Phylogenetic Systematics of the Family Bethylidae (Insecta: Hymenoptera) Part I. Higher Classification

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Abstract The higher phylogeny of the family Bethylidae was cladistically analyzed using the all possible subfamilies. The analysis yielded in a single most parsimonious tree. The following conclusions were reached: 1) six subfamilies are recognized; 2) Afgoioginae was included in Pristocerinae; 3) a new subfamily, Parapenesiinae, was proposed; 4) Epyrinae, Mesitiimae, and Galodoxinae were marked as sister-groups each other; 5) Galodoxinae was considered to the hold within the current position.

Introduction

The family Bethylidae, belonging to Chrysidoidea and known as a group of primitive aculeate Hymenoptera, is widely distributed from the tropics to the subarctic regions of the world. Extant species represented by about 1900 nominal species in 84 genera excluding fossile species as of 2002.

The wasps are small, 1-20 mm in body length, and most species are external parasites of lepidopterous and coleopterous larvae. Due to their host associations, bethylids are potentially beneficial in agriculture and forestry as biological control agents of various insect pests. On the other hand, some species, e.g. *Cephalonomia*, *Epyris*, and *Sclerodermus* species, have been well known as sanitary injurious pests that cause serious dermatitis for humans by their frequent stinging (Tachikawa, 1980a, b, 1985a, b; Terayama, 1997, 1999). Although this group is thus important in the agricultural, forestry, and medical fields, applied studies of bethylids have not been easily advanced by lack of taxonomic, phylogenetic and biological knowledge.

There are three opposing views about the recognition of subfamilies in Bethylidae: (1) six subfamilies, Pristocerinae, Afgoiogfinae, Epyrinae, Galodoxinae, Mesitiinae, and Bethylinae, are recognized (Argaman, 1988; Strejcek, 1990), (2) five subfamilies are recognized, and Afgoiogfinae is included in Pristocerinae (Gordh & Móczár, 1990), (3) four subfamilies are recognized, and two subfamiles, Afgoiogfinae and Galodoxinae, are unrecognizable (Finnamore & Brothers, 1993). Evans (1978) carried out the first phylogenetic analysis among three subfamilies based on the New World's materials and indicated that Bethylinae is a sister-group of (Pristocerinae + Epyrinae).

The present study aims to clarify the internal relationships of Bethylidae at subfamily level and contribute to the taxonomy of this family.

Historical background

Higher classification

The name Bethylidae was first used in 1839 by Halliday. Förster (1856) used a different name Bethyloide, for the same group this name was corrected into Bethylidae by Ashmead (1902). In 1883 Cameron incorporated the subfamily Bethylinae into the family Proctotrupidae. Dalla Torre (1898) divided Cameron's Bethylinae into two subfamilies, Bethylinae and Pristocerinae. On the other hand Ashmead (1902) and Brown (1906) placed Bethylidae or Bethylinae in the superfamily Vespoidea.

In the early 20th century, many genera and species were described by Kieffer. In 'Genera Insectorum' (1908) he gave descriptions for 491 species in 58 genera of Bethylidae in the world. Furthermore, in 'Das

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Tierreich' (1914) he recognized 660 species in 102 genera, and presented a key to known species. He also established 5 tribes in it, namely Pristocerini, Sclerodermini, Epyrini, Mesitiini, and Bethylini. In 1928 Berland separated superfamily Bethyloidae from superfamily Proctotrupoidea (= Proctotrupidae in Cameron (1883)). At the same time he raised Kieffer's 5 tribes to subfamily rank. Evans has published several important papers on the New World fauna, and he reviewed the species of this zoogeographical region in 1964 and 1978. In the 1964 revision, he recognized 4 subfamilies in the Bethylidae, namely Pristocerinae, Epyrinae, Mesitiinae and Bethylinae, and regarded Berland's subfamily Scleroderminae as a tribe of subfamily Epyrinae. Recently Nagy (1974) and Argaman (1988) established the subfamily Galodoxinae based on the material from the Philippines, and subfamily Afgoiogfinae, which consists of genera *Afgoigfa* and *Parascleroderma*.

The recent checklist of Gordh & Móczár (1990) outlined bibliographic information and distribution of each species, treating 1794 species in 91 genera in 5 subfamiles excluding fossile records. In this checklist they rejected the segregation of subfamily Afgoiogfinae from Pristocerinae. In 'Hymenoptera of the world' Finnamore & Brothers (1993) did not recognize subfamilies Afgoiogfinae of Argaman and Galodoxinae of Nagy. Recently, Terayama (1996) was provisionally synonymized Afgoiogfinae with Pristocerinae by the cladistic analysis. About 1900 nominal species in 84 genera belonging to 4 to 6 subfamilies are known up to the present .

Phylogeny

The internal phylogeny of Bethylidae remains unsolved. Systematic work at the subfamily level has been presented by only Evans (1964). In his analysis treating three subfamilies, Bethylinae was regarded as a sister-group of the others (Pristocerinae + Epyrinae). He also offered a hypothesis about the relationships among genera in each subfamily (1964, 1978). Unfortunately, however, few apomorphic characters were indicated to explain the relationships. Nagy commented that subfamily Galodoxinae established by him is most closely related to the fossil subfamily Protopristocerinae established also by him in 1974. Recently, the phylogenetic analyses using the cladistic method have been made on the Pristocerinae (Terayama, 1996), Sclerodermini (Terayama, 1995a), and Bethylinae (Polaszek & Krombein, 1994; Terayama, 1995b) at genus level. However, up to the present no phylogenetic study using the cladistic method has been made on the Bethylidae at subfamily level.

