

The Phylogeny of the Bethylid Wasp Tribe Sclerodermini (Hymenoptera, Bethylidae)

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ABSTRACT The bethylid wasp tribe Sclerodermini is revised, 9 genera are recognized, and possible phylogenetic relationships are discussed. The genus *Nesepyrus* is synonymized with *Allobethylus*. The genus *Bethylopsis*, which has long been unknown of its precise taxonomic position, is found to be a member of this tribe. A key to the genera of the world is also provided.

The family Bethylidae, belonging to the Chrysidoidea and known as a group of primitive aculeate Hymenoptera, is widely distributed from the tropics to the subarctic regions of the world. It is represented by 1796 nominal species in 89 genera belonging to 4 to 6 subfamilies excluding fossil records as of 1992 (GORDH & MÓCZÁR, 1990; STREJČEK, 1990; KROMBEIN, 1992; ARGAMAN, 1990; AZEVEDO, 1992).

The tribe Sclerodermini of the subfamily Epyrinae was established by KIEFFER (1914). In 1928 BERLAND raised this tribe to full subfamily rank. Later EVANS (1964) regarded BERLAND's subfamily Scleroderminae as a tribe of subfamily Epyrinae.

The internal phylogeny of Sclerodermini remains unsolved. Only systematic work treating New World genera was presented by EVANS (1964). In his hypothesis about the relationships among genera or tribes, the tribe Epyrini is the least specialized group, and the Sclerodermini is more specialized one and may have arisen from the Epyrini. Unfortunately few apomorphic characters were indicated to explain the relationships, and no phylogenetic study using the cladistic method has been made on the Epyrinae up to the present.

The present study aims to clarify the internal relationships of tribe Sclerodermini at genus level and to contribute to the taxonomy of this taxon.

Materials and Methods

Taxa included in the analysis

Nine genera are treated. Five genera are examined with specimens. As for the remaining genera, I checked the character states based on the extensive literature (EVANS, 1964, 1973, 1978; MÓCZÁR, 1966; KIEFFER, 1914; AZEVEDO, 1992). Three genera, *Ateleopterus*, *Discleroderma* and *Scaphepyris*, are excluded from the present analysis because of not only lack of the types or voucher specimens, most of which were presumably lost during the World Wars, but also insufficient information due to the poor original descriptions. The species examined in this study are listed in the appendix together with the institutions preserving the materials.

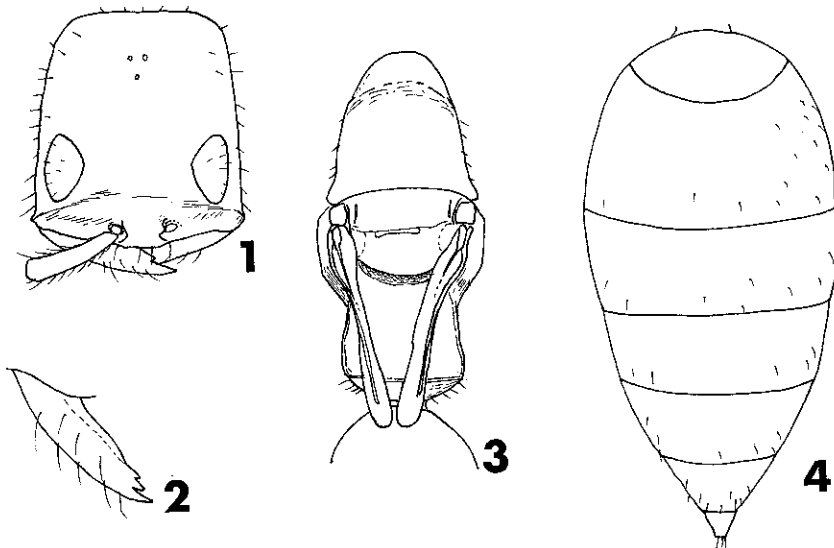
Methods of cladistic analysis

The cladistic analysis was performed by PAUP Ver. 3.0 b drawn by SWOFFORD (1989). 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 Hymenoptera (CARPENTER, 1986; 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 of aculeate Hymenoptera which had the plesiomorphic state in every character as an outgroup.

