
Goniozus	010000010	01P0110011	P011
Prosierola	010001111	0101100011	0011
Odontepyris	010001010	1001100011	P011
Eupsenella	000000000	0010100000	0111
Lytopsenella	000000000	0100000000	0?11
Outgroup	000000000	0000000000	0000



Figs. 1-4. *Bethylus* spp. Figs. 1, 3, *Bethylus boops* from Sweden - 1, head, frontal view; 3, forewing. Figs. 2, 4, *Bethylus* sp. from Japan - 2, head, frontal view; 4, forewing.



Figs. 5-13. Forewings of Bethylinae. 5, *Goniozus japonicus* from Japan; 6, *Goniozus* sp. from Taiwan; 7, *Sierola* sp. from Japan; 8, *Eupsenella diemenensis* from Australia; 9, *Odontepyris* sp. from Japan; 10, *Odontepyris* sp. from Taiwan; 11, ditto; 12, ditto; 13, *Prosierola* sp. from Trinidad.

with 5 segments (character 2), notauli absent (character 3), and marginal cell opened (character 19), while there is only one autoapomorphy (hind trochanthers with spine; character 21) in *Eupsenella* and no unequivocal apomorphies emerge for the *Lytopsenella*.

Prosierola and *Odontepyris* constitute a monophyletic assemblage by character 6 (moderately to strongly expand mesopleura) and 13 (Long rs-vein). The geographical distribution of these genera is allopatric; *Prosierola* is distributed in the New World, while *Odontepyris* in the Ethiopian, Oriental, and southern Palaearctic Regions.

The following characters support the monophyly of the genus *Bethylus*: antennae with 12 segments (character 1), head rather flat and rectangular (character 4), anterior border of clypeus broadly rounded (character 5), basal vein forming a distinct angle with a short branch (character 16), and anal and transverse median veins angulate (character 17).

Odontepyris, *Prosierola* and *Goniozus* were each found to possess unicquely derived character conditions demonstrating that each genus is monophyly. The autoapomorphy for *Odontepyris* is character 10 (presence of a pair of pits in basal outer portion of propodeum), that for *Prosierola* is characters 7 (posterior margin of pronotum slightly produced backward medially) and 9 (presence of a pair of pits of basal inner portion of propodeum), and that for *Goniozus* is character 15 (large and triangular prostigma). However, the present analysis did not reveal any unequivocal apomorphic character condition for *Sierola*.

Evans (1978) established 2 tribes, Bethylini and Sierolini, in this subfamily. However, the present results did not support his system. The genus *Bethylus*, although having more apomorphic characters, is not clearly separated as the sister-group of all the other genera combined. On the other hand, *Eupsenella* and *Lytopsenella* are separated from the other 5 genera. But I did not establish new tribes for these genera since this subfamily consists of compact genera in morphology. *Eupsenella* and *Lytopsenella* are the most primitive of the Bethylinae with respect

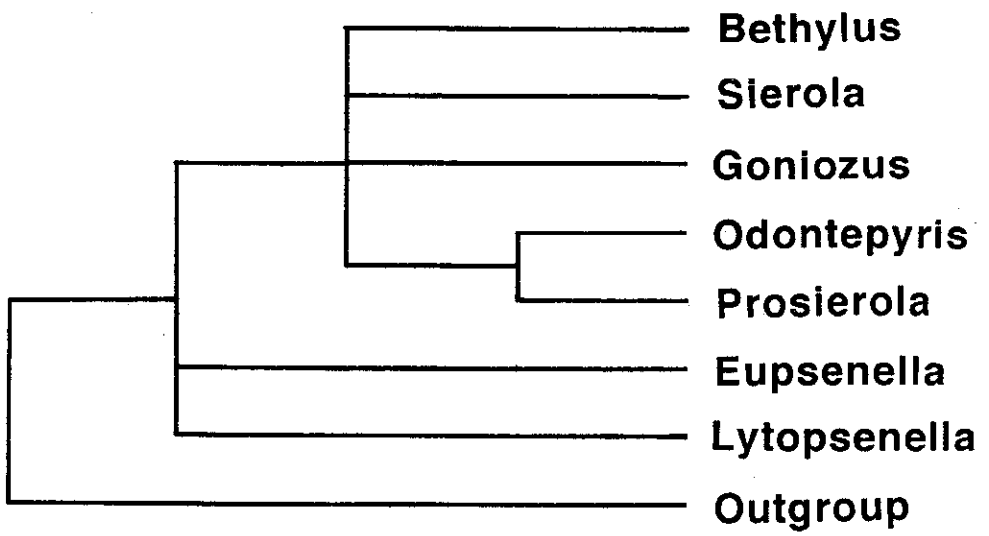


Fig. 14. Strict consensus cladogram calculated from the 12 equally most parsimonious cladograms.