Materials and methods

Material examined

Sixty-nine out of 84 valid genera were treated. Fifty-five genera were examined with specimens. As for the remaining 14 genera the states of their characters were extracted from extensive literature (Azevedo, 1992, 1999; Evans, 1964, 1978; Königsmann, 1979; Móczár, 1970a, b, 1971; Nagy, 1972; Strejcek, 1990). Fifteen genera were 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 specimens in this study are listed in the appendix together with institutions preserving the materials.

Taxa included in the analysis

All the possible subfamilies, Pristocerinae, Afgoioginae, Epyrinae, Galodoxinae, Mesitiinae, and Bethylinae, were treated. In the course of my examinations of 69 genera, the genus *Parapenesia* belonging

to Pristocerinae has many unique characteristics. After the examination of this type material, I was found that the specimen has strongly different shape of mesosoma which is unique in the Bethylidae. For this reason *Parapenesia* is treated as a separate taxon in the analysis.

Table 1. Characters and their status used in the analysis of Bethylidae.
0, plesiomorphic; 1, apomorphic.

Both Sexes
1. Strong sexual dimorphism. Absent [0]; present [1].
2. Head form. Not prognathous [0]; prognathous [1].
3. Clypeus. Whitout longitudinal median carina [0]; with a longitudinal median carina [1].
4. Pronotum. Shorter than mesoscutum [0]; longer than mesoscutum [1].
5. Metasternum. Not broad anterioly [0]; broad anteriorly [1].
6. Anteromedian portion of propodeum. Not strongly carinate [0]; strongly raised, carinate and extending to the metanotum [1].
7. Posterolateral corners of propodeum. Without spine [0]; with a strong spine [1].
8. Second gastral tergum. Usual in size [0]; large [1].
9. Pterostigma. Present at 1/2 of distance or more of wings [0]; less than 1/2 of distance of wings [1].
10. Basal vein. Cubitus with a base [0]; simple [1].
11. Strong notch on the anterior marbin near the base of the hind wings. Absent [0]; present [1].
12. Tarsal claws. Weakly to moderately curved [0]; strongly curved [1].
Male
13. Anterior portion of propleuron. Short [0]; elongate [1].
14. Metanotum. Developed [0]; reduced [1].
15. Small emargination of fovea on the anterior portion of metanotum. Absent [0]; present [1].
Female
16. Body shape. Not flattended [0]; extremely flat dorsoventrally [1].
17. Eyes. Large [0]; reduced [1].
18. Scutellum. Usual in size [0]; extremely broaded [1].
19. Mesopleura and mesonotum. Not fused [0]; fused [1].
20. Width of mesescutum. Almost the same as pronotal width [0]; shorter than the poronotal width [1].
21. Metanotum. developed [0]; reduced [1].
22. Propodeum. Long, lateral sides more or less parallel. [0]; broad, lateral sides strongly convex [1].
23. Forth gastral sternum. Simple [0]; with a pair of large cornicles [1].
24. Fifth gastral sternum. Simple [0]; with a pair of large cornicles [1].

Table 2. Character coding for the analysis of the subfamilial relationships.
? = status unknown, P = polymorphic.

Taxon	1 1 1 1 1 1 1 1 1 1 2 2 2 2 2 1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4
Pristocerinae	1 1 1 0 1 0 0 0 P 1 0 0 1 0 1 0 1 0 0 1 1 0 0 0
Afgoioginae	1 1 1 0 1 0 0 0 0 1 0 0 1 0 1 1 1 0 0 1 1 0 0 0
Epyrinae	0 1 1 1 1 0 0 0 1 1 0 0 0 1 0 P 0 0 0 0 P 0 0 0
Mesitiinae	0 1 1 1 1 1 1 1 1 1 0 0 0 1 0 0 0 0 0 0 0 0 0 0
Bethylinae	0 1 1 0 1 0 0 0 0 1 0 1 1 0 1 0 0 0 0 0 0 0 0 0
Galodoxinae	? 1 1 1 1 0 0 0 1 1 0 0 ? ? ? 0 0 0 0 0 0 0 1 1
Parapenesia	? 1 1 0 ? 0 0 0 ? ? ? 0 ? ? ? 0 1 1 1 0 1 1 0 0
Chrysididae	0 0 0 0 0 0 P 1 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0 0

Methods of cladistic analysis

The cladistic analysis was performed by PAUP* Ver. 4.0b (Swofford, 2001) on a Macintosh Power Book G4 computer. All the search for the shortest tree(s) was made by the exact branch-and-bound algorithm with 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).

Twenty-four characters are used (Table 1). Their character states are shown in Table 2. The definitions of character states and interpretation of the polarities largely followed prevailing views of evolutionary change within the aculeate Hymenoptera (Brothers, 1975; Brothers & Carpenter, 1993; Carpenter, 1986, 1990). Since the phylogenetic relationships between the bethylids and other wasps have not been fully resolved, I examined two data sets which adopted different outgroups as follows: Data set 1: Chrysididae which is regarded as the sister-group of Bethylidae by Brothers & Carpenter (1993) and Carpenter (1986); Data set 2: hypothetical ancestor which had the all plesiomorphic state in every character.