Results and Discussion*Taxonomic changes*

After examinations of sample material, I arrived at the following conclusions: 1) the genus *Nesepyrus* is synonymized with *Allobethylus*, and 2) the genus *Bethylopsis*, which has long been unknown of its precise taxonomic position, is a member of this tribe.



Figs. 1-4. *Bethylopsis fullawayi* FOUTS, 1939 (holotype).—1, Head, frontal view; 2, mandible; 3, alitrunk, dorsal view; 4, gaster, dorsal view.

Genus *Allobethylus* KIEFFER

Allobethylus KIEFFER, 1905, p. 247. Type species: *Allobethylus multicolor* KIEFFER, 1908. Designated by KIEFFER (1908).

Nesepyrus BRIDWELL, 1920, pp. 309–310. Type species: *Nesepyrus ewa* BRIDWELL, 1920. Original designation. **Syn. nov.**

The genus *Allobethylus* which consists of a single species, *A. multicolor*, is recorded from Papua New Guinea, and the genus *Nesepyrus*, consisting of 4 species, from the North to Central Americas and the Hawaiian Islands. In his 1920 paper, BRIDWELL indicated that the characters that separate *Nesepyrus* from *Allobethylus* as follows: 1) eyes with hairs, 2) submedian cell closed, 3) pterostigma weakly developed, 4) fossae of scutellum different, and 5) propodeum with a single imperfect median carina. However, the characters 1), 4) and 5) should be only species level differences in the Epyrinae, and the character 2) is erroneously cited, because the submedian cells are opened at the tip of anal vein in both genera. The character 3) is continuous; both genera have more or less small pterostigma. For the reason above mentioned, there is no distinct character to separate these genera, so I regard *Nesepyrus* as a junior synonym of *Allobethylus*.

The following 4 species are transferred to the genus *Allobethylus*: *A. antelleanus* (EVANS), comb. nov., *A. ewa* (BRIDWELL), comb. nov., *A. floridanus* (EVANS), comb. nov., and *A. virginianus* (EVANS), comb. nov.

Genus *Bethylopsis* FOUTS

Bethylopsis FOUTS, 1939, pp. 156–157. Type species: *Bethylopsis fullawayi* FOUTS, 1939. Monotypic.

This genus is firstly described by Fouts in 1939 from the Marquesas Islands. However, its precise taxonomic place has long been unknown. I have examined the type species, *B. fullawayi*, which is deposited in the collection of the Bernice P. Bishop Museum, and concluded that this genus should be placed in the tribe Sclerodermini of the subfamily Epyrinae. This genus is similar to the genus *Allobethylus* in general appearance, but is separated from the latter by the reduction in wing size and absence of notauli (Figs. 1–4).

The measurements of the type (female) are as follows: HL 0.67 mm; HW 0.62 mm; LE 0.23 mm; LA 1.05 mm; LPD 0.35 mm; WPD 0.38 mm; FWL 0.63 mm; TL 3.0 mm.

Cladistic analysis

Nine genera in the tribe are used for the analysis. Exact analysis of the matrix in Table 2 resulted in one cladogram (Fig. 5). Tree length is 36, with a consistency index of 0.778 and a retention index of 0.692. *Nothepyrus*, *Chilepyrus*, and (*Thlastepyrus*+*Alongatepyrus*) are positioned basally, and after that there is a division into *Allobethylus* and the remaining 4 genera. However, these relationships involved many reversed character transformations. *Bethylopsis* may be the sister-group of (*Glenosema*+(*Lepidosternopsis*+*Sclerodermus*)), but no autapomorphy has been revealed for this genus in the present analysis. *Sclerodermus* and *Lepidosternopsis* constitute a monophyletic assemblage by the characters 18 (absence of lateral and transverse carinae of propodeum) and 19 (absence of transverse carina of propodeum), and this has sister-group relationship to *Glenosema*.

