「Phylogenetic Systematics of Bethylidae (Hymenoptera: Chrysidoidea), with a Taxonomic Revision of the Japanese Species and Descriptions of New Taxa from Asia, Australia, South America and Africa」

（和訳：アリガタバチ科（膜翅目、セイボウ上科）の系統分類付、日本産アリガタバチ類の総括及びアジア、オーストラリア、南米、アフリカ産種の記載）

Mamoru Terayama

寺山　守

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Mamoru Terayama

寺山　守

To my wife

Meifui

in love and gratitude

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Introduction

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. They are represented by 1796 nominal species in 89 genera excluding fossile species as of 1992 (Gordh & Moczar, 1991; Strejcek, 1990; Krombein, 1992; Argaman, 1990; Azevedo, 1992).

The wasps are small, 1-20 mm in body length, and mostly external parasites of lepidopterous and coleopterous larvae. Due to their host associations, bethylids are potentially benefical in agriculture and forestry as biological control agencies of various pests in the forementioned groups. Many active studies have been carried out using Goniozus species against leaf-eating lepidopterous larvae (Yukinari, 1976, 1977, 1979, 1984; Gordh, 1982, 1984, 1988; Gordh & Evans, 1976; Chen & Hung, 1962; Danthanarayana, 1980, etc.), Sclerodermus species against forest pests of cerambicid beetles (Okada, 1960; Okada & Ido, 1965, 1966; Ido & Takagaki, 1968, 1969; Oda et al., 1981; Lee & Chang, 1965; Enda, 1992; Xiao & Wu, 1983; Zhang et al., 1989, etc.), Prorops species against coffee berry-borer pests of Scolytid beetles (Clausen, 1978; Hempel, 1934; Toledo, 1978, etc.), and Laelius species against woollen pests of coleopterous larvae (Yamada, 1942, 1955, etc.).

On the other hand, some species, e.g. Cephalonomia, Epyris, Laelius, and Sclerodermus species, have been well known as sanitary injurious pest insects and cause serious problems by their frequent stings responsible for dermatitis in houses (Wssig, 1932; Geldern, 1927; Essig & Michelbacher, 1932; Asahina, 1953; Judd, 1960; Kawashima, 1959; Matusura, 1981; Yamazaki, 1982, etc.). In short, they have two aspects, one being as useful insects for the biological control of agricultural and forest pests and the other as sanitary pests injurying to human.

Although this group is important in the agricultural, forestry, and medical fields as mentioned above, applied studies of bethylids have not been easily advanced by a lack of basic taxonomic, phylogenetic and biological knowledge. Undoubtedly an essential step toward a comprehensive understanding of biology and behavior of these wasps is to establish a sound classification system of them.

The present study aims to clarify the internal relationships of Bethylidae at subfamily, tribe, and genus level in the part I, and to contribute to the taxonomy of this family in the pooly studied countries in the parts II and III.

Part I. The Internal Phylogeny of Bethylidae

Historical background

Taxonomy

The history of taxonomy of Bethylidae downed in the beginning of the 19th century, Panzer's description of Bethylus hemipterus (described as Tiphia hemiptera)(1801). In the next year, Latreille established the genus Bethylus based on the Panzer's species, then producing the family name, Bethylidae. However, later, Bethylus fuscicornis (= Omalus fuscicornis) is re-designated as the type species of this genus by ICZN opinion 153 (1944). In 1806 Latreille placed the genus Bethylus in the Oxyures group of the family Proctotrupiidae. Five genera, Pristocera Klug 1808, Epyris Westwood 1832, Calyoza Westwood 1837, Cephalonomia Westwood 1933, Sclerodermus Latreille 1809 and Bethylus Latreille 1802, were established until 1850, and the following 10 genera were added untill 1900 excluding synonymized genera or transferred to other subfamilies: Sielora Cameron 1881, Eupsenella Westwood 1874, Anoxus Thomson 1862, Ateleopterus Foerster 1856, Laelius Ashmead 1893, Mesitius Spinola 1851, Heterocoelia Dahlbom 1854, Dicrogenium Stadelmann 1894, Apenesia Westwood 1874, and Dissomphalus Ashmead 1893. The definitions of these genera were unsuitable because of incompleteness of higher classification of subfamily or family level in Hymenoptera during 19th century.