I have not made use of the fossil subfamily Protopristocerinae defined by Nagy in 1974 as an outgroup, since states of many of the important characters cannot be assessed for this group, and monophyly of this group is not confirmed.

Results

Data set 1 produced a single most parsimonious tree (Fig.1; tree length (TL) = 30, consistency index (CI) = 0.933, and retention index (RI) = 0.857). Of the 24 characters studied, 11 were cladistically informative. Data set 2 also produced the single most parsimonious tree which presents the same topological relationships as the data set 1 (TL = 28, CI = 0.964, RI = 0.923). The following results are consistent to both data sets: 1) the tree has two major monophyletic groups, (*Parapenesia* + (Pristoceninae + Afgoioginae)) and (Bethylinae + (Epyrinae + Mesitiinae + Galodoxinae)); 2) *Parapenesia* is a sister-group of (Pristocerinae + Afgoioginae); 3) Bethylinae is a sistrer-group of (Epyrinae + Mesitiinae + Galodoxinae); 4) Epyrinae, Mesitiinae and Galodoxinae are shown to form a remaining equivocally

resolved clade. Monophyly of *Parapenesia*, and Pristocerinae and Afgoiginae supported by 4 characters (1, 13, 15, 21), and that of Bethylinae, Epyrinae, Mesitiinae and Galodoxinae by 2 characters (9, 14).

The *Parapenesia* has the following autapomorphic characters: scutellum broaden and metanotum fused (character 18), mesopleura and mesonotum fused (character 19), broad and posteriorly rounded propodeum (character 22).

The clade (Pristocerinae + Afgoioginae) is characterized by the apomorphic condition of characters 17 (reduced eyes in the female) and 20 (small mesoscutum in female). The autoapomorphic character of Afgoioginae is its extremely flat body in the female (character 16), and the analysis did not reveal apomorphic characters for Pristocerinae.

The following two characters support the monophyly of Bethylinae: a strong notch on the anterior margin near the base of hind wing (character 11), strongly curved tarsal claws (character 12). The well developed median clypeal carina which extends a short distance from clypeus to frons is a possible autapomorphy. The monophyly of the group (Epyrinae + Mesitiinae + Galodoxinae) is supported by the proportionally long mesonotum (character 4), but there are no unequivocally shared apomorphies among two of the constituent taxa. Two autapomorphic characters are characterized the subfamily Mesitiinae: strongly carinate anteromedian portion of propodeum (character 6) and strong spines of posterolateral corners of propodeum (character 7). Two autapomorphies support the monophyly of Galodoxinae: the large cornicles of the 4th and 5th gastral sternites respectivelly (characters 23 and 24).

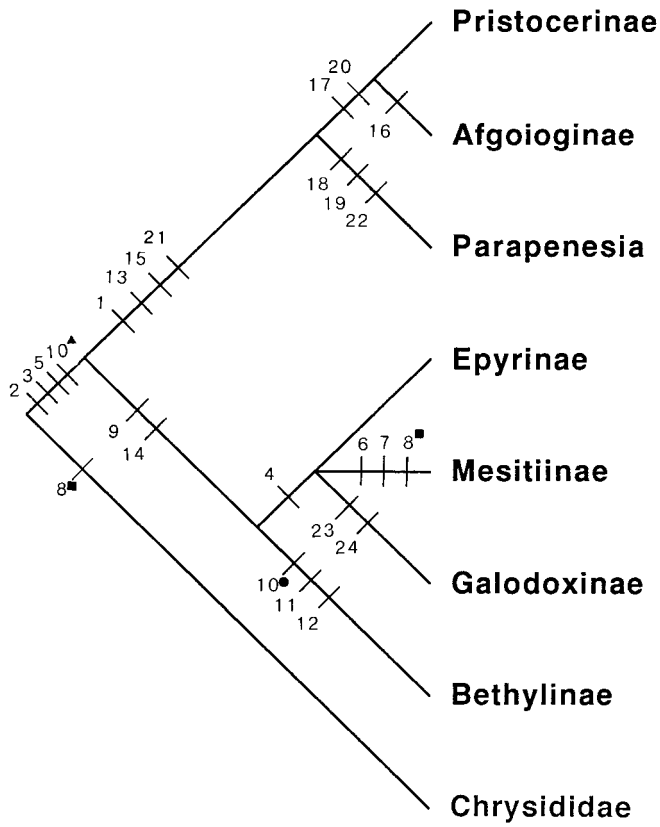


Fig. 1. Proposed phylogeny of the subfamilies of Bethylidae.
▲: showing later reversal. ●: reversal of previous change. ■: convergence elsewhere on tree.

Discussion

Internal phylogeny of Bethylidae

The *Parapenesia* has three autapomorphic characters (18, 19, 22). These are morphologically informative characters to separate it from the other subfamilies. So it may reasonably constitute a separate subfamily. However, its phylogenetical position which form a sister-group with Pristocerinae is not robust, since the 3 of 4 characters (1, 13, 15) which support the monophyly of *Parapenesia* + Pristocerinae are based on the male characters. The *Parapenesia* has been known in female only. Rather, the 13-segmented antennae, the truncated anterior margin of clypeus and the relatively large eyes of *Parapenesia* look resembling to the tribe Sclerodermini in Epyrinae. For the '*Parapenesia* problem', discovery of male of this genus is needed.