Table 1. Characters and their states used in the analysis of the tribe Sclerodermini (based on the female).
0, plesiomorphic; 1, 2, apomorphic.

1.	Occiput of head.	Shorter [0]; elongate [1].
2.	Size of head.	Smaller [0]; much wider than maximum width of pronotum [1].
3.	Lateral borders of head in frontal view.	Convex [0]; parallel to subparallel [1].
4.	Mandibles.	Short and broad [0]; long and slender [1].
5.	Number of teeth of masticatory margin of mandibles.	Less than 7 [0]; 7 [1].
6.	Upper margin of mandibles.	Without denticles [0]; with small denticles [1].
7.	Eyes.	Situated on lateral sides [0]; situated forward [1].
8.	Eyes.	Situated almost at middle [0]; situated anterior portion [1].
9.	Ocelli.	Present [0]; absent [1].
10.	Occipital carina.	Present [0]; absent [1].
11.	Notauli.	Present [0]; absent [1].
12.	Parapsidal furrows.	Present [0]; absent [1].
13.	Tegulae.	Large [0]; small [1].
14.	Scutellum.	Long [0]; short [1].
15.	Basal transverse groove of scutellum.	Present [0]; absent [1].
16.	Scutellum.	Not separated from mesoscutum by a transverse streak [0]; separated from mesoscutum by a transverse streak [1].
17.	Propodeum.	Longer than wide [0]; wider than long [1].
18.	Lateral carinae of propodeum.	Present [0]; absent [1].
19.	Transverse carina of propodeum.	Present [0]; absent [1].
20.	Median carina of propodeum.	Present [0]; absent [1].
21.	Gastral sternites 4-6.	Simple [0]; biemarginate [1].
22.	Posterior border of abdominal sternites.	Simple [0]; with scales [1].
23.	Wings.	Fully developed [0]; dimorphic [1]; very small [2].
24.	Submedian cell.	Long [0]; extremely short, less than half length of median cell [1].
25.	Median vein.	Long [0]; short, not divided into median and submedian cells [1].
26.	Costal cell.	Present [0]; absent [1].
27.	Body shape.	Not depressed [0]; extremely depressed dorsoventrally [1].

Thlastepyris and *Alongatepyris* constitute a monophyletic assemblage by the characters 24 (extremely short median cell of forewings) and 27 (extremely depressed body shape). These genera closely resemble each other, but the former differs from the latter in having short marginal and median veins, and lacking costal cell in forewings.

EVANS (1964) regarded the tribe Epyrini as a generalized element and Sclerodermini as specialized stock. The wing vein reduction and simplification of the body surface sculpture seen in the genera of this tribe support his hypothesis. In this cladistic analysis with the external morphologies, however, there have been found many homoplasious character states. I have no doubt that the additions of new characters will lead to further changes and improved resolutions.

Zoogeographical distribution

The number of described species in each genus is shown in Table 3. This tribe is distributed evenly at generic level in the world. At specific level, however, the

Table 2. Character coding for the analysis of the generic relationships in the tribe Sclerodermini.

Taxa	Character coding																											
	1	2	3	4	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9	0	1	2	2	2	2	2	2	2
<i>Allobethylus</i>	1	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Alongatepyris</i>	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
<i>Bethylopsis</i>	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0
<i>Chilepyris</i>	0	1	0	0	0	0	1	0	0	1	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0
<i>Glenosema</i>	1	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0
<i>Lepidosternopsis</i>	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	1	2	0	0	0	0
<i>Nothepyris</i>	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
<i>Sclerodermus</i>	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0
<i>Thlastepyris</i>	1	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1
Outgroup	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	0