Table 3. Zoogeographic synopsis of Bethylinae. The number of currently recognized species-level taxa (until 1994) in each genus is shown by zoogeographical region. In case where no published record is available but the author has reliable information, "X" is applied there. The Hawaiian subdivision is separately shown but the Maragacy Region is included in the Ethiopian Region in this table. The zoogeographical regions are abbreviated as follows: PAL, Palaearctic; ORI, Oriental; AUS, Australian; ETH, Ethiopian; NEA, Nearctic; NET, Neotropical; HAW, Hawaiian.

Genus	PAL	ORI	AUS	ETH	NEA	NET	HAW	Total no. of species
Lytopsenella						2		2
Eupsenella			3					3
Bethylus	29	X			3			32
Goniozus	12	35	10	11	41	40	1	136
Odontepyris	2	7	4	3				16
Prosierola					1	8		8
Sierola	X	1	4		1		190 .	196

to the wing venation, palpal formula, and presence of notauli.

Zoogeographical distribution

The number of described species in each genus is shown in Table 3. This subfamily has been recorded from all zoogeographical regions. The genus *Bethylus* is principally distributed in the Palaearctic Region (Fig. 15-A). Two closely related genera *Prosierola* and *Odontepyris* show allopatric distribution pattern (Fig. 15-B): *Prosierola* is distributed in the New World and *Odontepyris* in the Ethiopian, Oriental and southern Palaearctic regions. The genus *Eupsenella* is restricted to the Australian Region (Fig. 15-C). *Lytopsenella* is known only from the southern region. However, fossil species were found in the Eurasia in the Oligocene (Brues, 1923, 1933; Evans, 1964).

Key to the genera of subfamily Bethylinae

The zoogeographical distribution for each genus is shown in parentheses. The abbreviations of zoogeographic regions as follows: PAL, Palaearctic Region; ORI, Oriental Region; AUS, Australian Region; ETH, Ethiopian Region; NEA, Nearctic Region; NET, Neotropical Region.

1. Forewings with 6 closed cells, marginal and submarginal cell closed; notauli present 2
- Forewings with at most 4 closed cells; notauli absent 3
2. Propodeum with a median longitudinal canna; pterostigma broad .....*Eupsenella* [AUS]
- Propodeum without median longitudinal carina; pterostigma thin .....*Lytopsenella* [NET]
3. Marginal cell closed .....*Sierola* [PAL, ORI, AUS, NEA; abundant on the Hawaiian Islands]
- Marginal cell open apically 4
4. Antennae with 12 segments; basal vein forming almost a right angle; its portion appearing as a continuation of the median vein; transverse median vein thus far based of the apparent basal vein; brachypterous or micropterous species are present .....*Bethylus* [PAL, ORI, NEA]
- Antennae with 13 segments; basal vein oblique, only slightly angled, leaving median vein at about the same point as the transverse median vein; always fully winged