Afgoioginae is separated from Pristocerinae by character 17 (flat female body). However, this character is also seen in the genera *Thlastepyris*, *Alongtepyris*, *Plastanoxus* and *Cephalonoma* of Epyrinae. Presumably these extremely depressed from is due to adaptation to life under barks. So this character is not suitable to support a separate subfamily. Argaman (1988) indicated the following characters to separate Afgoioginae from Pristocerinae: 1) palpal formula 6-3, 3-2; 2) mesosternum without acetabular carina; 3) costal margin of pterostigma emarginate; 4) eyes of female large. As for the character 2 some other genera of Pristocerinae, e.g. *Dicrogenium*, also have the same condition. Character 3 is variable within the genus, and some species have straight costal margin of pterostigma. The characters 1 and 4 presumably represent generic level differences. As a conclusion, I support the Gordh & Móczár view (1990) that Afgoioginae should be included in the Pristocerinae.

Evans (1964) presented the probable relationships among the three subfamilies as follows: (Bethylinae + (Pristocerinae + Epyrinae)). However, the present analysis indicated that the Bethylinae constitute a clade with Epyrinae. Pristocerinae is separated basally from the clade Bethylinae + Epyrinae. The character 17 on the Table 2 is autapomorphic character and characters 1, 13, 15, 17, 20 and 21 are possible ones in Pristocerinae.

Epyrinae, Mesitiinae and Galodoxinae are shown to form a monophyletic group. The latter two may be held to constitute separate subfamilies by the autapomorphic characters 6 and 7, and 23 and 24, respectively, while no unequivocal apomorphies emerge for the Epyrinae.

Nagy (1974) stated that the subfamily Galodoxinae is allied on the ground of some features to the fossil subfamily Protopristocerinae, which is very much like the genus *Pristocera* of Pristocerinae but have the winged female. The results of the present phylogenetic analysis did not support his view; namely the subfamily is closely related to the Epyrinae or Mesitiinae rather than to the Pristocerinae.

I did not find any autapomorphy for the subfamily Epyrinae in the present analysis. This subfamily is most diverse group in external morphology in the Bethylidae. It has the largest number of genera (39), which contain medium to minute sized genera. The size reduction of those genera may follow many of the degenerative specializations in external morphology. The tendency of the specialization are: 1) simplification of the body sculpture; 2) reduction in wing veins or loss of wings; 3) reduction in the number of antennal and palpal segments. Those continuous specialization among genera would prevent to find synapomorphies of this subfamily. I tentatively treat Epyrinae as a single independent subfamily.

The detailed phylogenetic relationships among Epyrinae, Mesitiinae and Galodoxinae will be revealed by further studies. Also examining males of *Parapenesia* and Galodoxinae will provide more phylogenetic information.

Constituent of Subfamilies

The following conclusion has been reached: 1) six subfamilies are recognized; 2) Afgoiobinae is included in the Pristocerinae; 3) a new subfamily, Parapenesiinae, is proposed although the '*Parapenesia* problem' has been unsolved; 4) Epyrinae, Mesitiinae, and Galodoxinae are marked as sister-groups each other, and Galodoxinae should be positioned as subfamily rank. The revised taxonomic system of subfamilies of Bethylidae is proposed as follows based on the present phylogenetic analysis:

(1) Subfamily Pristocerinae

Pristocerinae Dalla Torre, 1898: 561. Type genus: *Pristocera* Klug, 1808.

Pristoceriini; Kieffer, 1914: 451. [As a tribe.]

Pristocerinae; Berland, 1928: 103. [Raised to subfamily status.]; Evans, 1963: 19.

Afgoioginae Argaman, 1988: 140. Type genus: *Afgoiogfa* Argaman, 1988. [Provisional synonymy by Terayama, 1996] **Syn. nov.**

(2) Subfamily Parapenesiinae, new subfamily

Type genus: *Parapenesia* Kieffer, 1910.

Diagnosis. Small apterous wasps (female) with the following combinations of characters. 1, Antenna with 13 segments; 2, clypeus with a medium carina; anterior margin truncate; 3, eye medium sized, situated forward on head; 4, mesoscutum and mesopleuron fused, but the mesopleuron produced laterally in dorsal view; 5, mesoscutum broaden; 6, notauli present but shallow; 7, parapsidal lines absent; 8, tegla absent; 9, metanotum reduced; 10, propodeum oval, wider than long; 11, middle tibia spinose; 12, gaster depressed dorsoventrally.

Remarks. The characters 4, 5, and 10 are autapomorphic in Bethylidae. Male is not known.

***Parapenesia unicolor* Kieffer, 1910** (Figs. 2-4)

Redescription of type. Female. Head length 0.77 mm; head width 0.68 mm; length of mesosoma 1.31 mm; dorsal length of propodeum 0.45 mm; dorsal width of propodeum 0.56 mm; total body length 3.8 mm.

Body and legs yellowish brown; tip of mandible reddish brown.