The name, subfamily Bethylidae, had already been used in 1839 by Halliday. Foerster (1856) also used the name family Bethyloide, and later this name was corrected into Bethylidae by Ashmead (1902). In 1883 Cameron incorporated the subfamily Bethylinae into the family Proctotrupidae. Dalla Torre (1897) divided Cameron's Bethylinae into two subfamilies, Bethylinae and Pristocerinae. On the other hand Ashmead (1902) and Brown (1906) included Bethylidae or Bethylinae in the superfamily Vespoidea.

In the early 20th century, descriptions of many genera and species were presented by a series of Kieffer's papers. In "Genera Insectorum" (1908) he gave 491 species in 58 genera of Bethylidae in the world. Furthermore, in "Das Tierreich" (1914) he recognized 660 species in 102 genera, and presented a key to known species. He also established 4 tribes in it, namely Pristocerini, Sclerodermini, Epyrini, and Bethylini. In 1928 Berland separated superfamily Bethyloidae from superfamily Proctotrupoidea. At the same time he raised Kieffer's 4 tribes to full subfamily rank and established subfamily Mesitiinae. Benoit (1963) established 3 tribes, Pristocerini, Dicrogeniini and Usakosiini, in the subfamily Pristocerinae. 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. At the same time he added 2 tribes, Epyrini and Cephalonomini, in the subufamily Epyrinae. In 1978 he also established the tribes Bethylini and Sielonini in the subfamily Bethylinae. Recently Nagy (1988) 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 & Moczar (1990) outlined bibliographic information and distribution of each species, treating 1794 species in 91 genera in 5 subfamilies excluding fossile records. In this checklist they rejected the segregation of subfamily Afgoiogfinae from Pristocerinae. Further new genera, Acephalonomia and Alongatepyris, are described by Sterjcek (1990) and Azevedo (1992) respectively, while 4 genera, Calyoza, Paracalyoza, Pseudocalyoza and Calyozella, were synonymyzed with the genus Epyris by Krombein (1992). The genus Proscleroderma was transferred to the subfamily Sierolomorphidae by Argaman (1990). In "Hymenoptera of the world" Finnamore & Brothers (1993) did not recognize subfamilies Afgoiogfinae of Argaman and Galodoxinae of Nagy.

In total 1796 nominal species in 89 genera belonging to 4 to 6 subfamilies are known up to the present.

Fossil record

Forty-one species in 23 genera have been recorded mostly from the Oligocene (Baltic amber) and few from the Miocene (Burmese Amber) and Upper Cretaceous (Spahr, 1987; Gordh & Moczar, 1990) (Apendix IV). Twelve of the 23 genera are known only from fossils. The oldest forms, Archaepyris minutus and Celonophamia taimyria, were found in Upper Cretaceous amber from the Taimyr Peninsula, Siberia, and Upper Cretaceous Canadian amber respectively.

A single fossil subfamily, Protopristocerinae, defined by Nagy in 1974 containes 5 genera, Archaepyris, Bethylitella, Bethylopteron, Palaeobethyloides and Protopristocera (Gordh & Moczar, 1990). However, this subfamily is ambiguous in terms of cladistics because it seems to be polyphyly.

The fossil genera Palaeobethylus and Uromesitius (Brues, 1923, 1933) are possibly more close to the Chrysididae than to the Bethylidae by the gastral structures.

Phylogeny

The internal phylogeny of Bethylidae remains unsolved. Only systematic work at subfamily level is presented by Evans (1964). In his analysis treating three New World subfamilies, Bethylinae was a sister-group of the others (Pristocerinae + Epyrinae). He also offered a hypothesis about the relationships among genera in each subfamily (1963, 1964). Unfortunately few apomorphic characters were indicated to explain the relationships. Nagy (1974) commented that the subfamily Galodoxinae established by him is most closely related to the fossil subfamily Protopristocerinae established also by him in 1974. However, up to the present no phylogenetic study using the cladistic method has been made on the Bethylidae.

General Morphology

The family Bethylidae is grouped with the other chrysidoid families by: 1) modificated head capsule which is associated with prognathy; 2) clypeus with longitudinal median carina; 3) anteriorly broaded metasternum ; 4) hind wing vein C absent except extreme base and vein S + R + S very short (Carpenter, 1986; Brothers & Carpenter, 1993).

In Bethylidae, numerous characters have been used in taxonomy. Important characters are discussed especially in Kieffer (1914), Moczar (1970a, b, 1971) and Evans (1964, 1978). The wing venation, structure of alitrunk, shape of tarsal claws, and position and size of eyes are useful in the tribe and subfamily level taxonomy. The wing venation, shape of scutellar pits of fovea, palpal formula, notauli, and structure of male genitalia are also important in the definition of genera. Shape of head, clypeus, mandibles, antennae, eyes, and ocelli, and shape and sculpture of propodeum and other body parts are mostly efficient in specific level taxonomy.