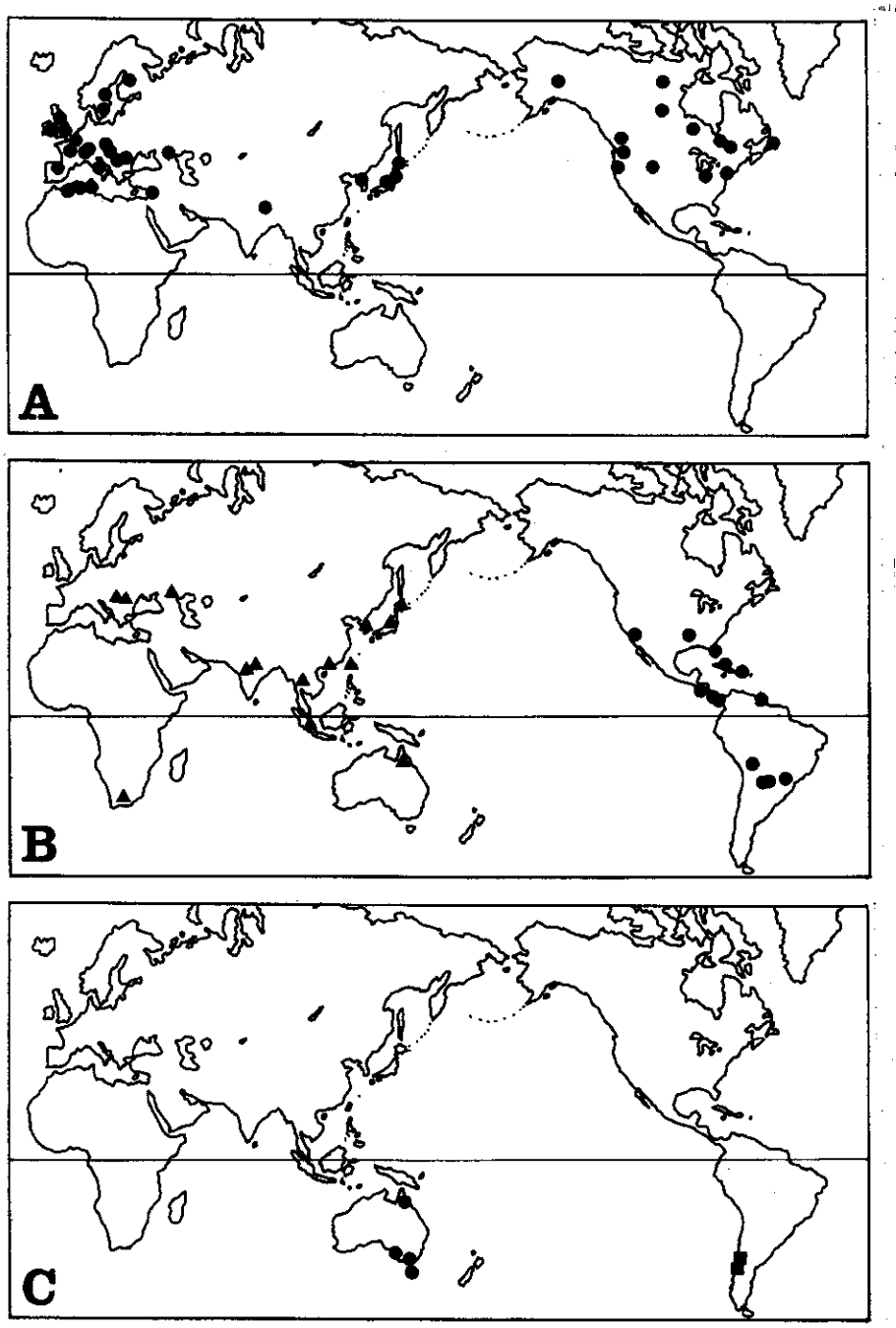


Fig. 15. Geographical distributions of 5 genera of Bethylinae. 15-A; Genus *Bethylus*. 15-B; Genera *Prosierola* (●) and *Odontepyris* (▲). 15-C; Genera *Eupsenella* (●) and *Lytopsenella* (■).

.....5

5. Prostigma large, foming a subtriangle; median carina of clypeus short, extending up to the frons at most for short distance
.....*Goniozus* [PAL, ORI, AUS, ETH, NEA, NET]

- Prostigma small, not forming a triangle; median carina of clypeus long, continueing on well up to the frons

.....6

6. Complete median carina of propodeum present; base of propodeal disc with a pair of small pits at the outermost part of basal triangular area
.....*Odontepyris* [PAL, ETH, ORI, AUS]

- Median carina of propodeum absent; base of propodeal disc with a pair of pits at the extreme base medially
.....*Prosierola* [NEA, NET]

Acknowledgements

I wish express my thanks to Sk. Yamane (Kagoshima University) and N. Minaka (National Institute of Agro-Environmental Sciences) for improving the earlier drafts of the manuscript. N. Minaka in particular kindly helped in analyzing the data by cladistic method using PAUP.

I am also grateful to the following biologists or institutions for lending valuable materials or giving useful information: M. L. Thakur (Indian Forest Research Institute, Dahra Dun), J. Huber and J. Poirier (Biosystematic Research Center, Ottawa), A. T. Finnamore (Provincial Museum of Alberta), A. Menke (United States National Museum, Washington), G. F. Hevel (National Museum at Natural History, Washington), K. Arakaki (Bernice P. Bishop Museum, Honolulu), A. Polaszek (Landbouwuniversiteit, Wageningen), F. Ronquist (Swedish Museum of Natural History), J. Forrest (South Australian Museum, Adelaide), S. Akimoto (Hokkaido University, Sapporo), K. Konishi (National Institute of Agro-Environmental Sciences, Tsukuba), S. Miyano (Natural History Museum & Institute, Chiba), A. Shinohara (National Science Museum, Tokyo), K. Yamagishi (Meijyo University, Aichi), T. Tachikawa (Ehime University, Matsuyama), S. Nomura (Kyushu University, Fukuoka), K. Kusigemati (Kagoshima University, Kagoshima).