Head longer than wide, with weakly convex posterior margin in full face view; posterolateral corner not forming an angle; frons and vertex smooth and shining. Mandible with 3 teeth, apical tooth most projecting and basal two dull. Eye 0.19 mm in length. Antenna short; scape robsut and short; 2nd to 5th segments each as long as wide; 6th to 13th segments each slightly longer than wide.

Mesosoma smooth and shining; pronotum 0.5 times as long as wide, anterior margin semicircular, posterior margin straight in dorsal view; mesothorax including mesopleuron 0.71 mm in maximum width; propodeum oval, 0.80 times as long as wide in dorsal view.

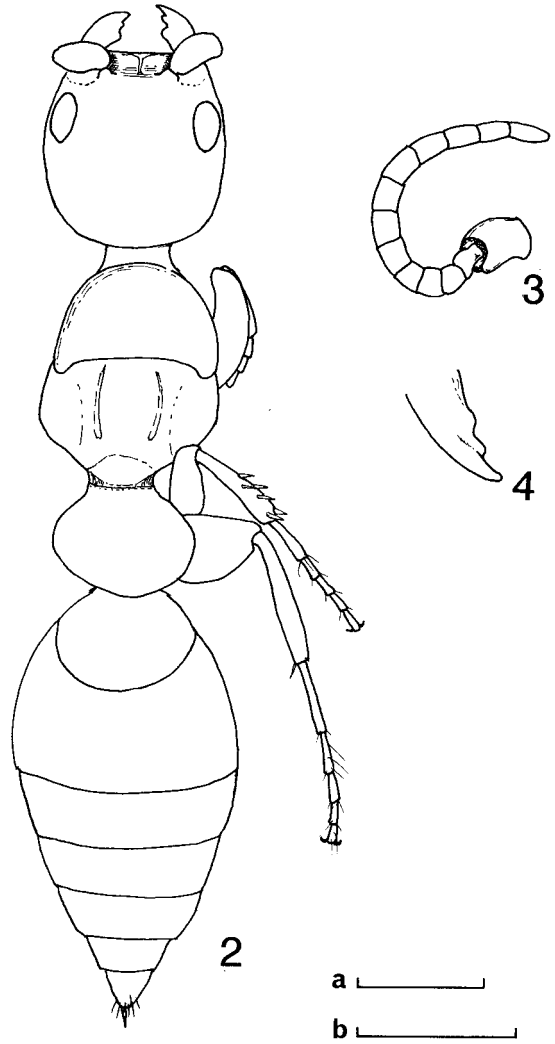
Middle and hind femora broad; middle tibia with 8 spines; claws simple.

Metasoma rather smooth but weakly microreticulate.

Holotype. Female, Cap. Srege (Africa).

Type depository. Zoological Museum, Berlin.

Remarks. This genus is monotypic, known from *P. unicolor* only.



Figs. 2-4. Parapenesiinae new subfamily, *Parapenesia unicolor* Kieffer, female. 2, body, dorsal view; 3, antenna; 4, right mandible. Scale bars: a, 0.5 mm in figure 2; b, 0.5 mm in figures 3 & 4.

(3) Subfamily Epyrinae

Epyrini Kieffer, 1914: 308. [As a tribe.] Type genus: *Epyris* Westwood, 1832.
Epyrinae; Berland, 1928; 111. [Raised to subfamily status.]; Evans, 1964: 89.
Sclerodermini Kieffer, 1914: 238. [As a tribe.]
Scleroderminae; Berland, 1928: 121. [Raised to subfamily status.]
Sclerodermini; Evans, 1964: 89. [As a tribe of Epyrinae.]

(4) Subfamily Mesitiinae

Mesitiini Kieffer, 1914: 288. [As a tribe.]
Mesitinae [sic.] Berland, 1928: 108. [Raised to subfamily status.] Type genus: *Mesitius* Spinola, 1851.
Mesitiinae; Kurian, 1954: 266.

Remarks. The name Mesitinae was given initialy by Berlands (1928), and then, Móczár (1970a, b, 1971) or Nagy (1969, 1972) employed it. However, Mesitinae should be corrected as Mesitiinae, according to the International Code of Zoological Nomenclature (4th Edition) by Articles 32.2, 32.5 and 35.4.

(5) Subfamily Galodoxinae

Galodoxinae Nagy, 1974: 126. Type genus: *Galodoxa* Nagy, 1974.

(6) Subfamily Bethylinae

Bethylinae Dalla Torre, 1898: 547. Type genus: *Bethylus* Latreille, 1802.

Bethylinae; Berland, 1928: 99. [Raised to subfamily status.]; Evans, 1964: 180.

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Appendix. Specimens examined for the cladistic analysis.

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

Institutional codes:

ASB: Academia Sinica, Beijing, China

BFRI: Research Institute of Forestry, Beijing, China

BMNH: Natural History Museum, London, U.K.

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

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

DEI: Deutsches Entomologisches Institut, Berlin, Germany

EUM: Entomological Laboratory, Ehime University, Matsuyama, Japan

FSM: Forest Department of Sarawak, Kuching, Malaysia.