The morphological terminology employed here follows largely that of Evans (1964, 1978) with some modifications.

Head. The maxillary palpi have 1 to 6 segments (usually 6), the labial palpi 1 to 3 segments (usually 3). The mandibles are usually subtriangular and have 1 to 7 teeth; in several genera sickle-shaped. Shape of clypeus is variable and important in classification at specific level, but sometimes at tribal or generic level. The number of antennal segments is usually 13, but 12 in some genera and 9 in Acephalonomia. Antennal scape and pedicel are excluding the basal constriction or neck. Eyes are usually large, but in the females of Pristocerinae extremely reduced or absent. Ocelli are usually developed, but in several genera small, indistinct or absent. Head shape, and the size and position of eyes and ocelli are of special importance in the classification mostly at specific level. Fig. 2 illustrates certain head measurements.

Alitrunk. The alitrunk or mesosoma is used to mean the true thorax plus propodeum (true 1st abdominal segment). The pronotum has an anterior collar. The measurements of pronotum is made excluding the collar. The mesonotum is divided into two parts, mesoscutum and scutellum. The mesoscutum usually has notauli and parapsidal furrows; in several genera these are indistinct or absent. In this paper the area between notauli are called "median area" and the areas between notauli and outer margin of mesonotum "lateral areas". The scutellum has a central, elevated disc which may have a transverse groove or a pairs of pits at its base. The shape of metanotum is useful in the subfamily level classification. The mesopleura is simple, but in certain genera it has a sharply defined, depressed area near the top, called the upper fovea, and a larger one below this fovea, called the lower fovea. The shape and sculpture of propodeum is of great importance in the classification at specific level. In the subfamily Mesitiinae posterolateral borders of propodeum form a distinct spine. Several special terms for the propodeum are used as shown in Fig. 4.

Discal carinae: major longitudinal carinae except lateral and sublateral ones.
Median carina: a discal carina running on the midline.
Submedian carinae: the discal carinae excepting the median carina.
Lateral carinae: the longitudinal carinae margining the sides of the disc.
Sublateral carinae: the longitudinal carinae closely paralleling the lateral carinae.
Transverse carina: the carina margining the disc behind.
Lateral area: the part of disc surrounded by the lateral and sublateral carinae.
Sublateral area: the part of disc surrounded by the sublateral and submedian carinae.
Median area: the median portion of disc limited by outest two sublateral areas. In some species, this area form a subtriangle and is called the basal triangular area.

Gaster. The term gaster is used to mean the abdomen or metasoma. Morphologically, the 1st gastral segment corresponds to the 2nd abdominal segment. Each gastral segment consists of upper plate (tergite) and lower plate (sternite). The gaster is said to be petiolate if the first tergite does not attain the extreme base of the 1st segment; it is said to be sessile if the 1st tergite reach the base. The apical sternite of the male is called the subgenital plate. The male genitalia (Figs. 8-11) are described according to the terminology employed by Evans (1964).

Forewing. Names for the forewing used in the present paper are shown in Fig. 12 which is slightly modified from Evans (1964, 1978). The wing venation is variable and much useful in subfamily to genus level classification. The discoidal cell of Bethylidae is actually homologous to the 2nd discoidal cell of other Aculeata. In some genera the subcosta is greatly thickened apically (Fig. 13) so as to simulate a second stigma; this is called a prostigma. In Bethylinae there may be a small vein arising from the basal vein which is usually simply called the stub vein; in some cases this loops go down to join the discoidal vein to form an areolet (pl. areola), which is presumably equivalent to the 1st discoidal cell.

Abbreviations are used for the following measurements and formula:

Palpal formula (PF): the number of segments in the the maxillary and labial palpi; always expressed in the order of maxillary and labial palpi.

Head length (HL): maximum length of head excluding mandibles, in frontal view.

Head width (HW): maximum width of head including eyes, in frontal view.

Width of front (WF): minimum width between eyes, in frontal view.

Height of eye (HE): maximum height or length of eye, in lateral view.

Daiameter of anterior ocellus (DAO): maximum diameter of anterior ocellus.

Width of ocellar triangle (WOT): distance across and including posterior

ocelli.

Posterior ocello-line (POL): shortest distance between posterior ocelli.