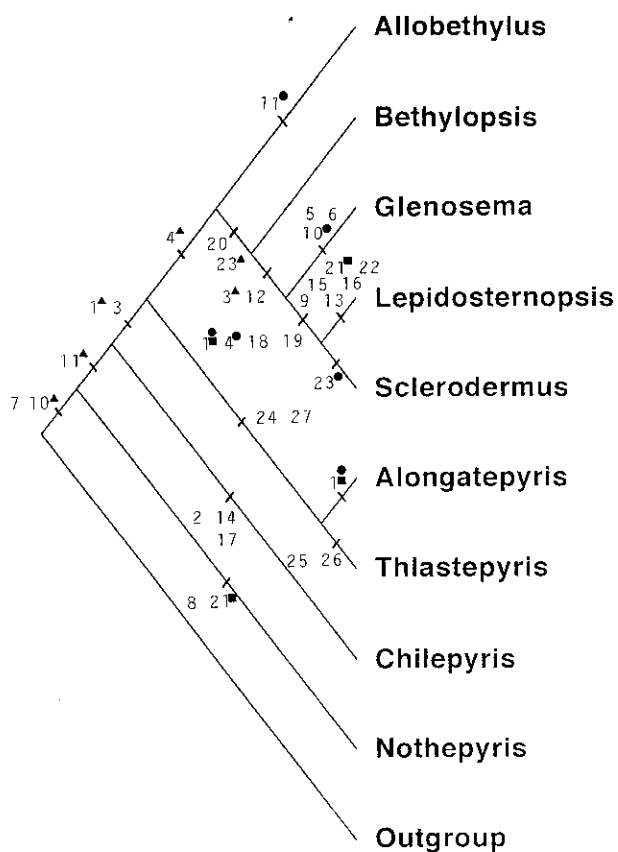


Fig. 5. Most parsimonious cladogram of the tribe Sclerodermini.
 ■: convergence elsewhere on tree. ●: reversal of previous change. ▲: showing later reversal.

genus *Sclerodermus* is abundant in the Palaearctic Region and Oceania. *Chilepyris* and *Lepidosternopsis* are restricted to the Australian and the southern Neotropical Regions. The Neotropical Region has three endemic genera, *Alongatepyris*, *Thlastepyris* and *Nothepyris*, of which the latter two are phylogenetically most closely related in this analysis.

Table 3. Zoogeographical synopsis of the tribe Sclerodermini.

The number of species occurring in each region is given. "X" shows unpublished data. The Hawaiian subdivision is separately shown but the Malagasy Region is included in the Ethiopian Region in this table. The zoogeographic regions are abbreviated as follows: PAL, Palaearctic; ORI, Oriental; AUS, Australian; ETH, Ethiopian; NEA, Nearctic; NET, Neotropical; HAW, Hawaiian.

Genera	PAL	ORI	AUS	ETH	NEA	NET	HAW	Total
<i>Allobethylus</i>	X	X	1		2	1	1	5
<i>Alongatepyris</i>						1		1
<i>Ateleopterus</i>	1							1
<i>Bethyloysis</i>							1	1
<i>Chilepyris</i>			1			1		2
<i>Discleroderma</i>		1						1
<i>Glenosema</i>	5	X	1	2	1			9
<i>Lepidosternopsis</i>			2			1		3
<i>Nothepyris</i>						1		1
<i>Scaphepyris</i>		1						1
<i>Sclerodermus</i>	26	10	2	4	4	6	18	68
<i>Thlastepyris</i>						1		1

Key to Genera of the Tribe Sclerodermini

This tribe is characterized in Epyrinae by 13-segmented antennae, short and truncate clypeus, situation of eyes (forward on head), 6 or 5 segmented maxillary palpi, and 3 or 2 segmented labial palpi.

The zoogeographical distribution for each genus is shown in brackets; for the abbreviations of zoogeographic regions, see Table 3. Ambiguous genera are excluded in the key to avoid unnecessary confusions.