HNM: Hungarian Natural History Museum, Budapest, Hungary

HUS: Entomological Institute, Hokkaido University, Sapporo, Japan

IAVH: Instituto para Investigación de Recursos Biologicos 'Alexander von Humboldt' Villa ole Leyva, Colombia

KU-K: Kusigemati collection, Entomological Laboratory, Kagoshima University, Kagoshima, Japan

KUF: Entomological Laboratory, Kyushu University, Fukuoka, Japan

LU-P: Polaszek collection, Landouwuniversiteit, Wageningen, Netherlands

MCSN: Museo Civico di Storia Naturale, Genova, Italy

MNHN: Museum National d'Histoire Naturelle, Paris, France

MU-Y: Yamagishi collecion, Entomological Laboratory, Meijo University, Nagoya, Japan

MRAC: Musee Royal de I'Afrique Centrale, Tervuren, Belgium

NASM: National Science Museum, Tokyo, Japan

NHMC: Natural History Museum and Institute, Chiba, Japan

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

OMNH: Osaka Museum of Natural History, Japan

PMA: Provintial Museum of Alberta, Alberta, Canada

SAM: South Astralian Museum, Adelaide, Astralia

SMNH: Swedish Museum of Natural History, Stockholm, Sweden

TARI: Taiwan Agricultural Research Institute, Taichung, Taiwan

TE: Terayama collection, Division of Agriculture & Agricultural Life Sciences, University of Tokyo, Tokyo, Japan

USNM: United States National Museum, Washington D.C., U.S.A.

ZMC: Zoologisk Museum, Copenhagen, Denmark

ZMHU: Zoologisches Museum an der Humboldt-Universität zu Berlin, Germany

ZUC: Zhejiang University, Zhejiang Province, China

Specimen code:

(T): holotype, paratypes or syntypes examined.

List of species examined

Subfamily Pristocerinae

Afrocera: A. bamboutoana [Cameroun, MNHN(T)]

Apenesia: A. bishamon [Japan, NIAES(T), KU-K]; A. daikoku [Japan, NIAES(T), KU-K]; A. elegans [Japan. NIAES(T), KU-K]; A. kisigematii [Japan, NIAES(T), NASM, KUF, KU-K, HUS, MU-Y, EUM]; A. okinawensis [Japan, NIAES(T), KU-K]; A. otohime [Japan, NIAES(T)]; A. formosimonticola [Taiwan, NASM(T), NIAES, TE]; A. liukueiens [Taiwan, NASM(T)]; A. meifuiae [Taiwan, NIAES(T), NASM]; A. takasago [Taiwan, NASM(T)]; A. pingtungensis [Taiwan, NASM(T)]; A. sinensis [China, ZUC(T)]; A. tianmuensis [China, ZUC(T)]; A. clara [China, ZUC(T)]; A. sarawakensis [Borneo, FSM(T)]; A. bicolor [Colombia, IAVH(T)]; A. formosa [Colombia, IAVH(T)]; A. catalinae [Colombia, IAVH(T)]; A. spp. [Thailand, PMA]; A. spp. [Nepal; CNC]; A. sp. [Philippines, PMA]

Caloapenesia: C. philippinensis [Philippines, ZMC(T)]; C. thailandensis [Phillippines, CNC(T)].

Dicrogenium: D. rosmarum [Camerun, ZMHU(T)]; D. alberti [Zaire, MRAC(T)]

Diepyris: D. brunneus [Zaire, MRAC(T)]

Dissomphalus: D. kyushuensis [Japan, KUF(T), HUS]; D. minutulus [Japan; NIAES(T)]; D. wusheanus [Taiwan, PMA(T)]; D. chipenensis [Taiwan, NIAES(T)]; D. minor [Borneo, FSM(T), NIAES]; D. spp. [Taiwan, NIAES, PMA]; D. philippinensis [Philippines, CNC(T)]; D. browni [Philippines, CNC(T)]; D. kinabarensis [Indonesia, NIAES(T)]; D. malaysianus [Indonesia, NIAES(T)]; D. khaoyaiensis [Thailand, PMA(T)]; D. changmaiensis [Thailand, PMA(T)]; D. thaianus [Thailand, PMA(T)]; D. nepalensis [Nepal, CNC(T)]; D. luteus (= Psilobethylus luteus) [Italy, MCSN(T)]

Kathepyris: K. basutoensis [Lesotho, MRAC(T)]; K. uelensis [Zaire, MRAC(T)]

Neodicrogenium: N. superbum [Zaire, RMAC(T)]

Neoapenesia: N. leytensis [Philippines, CNC(T)]

Neusakosia: N. schoutedeni [Southwest Africa, MRAC(T)]

Pristocera: P. formosana [Taiwan & Korea, TARI(T), KUF, EUM, EUM, NASM]; P. carinata [Myanmer, MCSN(T)]; P. kinabarensis [Indonesia, PMA(T)]; P. sarawakensis [Indonesia, PMA(T)]; P. sumatrensis [Indonesia, PMA(T)]; P. changmaiensis [Thailand, PMA(T)]; P. sp. [India, PMA]; P. spp. [Nepal, CNC]; P. sp. [Sri Lanka, CNC]

Acrepyris: A. japonicus [Japan, KUF(T), HUS, NIAES]; A. ishigakiensis [Japan, KUF(T)]; A. minutus [Japan, KUF(T)]; P. ryukyuensis [Japan, NIAES(T)]; P. orihime [Japan, NIAES(T)]; P. antennata [Myanmar, MCSN(T)]; P. mieae [Taiwan, NASM(T)]; A. takasago [Taiwan, NASM(T)]; A. tainanensis [Taiwan, NASM(T)]; A. sinensis [China, ZUC(T)]; A. zhejiangensis [China, ZUC(T)]; A. rugulosus [China, ZUC(T)]; P. sp. [Nepal, CNC]; P. sp. [Indonesia, CNC]; P. spp. [India, PMA, CNC]