Antero-posterior ocello-line (AOL): shortest distance between anterior ocellus and posterior ocellus.

Ocello-ocular line (OOL): shortest distance from a posterior ocellus to nearest eye margin.

Length of alitrunk (LA): maximum diagonal length of the alitrunk excluding the pronotal collar, in lateral view.

Length of propodeal disc (LPD): measured along the midline excluding posterior declivity, in dorsal view.

Length of propodeum (LP): measured along the midline including posterior declivity, in dorsal view.

Width of propodeal disc (WPD): maximum width of the disc excluding the anterior potion from the level of propodeal spiracles, in dorsal view.

Forewing length (FWL): maximum length of forewing.

Total length (TL): total length of outstretched individual, from the manidbular apex to the gastral apex.

Taxa included in the analysis

All the possible subfamilies are examined. At generic level, 74 out of 91 valid genera including 3 new ones described hereinafter are treated. Fifty-two genera are examined with specimens. As for the remaining 22 genera, I checked the states of these characters based on the extensive literature (Evans, 1955, 1958, 1959, 1961, 1962a, b, 1963; Moczar, 1970a, b, 1971; Nagy, 1971, 1974; Kieffer, 1914; Argaman, 1988; Azevedo, 1992). Seventeen genera are excluded from the present analyses because of not only luck 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 examined in this study are listed in the appendix I of this part together with institutions preserving the materials.

Methods of cladistic analysis

The cladistic analysis was performed by PAUP Ver. 3.0b drawn by Swofford (1989). 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). I also used MacClade Ver. 2.1 by Maddison & Maddison (1987) for graphic display of the number of

synapomorphies on different branches of the cladogram and for tracing of selected characters.

I made a character analysis determining the polarity and the characters used in this analysis, and the character state matrices for the taxa are given in the tables in each section. The character state definitions and polarities largely followed prevailing theories of evolutionary change within the aculeate Hymenoptera (Carpenter, 1986, 1991; Brothers, 1975; Brothers & Carpenter, 1993; Koenigsmann, 1978). Since the phylogenetic relationships between the bethylids and other wasps have not been fully resolved, I used two outgroups: Chrysididae which is regarded as the sister-group of Bethylidae by Carpenter (1986) and Brothers & Carpenter (1993) and hypothetical ancestor which had the all-plesiomorphic state in every character.

In subfamily level analysis, I processed two sets of data, one is Chrysididae as a outgroup, and the other is hypothetical ancestor as a outgroup and calculated the parsimonious trees separately for each. In tribe and genus level analyses, I used hypothetical ansestor as an outgroup.

I have not made use of the fossil subfamily Protopristocerinae as an outgroup since many of the characters of interest in my data matrices cannot be assessed in this group and monophyly of this group is not confirmed.

Results and Discussions

Phylogeny between subfamilies

First cladistic analysis

There are 3 hypotheses about establishment of subfamilies in Bethylidae. These are as follows: (1) Six subfamilies, Pristocerinae, Afgoiogfinae, Epyrinae, Galodoxinae, Mesitiinae, and Bethylinae, are recognized (Argaman, 1988; Nagy, 1988), (2) Five subfamilies are recognized, Afgoiogfinae is included in Pristocerinae (Gordth & Moczar, 1990), (3) Four subfamilies are recognized, and two subfamilies, Afgoiogfinae and Galodoxinae, are unrecognizable (Goulet & Huber, 1993). Evans (1964) carried out the first phylogenetic analysis among three New World's subfamilies. He indicated Bethylinae is a sister-group of (Pristocerinae + Epyrinae).

In the course of my examinations, it has been known that the genus Parapenesia belonging to Pristocerinae has many unique characteristics. For this reason Parapenesia is treated as a separate taxon in the analysis.

Twenty-four characters are used in the subfamily level analysis (Table 1). Their character states are shown in Table 2. Each data set utilized a different outgroups, as follows: Data set 1: Chrysididae as suggested by Carpenter (1986) and Brothers & Carpenter (1993); Data set 2: a hypothetical ancestor, with all the characters scored as the plesiomorphous states.