1. Mandibles thin and elongate, terminating in 2-3 teeth; head rectangular, distinctly longer than wide in frontal view 2
- Mandibles thick and broad; head at most slightly longer than wide in frontal view 3
2. Wings fully developed; notauli distinct *Allobethylus* [PAL, ORI, AUS, NEA, NET]
- Wings reduced, not reaching the posterior border of propodeum; notauli indistinct *Bethyloysis* [Marquesas Isls.; known from female only]
3. Mandibles with 7 small teeth, upper margin denticulate; wings fully developed or brachypterous; female only (see also couplet 8)

- *Glenosema* [PAL, ORI, AUS, ETH, NEA]
 — Mandibles with less than 7 teeth, upper margin without denticule 4
 4. Gastral sternites 4–6 deeply bimarginate, with broad median apical plates and narrower lateral plates; wings present but minute, not reaching the anterior border of propodeum
 *Lepidosternopsis* [NET, AUS; known from females only]
 — Gastral sternites 4–6 simple or their margins shallowly sinuate 5
 5. Body extremely depressed dorsoventrally 6
 — Body at most weakly depressed dorsoventrally 7
 6. Costal vein and costal cell present; median vein dividing median and submedian cells *Alongatepyris* [NET]
 — Costal vein and costal cell indistinct; median vein short, median and submedian cells not separated by median vein *Thlastepyris* [NET]
 7. Radial vein present 8
 — Radial vein absent, at most indicated by a very faint line; apterous female present in some species 9
 8. Mandibles with 2–3 teeth; occipital carina absent *Nothepyris* [NET]
 — Mandibles with 5 teeth; occipital carina present; male only (see also couplet 3)
 *Glenosema* [PAL, ORI, AUS, ETH, NEA]
 9. Pterostigma large and almost circular; head very large, wider than long, much wider than maximum width of thorax in dorsal view
 *Chilepyris* [NET, AUS]
 — Pterostigma smaller and longer than wide; head slightly wider than long, almost as long as wide or only slightly wider than maximum width of thorax; winged and apterous forms present in both sexes but female usually apterous *Sclerodermus* [PAL, ORI, AUS, ETH, NEA, NET]

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摘 要

寺山 守 (東京大学教養学部生物学教室)——アリガタバチ類の Sclerodermini 族の系統 (ハチ目, アリガタバチ科).

アリガタバチ科 Epyrinae 亜科の Sclerodermini 族を属レベルで点検し, 系統関係を推定した. *Nesepyrus* 属は *Allobethylus* 属の異物同名とみなした. また, 原記載以降長い間所属亜科が不明であった *Bethylopsis* 属は, 基準標本を点検した結果, 本族の一員であることが判明した. さらに, 本族の属の検索表を提供した.

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Appendix. Species examined.

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

Tribe Sclerodermini

Allobethylus: *A. multicolor* [New Guinea, HNM]

Bethylopsis: *B. fullawayi* [Marquesas Isls., BPBM]

Glenosema: *G. sp. A* [Thailand, PMA]; *G. sp. B* [Thailand, PMA]; *G. sp. C* [Thailand, PMA].

Nesepyrus: *N. sp.* [Japan, TE, NIAES, KUF]

Sclerodermus: *S. harmandi* [Japan, MNHP]; *S. nipponicus* [Japan, Korea, Taiwan, China, NIAES, KUF, HUS, NSMT, TE]; *S. guani* [China, ASB, BFRI]; *S. luteicolle* [Myanmar, MCSN]; *S. macrogaster* [U.S.A., KUF]; *S. carolinense* [U.S.A., KUF]; *S. sp. A* [Japan, NIAES, TE]; *S. sp. B* [Taiwan, TE]; *S. sp. C* [Taiwan, TE].

Institutional codes:

ASB: Academia Sinica, Beijing, China

BFRI: Research Institute of Forestry, Beijing, China

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

HNM: Hungarian Natural History Museum, Budapest, Hungary

HUS: Entomological Institute, Hokkaido University, Sapporo, Japan

KUF: Entomological Laboratory, Kyushu University, Fukuoka, Japan

MCSN: Museo Civico di Storia Naturale, Genova, Italy

MNHP: Muséum National d'Histoire Naturelle, Paris, France

NSMT: National Science Museum, Tokyo, Japan

NIAES: National Institute of Agro-Environmental Sciences, Tsukuba, Japan

PMA: Provincial Museum of Alberta, Alberta, Canada

TE: TERAYAMA collection, Department of Biology, University of Tokyo, Tokyo, Japan