Literature cited

Argaman, Q., 1990. Generic synopsis of Sierolomorphidae (Hymenoptera). Isurael Jour. Ent., **24**: 29-33.

Azevedo, C.O., 1992. Sobre os Sclerodermini (Hymenoptera, Bethylidae, Epyrinae) da região de São Carlos, São Paulo, Brasil. Revista bras. Ent., **36**: 561-567.

Berland, L., 1928. Bethylidae. *In* Faune de France - Hyménoptères Vespiformes II, **19**: 96-137.

Brothers, D. J., 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. Univ. Kansas Sci. Bull., **50**: 483-648.

Brothers, D. J. & J. M. Carpenter, 1993. Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). Jour. Hym. Res., **2**: 227-304.

Brues, C. T., 1923. Some new fossil parasitic Hymenoptera from Baltic amber. Proc. Amer. Aca. Arts & Sci., **58**: 327-346.

Brues, C. T., 1933. The parasitic Hymenoptera of the Baltic amber. Part 1. Bernstein-Forschungen, **3**: 4-172.

Carpenter, J. M., 1986. Cladistics of the Chrysidoidea (Hymenoptera). Jour. New York Ent. Soc., **94**: 303-330.

Carpenter, J. M., 1991. Phylogenetic relationships and the origin of social behaviour in the Vespidae. *In* K. G. Ross R. W. Matthews (eds.), The social biology of wasps, pp. 7-32. Cornell University Press.

Dalla Torre, C. G., 1898. Bethylinae, Pristocerinae. Catalogus Hymenopterorum, **5**: 547-562.

Evans, H, E., 1964. A synopsis of the American Bethylidae (Hymenoptera, Bethylidae). Bull. Mus. Comp. Zool., **133**: 67-151.

Evans, H, E., 1978. The Bethylidae of America North of Mexico. Mem. Amer. Ent. Inst., **27**: 1-332.

Gordh, G. & L. Móczár, 1990. A catalog of the world Bethylidae (Hymenoptera: Aculeata). Mem. Amer. Ent. Inst., **46**: 1-364.

Kieffer, J. J., 1904. Description de nouveaux Dryininae et Bethylinae. Du Musée Civique de Gênes. Ann. Mus. Civico Stor. Nat. Genova, Ser. 3, I: 351-412.

Kieffer, J. J., 1905. Proctotrypides. *In* E. André (ed.), Species des Hyménoptères d'Europe d'Algérie, **9**; 65-288. (Indirectly cited.)

Kieffer, J. J., 1911. Nouveaux Bethylides et Drynides exotiques du British Museum du Londres. Ann. Soc. Sci. Bruxelles, **35**: 200-233.

Kieffer, J. J., 1914. Bethylinae. Das Tierreich, **41**: 228-595.

Königsmann, E., 1978. Das phylogenetische System der Hymenoptera Teil 4: Aculeata (Unterordnung Apocrita). Deut. Ent. Zeitschr. (N. F.), **25**: 365-435.

Krombein, K. V., 1992. Systematics of the genera of Epyrinae with ramose male antennae (Hymenoptera: Bethylidae). Proc. Ent. Soc. Wash., **92**: 345-360.

Minaka, N., 1993. Algebraic properties of the most parsimonious reconstructions of the hypothetical ancestors on a given tree. Forma, **8**: 277-296.

Nagy, C. G., 1976. Bethylidae (Hymenoptera) parasitizing orchard caterpillars. Bull. Rev. Roumaine Biol., Ser. Biol. Anim., **21**: 103-108.

Polaszek, A. & K. V. Krombein, 1994. The genera of Bethylinae (Hymenoptera: Bethylidae). Jour. Hym. Res., **3**: 91-105.

Strejček, J., 1990. Beschreibung einer neuen Gattung und Art der Familie Bethylidae aus der Tschechoslowalei: *Acephalonomia cisidophaga* gen. et. sp. n. *Reichenbachia*. Staatliches Museum für Tierkunde Dresden, **28**: 47-50.