Data set 1 produced the single most parsimonious tree (tree length = 28, consistency index = 0.929, and retention index = 0.875) (Fig. 14). Of the 24

characters studied, 11 were cladistically informative. Data set 2 also produced the single most parsimonious tree which presents the same phylogenetic pattern as the data set 1 (tree length = 26, consistency index = 0.962, retantion index = 0.933). The following conclusions are consistent to both data sets: 1) the tree has two major monophyletic groups, (Parapenesia + (Pristoceninae + Afgoioginae)) and (Bethylinae + (Epyrinae + Mesitiinae + Galodoxinae)); 2) Prosapenesia is a sister-group of (Pristocerinae + Afgoioginae); 3) Bethylinae is a sister-group of (Epyrinae + Mesitiinae + Galodoxinae); 4) Epyrinae, Mesitiinae and Galodoxinae are shown to form a remaining equivocally resolved clade. The Parapenesia, and subfamilies Pristocera and Afgoioginae form a monophyletic group supported by 5 characters (1, 13, 15, 20, 21), and the subfamilies Bethylinae, Epyrinae, Mesitiinae and Galodoxinae by 2 characters (9, 14).

The Parapenesia has the following autoapomorphic characters: scutellum broaden and metanotum fused (character 18), mesopleura and mesonotum fused (character 19), broad and posteriorly rounded propodeum (character 22). These are morphologically informative characters to separate it from the other subfamilies. So it may reasonably constitute a separate subfamily. The clade (Pristocerinae + Afgoioginae) is characterized by the apomorphic condition of character 17 (reduced eyes in the female). The autoapomorphic character of Afgoioginae is its extremely flat body in the female (character 17), and the analysis did not reveal apomorphic characters for Pristocerinae. However, the flat female body is also seen in the genera Thlastepyris and Alongtepyris of

Epyrinae. Presumably these extremely depressed form is due to adaptations 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) PF = 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 & Moczar hypothesis that the Afgoioginae should be included in the Pristocerinae.

The following 2 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 autoapomorphy. The monophyly of the group (Epyrinae + Mesitiinae + Galodoxinae) is supported by the proportionately long mesonotum (character 4), but there are no unequivocally shared apomorphies among two of the constituent taxa. Two autoapomorphic characters support the subfamily Mesitiinae: strongly carinate anteromedian portion of propodeum (character 6) and strong spines of posterolateral corners of propodeum (character 7). Two autoapomorphies also support the monophyly of Galodoxinae: the large cornicles of the 4th and 5th gastral sternites respectivelly (characters 23 & 24). These two taxa may be

held to constitute separate subfamilies, while no unequivocal apomorpies 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. However the results of my phylogenetic analysis did not support his view. This subfamily strongly is related to the Epyrinae or Mesitiinae rather than to the Pristocerinae.

Second cladistic analysis

Since I did not find any autoapomorphy for the subfamily Epyrinae in the previous analysis, I have attempted a reanalysis at the subfamily level. Although Evans (1964) included Sclerodermini as a tribe in the subfamily Epyrinae, taxonomists before Evans, e.g. Kieffer (1914), Berland (1928), Kurian (1954), placed at the same level as Pristocerinae, Bethylinae and Mesitiinae. In the present analysis, the data of the 3 tribes in the subfamily Epyrinae, Epyrinii, Sclerodermini, and Cephalonomiini, are added and merged the Afgoioginae into the Pristocerinae. The characters and the data matrix which are slightly modified from those in the 1st analysis are shown in Table 3. Chrysididae is used as an outgroup.

A cladistic analysis based upon the new matrix generated a single most parsimonious tree (tree length = 34, consistency index = 0.941, retention index = 0.778) (Fig. 15). The phylogenetic relationships among 3 tribes, Mesitiinae, and Galodoxinae are polytomy. But both cladograms showed that the Sclerodermini and Cephalonomiini constitute a monophyletic assemblage by the characters 27 (loss of occipital carina). The autoapomorphies for Epyriini are character 26 (posterolateral corners of propodeum with a fovea) and Sclerodermini are characters 25 (position of eyes), and no exact autoapomorphy is found in Cephalonomiini. However, as these autoapomorphies have exceptions, they do not seem to guarantee to treat the above tribes as dependent subfamilies. Some species of Epyrinae lack propodeal fovea, but this is thought to be the secondary loss. Eyes situated well forward on head (possible autoapomorphy of Sclerodermini) are also seen in the Parapenesia and apterous females of the genus Cephalonomia in Cephalonomiini, but this state is thought to be results of the specialized body shape caused by the loss of wings and life on ground, and to be a convergent. The additional potential autoapomorphies of Cephalonomiini are 12-segmented antennae, reduced palpal segments and absence of anal vein. However, these characters are useful in the subfamily Epyrinae as will be shown in the analysis of relationships among tribes.