Prosapenesia: P. lacteipennis [Botswana, ZMHU(T)]; P. spp. [S.W. Africa, BMNH]

Protisobrachium: P. gracile [Zaire, MRAC(T)]; P. asianus [Thailand, PMA(T)]

Pseudisobrachium: P.sp. [Colombia, NASM]; P. ryukyuanum [Japan, KUF(T)]; P. onoyamai [Japan, NIAES(T)]; P. hongkongense [Hong Kong, NSMT(T)]; P. colombianum [Colombia, IAVH(T)]; P. luisae [Colombia, IAVH(T)]; P. spp. [Thailand, PMA]; P. spp. [Nepal, CNC]

Trichisus: T. wittei [Zaire, MRAC(T)]

Subfamily Afgoioginae (Synonymy of Pristocerinae)

Parascleroderma: P. atayal [Taiwan, NIAES(T)]; P. renaiensis [Taiwan, NIAES(T)]; P. okajimai [Taiwan, NIAES(T)]; P. maae [China, ZUC(T)]; P. thaiana [Thailand, PMA(T)]; P. sp. [Malaysia, PMA]; P. spp. [Japan, TE]

Subfamily Parapenesiinae (New subfamily)

Parapenesia: P. unicolor [Republic of South Africa, ZMHU(T)]

Subfamily Epyrinae

Tribe Epyrini

Anisepyris: A. spp. [Colombia, IAVH]

Bakeriella: B. spp. [Colombia, IAVH]

Calyozina: C. ramicornis [Taiwan, ZMHU(T)]; C. sp. [Thailand, PMV]; C, sp. [Nepal, CNC]; C. amazonica [Brazil, USNM(T)]; C. azurea [Brazil, CNC(T)]; C. neotropica [Panama, USNM(T)]

Disepyris: D. rufipes [India, MNHN(T)]

Epyris: E. apicalis [Japan, BMNH(T)]; E. staphylinoides (= Calyoza ashmeadi) [Camerun, ZMHU(T)]; E. sumatrana [Indonesia, ZMHU(T)]; E. sumatrensis (= Calyozella flavipennis) [Indonesia, ZMS(T)]; E. sauteri [Taiwan & Japan, ZMHU(T), TARI, NASM, HUS]; E. hirtipennis (= Calyozina flavipennis) [Indonesia, BMNH(T)]; E. sumatrana [Indonesia, ZMS(T)]; E. konishii [Japan, NIAES(T)]; E. hagoromonis [Japan, NIAES(T), NASM, EUM, KUF]; E. otome [Japan, NIAES(T)]; E. yakushimanus [Japan, NIAES(T)]; E. yamatonis [Japan, NIAES(T), NASM, KUF, EUM, MU-Y, KU-K, TE]; E. yasha [Japan, NIAES(T)]; E. spp. [Japan, HUS, NIAES, NASM, KYF, KU-K, MU-Y, TE, CNC]; E. spp. [Taiwan, NASM, NIAES, MU-Y, CNC, TE]; E. spp. [Korea, NASM, CNC, PMA]; E. spp. [Phillippines, CNC, MU-Y]; E. spp. [Thailand, PMA, CNC, TE]; E. spp. [Malaysia, PMA, CNC]; E. spp. [Nepal, CNC]; E. spp. [Sri Lanka, CNC]

Holopyris: H. atamensis [Japan & Taiwan, HSNM(T), NASM, NIAES, TE]; H. amamiinsulanus [Japan, NIAES(T), KU-K]; H. omotoensis [Japan, NIAES(T)]; H. matsumurai [Japan, NIAES(T)]; H. susanowo [Japan, NIAES(T)]; H. yambaru [Japan, NIAES(T)]; H. sylvanidis [Germany, Thailand, TE, NIAES]; H. sp. [Korea, TE]; H. spp. [Japan, HUS, NIAES, NASM, MU-Y, KUF, KU-K, EUM, TE]; H. spp. [Taiwan, NASM, TE, PMA]; H. spp. [Philippines, CNC]; H. spp. [Thailand, PMA]; H. spp. [Malaysia, MU-Y, PMA]; H. spp. [India, PMA]; H. spp. [Nepal, CNC]

Homoglenus (Synonymized with Epyris in the part II of the present study): H. punctatus [Iran, MHN(T)]; H. tripatitus [Guinea Bisseau, MCSN(T)]; H. montanus [India, HNM(T)]; H. indicus [India, HNM(T)]

Isobrachium: I. luzonicum [Philippines, MNHN(T)]; I. sp. [Thailand, PMA]

Laelius: L. micronerus [France, MNHN(T)]; L. spp. [Japan, HUS, NIAES, NASM, MU-Y, EUM, KUF, KU-K, TE]; L. sp. [China, ZUC]

Lytepyris: A. biscrensis [Algeria, HNM(T)]

Procalyoza (Synonymized with Anisepyris in the part II of the present study): P. westwoodi [Panama, BMNH(T)]

Rhabdepyris: R. sp. [India, PMA]]