Swofford, D. L., 1993. PAUP, Phylogenetic Analysis Using Parsimony, version 3. 1. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

(Terayama, M.: Department of Biology, College of Arts & Sciences, The University of Tokyo, Komaba, Meguro-ku, Tokyo 153, Japan)

アリガタバチ亜科の系統と分布（膜翅目：セイボウ上科：アリガタバチ科）

寺山　守

アリガタバチ亜科の系統関係を属レベルで解析し，その結果を踏まえて各属の分布を論じた．

本亜科に7属を認め，最節約法による系統解析の結果，*Eupsenella*属と*Lytopsenella*属が他の5属から最初に分岐し，さらに*Prosierola*属と*Odontepyris*属が姉妹群を形成した．本亜科は，属レベルでの形態的な分化の程度が低く，小数の属でまとまった一群とみなすことができることから，本亜科内にBethyliniとSierolini の2族を設定したEvans (1978) の取り扱いは支持されず，本亜科内には族を設定しない分類様式を提唱する．

*Bethylus*属は基本的に旧北区と新北区に分布が限られ，姉妹群関係にある*Prosierola*属と*Odontepyris*属は異所的分布を示し，それぞれ新世界と旧世界に分布が見られた．また，オーストラリアに分布する*Eupsenella*と南米南部に分布する*Lytopsenella*は，本亜科内で祖先形質を最も多く有する属であった．

(寺山　守：153 東京都目黒区駒場3-8-1 東京大学教養学部生物学教室)

Appendix

Specimens examined

All the specimens examined in this study are listed below, with institutional codes. Locality and institutional codes are indicated in brackets.

Institutional codes:

BPBM: Bernice P. Bishop Museum, Honolulu, U.S.

CNC: Biosystematics Research Center (Canadian National Collection), Ottawa, Canada

EUM: Entomological Laboratory, Ehime University, Matsuyama, Japan

HUS: Entomological Institute, Hokkaido University, Sapporo, Japan

KU-K: Kusigemati collection, Entomological

Laboratory, Kagoshima University, Kagoshima, Japan
KUF: Entomological Laboratory, Kyushu University, Fukuoka, Japan
LU-P: Polaszek collection, Landbouwuniversiteit, Wageningen, The Netherlands
MU-Y: Yamagishi collection, Entomological Laboratory, Meijo University, Nagoya, Japan
NSMT: National Science Museum, Tokyo, Japan
NHMC: Natural History Museum and Institute, Chiba, Japan
NIAES: National Institute of Agro-Environmental Sciences, Tsukuba, Japan
PMA: Provincial Museum of Alberta, Alberta, Canada
SAM: South Australian Museum, Adelaide, Australia
SMNH: Swedish Museum of Natural History, Stockholm, Sweden
TE: Terayama collection, Department of Biology, University of Tokyo, Tokyo, Japan
USNM: United States National Museum, Washington D.C., U.S.A.

List of species examined

Subfamily Bethylinae

Bethylus : *B.* spp. [Japan, HUS, TE]; *B.* sp. [Nepal, CNC]; *B.* sp. [Korea, NSMT]; *B. boops* [Sweden, SMNH]

Eupsenella : *E. diemenensis* [Australia, SAM]; *E.* spp. [Australia, SAM]

Goniozus : *G. japonicus* [Japan, Korea & Taiwan, USNM, HUS, NIAES, NSMT, MU-Y, EUM, KUF, KU-K, TE]; *G. marianensis* [Mariana Is., NHMC]; *G.* spp. [Japan, HUS, NIAES, NSMT, MU-Y, EUM, KUF, KU-K, TE]; *G.* sp. [Korea, NSMT, PMA]; *G.* spp. [Taiwan, NSMT, NIAES, PMA]; *G.* spp. [Thailand, PMA]; *G.* sp. [Malaysia, PMA]; *G.* spp. [Indonesia, NIAES, PMA]; *G.* sp. [Nepal, CNC]; *G.* spp. [India, PMA]

Odontepyris : *O.* sp. [Japan, HUS, NIAES, NSMT, TE]; *O.* spp. [Taiwan, NSMT, TE]; *O.* sp. [Korea, MU-Y, PMA]; *O.* sp. [Hong Kong, NSMT]; *O.* spp. [Thailand, PMA]; *O.* spp. [India, PMA, LU-P]; *O.* sp. [Nepal, CNC]

Prosierola : *P.* sp. [Trinidad, LU-P]

Sierola : *S. sinensis* [China, BPBM]; *S.* spp. [Japan, MU-Y, CNC, TE]; *S.* sp. [Thailand, PMA]; *S.* sp. [India, PMA]