The subfamily Epyrinae is morphologically most diverse group in the Bethylidae, and the average size reduces from Epyrini through Sclerodermini to Cephalonomiini. Such a size reduction may be led to many of the degenerative specializations in external morphology in each genus of different tribes. Tables 4 and 5 show some characters in the genera of epyrine tribes. According to the number of apomorphic characters from the Table 5, the Epyrinae are the least specialized group, and the Cephalonomiini are the most specialized. The

tend of the specialization are: 1) size reduction; 2) reduction in wing veins; 3) reduction in the number of antennal and palpal segments; 4) loss of wings, notauli and propodeal sculpture. I treat these taxa as in the subfamily Epyrinae rather than as indipendent subfamilies.

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.

2) Tribal and Generic Relationships

i) Subfamily Pristocerinae

The subfamily Pristocerinae has been reported to include 20 genera (Parapenesia is excluded but Afgoiogfa and Parascleroderma are included). After examinations of the material, the following two synonymies and two new genera are found.

Dissomphalus Ashmead

Dissomphalus Ashmead, 1893.

Type species: Dissomphalus xanthopus Ashmead, 1893.

Ecitopria Wasmann, 1899. [Synonymized by Evans, 1955.]

Thaumatepyris Kieffer, 1910. [Synonymized by Evans, 1964.]

Glenobethylus Kieffer, 1910. [Synonymized by Evans, 1964 .]

Parecitorpia Ogloblin, 1930. [Sunonymized by Evans, 1964.]

Psilobethylus Kieffer, 1906. Syn. nov.

The type species of the genus Psilobethylus, P. luteus Kieffer, is examined. General morphology is shown in Figs. 16-19. The measurements for the type specimen of the species are as follows: HL 0.33 mm; HW 0.28 mm; LA 0.45 mm; LP 0.19 mm; WPD 0.15 mm; TL 1.8 mm.

Type specimen. Female, Vallolucano (Italy), V. 1903, Solari, [MCSN].

Remarks. New combinations are as follows: Dissomphalus luteus (Kieffer, 1906) comb. nov. and Dissomphalus atriceps (Kieffer, 1910) comb. nov.

Genus Prosapenesia Kieffer

Prosapenesia Kieffer, 1910.

Type species: Prosapenesia lacteipennis Kieffer, 1910.

Neusakosia Benoit, 1981. Syn. nov.

Differences between Prosapenesia and Neusakosia are 1) number of mandibular teeth (5 in Prosapenesia (Fig. 21), 3 or 4 in Neusakosia (Fig. 27)); 2) shape of pronotal disc (anterior border emarginate in Prosapenesia (Figs. 22 & 23); not emarginate in Neusakosia (Fig. 28))(Benoit, 1981). However,

these are only species or species group level differences in comparison with the other generic characters in the Pristocerinae. So I regard Neusakosia as a junior synonym with Prosapenesia. Original description suggests that the genus Usakosia Kieffer, 1914, closely resembles the genus Prosapenesia. However, since the type material of the type species of Usakosia was lost during the World War I (Benoit, 1981; Huddleston, personal communication), I have no measures to conclude about the status of this genus.

The following two species are removed from the genus Neusakosia: Prosapenesia princeps (Benoit, 1981) comb. nov. and Prosapenesia schoutedeni (Benoit, 1981) comb. nov.

Among the 20 pristocerine genera, 4 genera, Anisobrachium, Apristocera, Parapristocera, and Usakosia, are known of ambiguous characters alone characters because of the lack of the types and sufficient descriptions. The genus Prisctocera consists of two subgenera, Pristocera and Acrepyris, which are separately used in the present analysis. The female characters are omitted, because up to the present only 7 genera, namely Afgoiogfa, Apenesia, Dissomphalus, Parascleroderma, Pristocera, Prosapenesia and Pseudisobrachium, have been known of their females (Evans, 1964, 1978; Argaman, 1988; Krombein, 1989). Thus, in total 17 supraspecific taxa are used in this analysis.

Results and Discussions

Tables 6 and 7 show the characters used in this analysis and character matrix respectively. Cladistic analysis yielded 3 equally most parsimonious trees, of a length of 75, consistency index of 0.747 and retention index of 0.716 (Fig. 48). One of the 3 trees (tree 2 in Fig. 48) has a zero length internode by ACCTRAN. Fig. 50 show the strict consensus tree from these 2 most parsimonious trees.