Trachepyris: T. indicus [Indonesia, TE]

Undescribed genus (Terayama, in prep.): spp. [Thailand, PMA]; sp. [Taiwan, NIAES]; sp. [China, ZUC]; sp. [India, CNC]

Tribe Sclerodermini

Allobethylus: A. multicolor [New Guinea, HNHM(T)]; A. tomoae [Japan, NIAES(T), KUF(T), TE(T)]; A. sp. [Thailand, NIAES]

Bethylopsis: B. fullawayi [Marquesas Isls., BPBM(T)]

Glenosema: G. siamensis [Thailand, PMA(T)]; G. chiangmaiensis [Thailand, PMA(T)]; G. doiinthanonensis [Thailand, PMA(T)]

Sclerodermus: S. harmandi (= S. nipponicus, = S. guani) [Japan, Korea, Taiwan & China, MNHN(T), NIAES, KUF, HUS, NASM, TE, BFRI, ASB]; S. luteicole [Myanmer, MCSN(T)]; S. macrogaster [U.S.A., KUF]; S. carolinense [U.S.A., KUF]; S. sp. [Japan, NIAES, TE]

Discleroderma: D. sp. [Japan & Taiwan, NIAES, TE]; D. sp. [Japan, NIAES].

Tribe Cephalonomiini

Cephalonomia: C. gallicola [Japan & Thailand, EUM, KUF, NIAES, TE]; C. tarsalis [Japan, EUM, TE]; C. shirahamana [Japan, KUF(T)]; C. spp. [Taiwan, NIAES, NASM]; C. sp. [Thailand, NIAES]

Islaelius: I. sp. [Thailand, PMA]

Plastanoxus: P. amamiensis [Japan, EUM(T), NIAES(T), OMNH(T), TE]; P. spp. [Thailand, PMA, NIAES]

Prorops: P. nasuta [Colombia, IAVH]; P. spp. [Japan, TE]

Undersribed genus A (Terayama, in prep.): sp. [Japan, TE]

Undescribed genus B (Terayama, in prep.): sp. [Thailand, PMA]

Subfamily Mesitiinae

Bradepyris (transferred from the subfamily Epyrinae): B. inermis [Morocco, HNM(T)]

Heterocoelia: H. brevicula [China, ZUC(T)]; H. vietnamensis [Thailand, PMA]; H. spp. [Japan, TE]; H. sp. [Thailand, PMA]

Sulcomesitius: S. haemorrhoidalis [Taiwan, NASM, MU-Y]; S. impressus [China, ZUC(T)]; S. punctulatus [China, ZUC(T)]; S. moczari [China, ZUC(T)]; S. rectus [China, ZUC(T)]; S. borneoensis [China, ZUC]; S. vechti [China, ZUC]; S. laosensis [China, ZUC]; S. thailandensis [Thailand, NASM, PMA]; S. spp. [India, PMA]; S. spp. [Nepal, CNC, PMA]

Metrionotus: M. hongkongensis [China, ZUC]; M. spp. [India; CNC, PMV]

Pycnomesitius: P. sp. [Sri Lanka, PMV]; P. spp. [India, PMA]

Subfamily Galodoxinae

Galodoxa: G. torquata [Philippines, ZMC(T)]

Subfamily Bethylinae

Bethylus: B. sinensis [China, ZUC(T)]; B. boops (= Anoxus boops) [Sweden, SMNH(T)]; B. fuscicornis [Japan, HUS, TE]; B. spp. [Japan, HUS, TE]; B. sp. [Nepal, CNC]; B. sp. [Korea, NASM]

Eupsenella: E. diemensis [Australia, SAM(T)]; E. spp. [Australia, SAM]

Goniozus: G. japonicus [Japan, Korea, Taiwan & China, USNM(T), ZUC, HUS, NIAES, NASM, MU-Y, EUM, KUF, KU-K, TE]; G. marianensis [Marian Isls., NHMC(T)]; G. ryukyuensis [Japan, NIAES(T)]; G. hoorai [Japan & Taiwan, CNC(T), KUF]; G. kusigematii [Japan, NIAES(T), KU-K]; G. tosaensis [Japan, NIAES(T), KUF]; G. yaeyamanus [Japan & Taiwan, NIAES(T), CUC]; G. xiaoi [China, ZUC(T)]; G. baishanzuensis [China, ZUC(T)]; G. lamprosemae [China, ZUC(T)]; G. spp. [Japan, HUS, NIAES, NASM, MU-Y, EUM, KUF, KU-K, TE]; G. sp. [Korea, NASM, PMA]; G. spp. [Taiwan, NASM, 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. marishi [Japan. NIAES(T)]; O. taiwanus [Taiwan, NIAES(T), NASM]; O. formosicola [Taiwan, NIAES(T), PMA]; O. liukueiensis [Taiwan, NIAES(T)]; O. koreanus [Korea, PMA(T), NIAES]; O. fujianus [China, ZUC(T)]; O. sp. [Japan, HUS, NIAES, NASM, TE]; O. sp. [Hong Kong, NASM]; O. spp. [Thailand, PMA]; O. spp. [India, PMA, LU-P]; O. sp. [Nepal, CNC]; T. sp. (= Trissomalus sp.) [India, PMA]; T. sp. (= Trissomalus sp.) [Thailand, PMA]

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

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