The clade ((Dicrogenium + Neodicrogenium) + Kathepyris) is positioned basally, and Pristocera and Acrepyris constitute the earlier branches of the cladogram. After that there is a division into two groups: Afgoiogfa, Parascleroderma, Prosapenesia and Diepyris, and the lest. The former group (((Afgoiogfa + Parascreroderma) + Prosapenesia) + Diepyris) constitute a monophyletic assemblage by the absence of the metacarpus vein of forewings (character 30), while the latter, which is characterized by the anteriorly well produced clypeus (character 3), has 4 unresolved dichotomies.

Protisobrachium, Pseudisobrachium and Neopenesia constitute a monophyletic assemblage by the character 16 (notauli lacking or indistinct) and character 40 (3-stalked subgenital plate), and this has sister-group relationship to the clade (Dissomphalus + Trichisucus). Dissomphalus and Trichius constitute a monophyletic assemblage by the characters 22 (broader and oval shape of gaster), 28 (rounded outermargin of forewings) and 31 (erect transverse median vein).

Benoit (1963, 1981) divided Pristocerinae into tree tribes, Dicrogeniini,

Pristocerini and Usakosiini, based mainly on the African material. But I do not recognize tribes in the subfamiliy for two reasons: first, there has been found no informative character to separate tribes in this analysis; second, the characters used in this analysis involved many reversals and parallelisms.

The single tribal character of Dicrogetiini presented by Benoit is a synapomorphfor Dicrogenium and Neodicrogenium (caracter 12 in this analysis). The group ((Dicrogenium + Neodicrogenium) + Kathepyris) constitutes a monophyletic assemblage by the shape of parameres (character 44). However, this condition also occurs in some species of the genus Pristocera.

Pristocera and Acrepyris present some difficulty in attempting to separate the two tribes, because they have intermediate species in character composition between the clade ((Decrogenium + Neodicrogenium) + Kathepyris) and the rest. The genus Prosapenesia of Usakosiini as recognized by Benoit is characteristic in having the following autoapomorphies: head truncate anteriorly (character 5), antennal sockets reduced (character 6), pterostigma extremely large (character 32), radial vein thin and weak (character 33), and posterior border of subgenital plate with a tergum (character 43). However the present analysis did not indicate it as a independent taxon.

Evans (1963) presented the probable relationships among the 8 New World species groups of Apenesia and 3 genera, Pristocera, Dissomphalus and Pseudisobrachium. He assumed that the 3 genera each may have arisen from a different species group of Apenesia. However, my analysis did not support his assumption, since the genus Apenesia may be a monophyletic taxon supported by the character 49 (shape of cuspis).

I treat Acrepyris as a genus.

Genus Acrepyris Kieffer gen. rev.

Acrepyris Kieffer, 1905.

Type species: Epyris reticulatus Kieffer, 1904.

Acrepyris: Evans, 1963. [As a subgenus of genus Pristocera.]

Neopristocera Yasumatsu, 1955. [Synonymized by Evans, 1963.]

This genus is distinguished from Pristocera by the following combination of characters in the male:

Acrepyris	Pristocera
Antennae long, extending to or beyond the posterior border propodeum	Antennae short, not reaching the anterior border of propodeum
Antennal funicular segments without distinct long erect hairs (Fig. 52).	Antennal funicular segments with distinct long erect hairs (Fig.51).
Subgenital plate simple (Fig. 54).	Subgenital plate deeply divided into two lobes (Fig. 53).
Aedoeagus of genitalia consistind of 3 sets of valves (Fig. 56 & 57).	Aedoeagus of genitalia simple, not consisting of 3 valves (Fig. 55).
Digiti of genitalia forming slender, curved rods	Digiti of genitalia forming broad, truncate plates.

The genus Acrepyris is distributed in the New World and the Oriental region (few in the eastern part of Palaearctic region), while the genus Pristocera is distributed from the Etiopian to the Oriental regions.

The following 24 species are removed from the genus Pristocera to the genus Acrepyris: A. antennata (Magretti) comb. nov., A. armifera (Say) comb. nov., A. atra (Klug) comb. nov., A. bridwelli (Evans) comb. nov., A. californica (Evans) comb. nov., A. chihuahua (Evans) comb. nov., A. cockerelli (Evans) comb. nov., A. dreisbachi (Evans) comb. nov., A. fraterna (Evans) comb nov., A. hyalina (Brues) comb. nov., A. intermedia (Evans) comb. nov., A. japonica (Yasumatsu) comb. nov. A. japonica ishigakiensis (Yasumatsu) comb. nov., A. minuta (Yasumatsu) comb. nov, A. nebulosa (Evans) comb. nov., A. otomi (Evans) comb. nov., A. palliditarsis (Cameron) comb. nov., A. parkeri (Evans) comb. nov., A. porteri (Evans) comb. nov, A. quiroga (Evans) comb. nov., A. sinaloa (Evans) comb. nov., A. tenochca (Evans) comb nov., and A. varidens (Cameron) comb. nov.

ii) Subfamily Epyrinae

This subfamily is the largest in the Bethylidae, and contains 43 living genera grouped into 3 tribes (Evans, 1964). After examinations of sample material, I arrived at the following conclusions: (1)Genus Laelius is synonymized with Allepyris as Perkins suggested (1976), (2) Genus Procaryoza is synonymized with Anisepyris, (3) Genus Homogrenus is synonymized with Epyris, (4) Genus Lytepyris is synonymized with Disepyris, (5) Genus Nesepyris is synonymized with Allobethylus, (6) Genus Orientepyris is established as new to science, (7) Genus Bethylopsis, which has long been unknown of its precise taxonomic position, is found to be a member of the tribe Sclerodermini of this subfamily, (8) Genus Odontepyris which is sometimes included in this subfamily should be moved to the subfamily Bethylinae, and (9) Genus Bradepyris is provisionally transferred to the subfamily Mesitiinae.

In total I recognize 39 genera. Since the type specimens of the type species of 13 genera have been lost, 26 genera are treated in the present analysis.

Genus Laelius Ashmead

Laelius Ashmead, 1893.

Type species: Laelius trogodermatis Ashmead

Paralaelius Kieffer, 1906. [Synonymized by Musebeck & Walkley, 1951.]

Allepyris Kieffer, 1905. [Provisinally synonymized by Perkins, 1976.] Syn. nov.

Remarks. Perkins (1976) suggested that the genus Allepyris is a junior synonym of Laelius, and Medvedev (1978, 1988) and Tachikawa (1980) followed his view. In fact these are sepatated only by the size of pterostigma. I also accept Perkins' suggestion. The following 5 species are transferred to the genus Laelius: L. berlandi (Benoit) comb. nov., L. mesitioides (Duchaussoy) comb. nov., L. microneurus (Kieffer) [Provisionally transffered to the genus Laelius by Perkins, 1976. comb. nov.], L. ruficrus (Kieffer) comb. nov., and L. seticornis (Duchaussoy) comb. nov.

Genus Epyris Westwood

Epyris Westwood, 1832.

Type species: Epyris niger Westwood

Dolus Motschulsky, 1863. [Synonymized by Krombein, 1987.]

Muellerella Saussure, 1892. [Synonymized by Evans, 1964.]

Parepyris Kieffer, 1913. [Synonymized by Evans, 1964.]

Psilepyris Kieffer, 1913. [Synonymized by Evans, 1964.]

Artiepyris Kieffer, 1913. [As subgenus of Epyris. Synonymized by Evans, 1969.]

Calyoza Westwood, 1837. [Synonymized by Krombein, 1992.]

Calyozella Enderlein, 1920. [Synonymized by Krombein, 1992.]

Paracalyoza Cameron, 1909. [Synonymized by Krombein, 1992.]

Pseudocalyoza Turner, 1915. [Synonymized by Krombein, 1992.]

Homoglenus Kieffer, 1904. Syn. nov.

Remarks. The generic character of Homoglenus is the presence of nebulous m-cu vein of forewings (Figs. 63-65) and no other distinct character to separate it from Epyris in known. This condition may not be useful to separate the genera, since the vein is completely absent to weakly recognizable in Epyris. The extremely long parameres of male genitalia of Homoglenus (Benoit, 1957) also suggest that this is phylogenetically related to the dodecatomus-group or staphylinoides-group of the genus Epyris. The 7 species including a fossil species are transferred to genus Epyris: E. bifossatus (Brues) comb. nov., E. indicus (Kieffer) comb. nov., E. montanus Kieffer comb. rev., E. punctatus (Kieffer) comb. nov., E. quadripartitus (Benoit) comb. nov., E. sanctus (Turner) comb. nov., and E. tripartitus (Kieffer) comb. nov.

Genus Anisepyris Kieffer, 1905

Anisepyris Kieffer, 1905.

Type species: Epyris amazonicus Westwood

Lophepyris Evans, 1959. [As subgenus of Rhabdepyris. Synonymized by Evans, 1964.]

Procalyoza Kieffer, 1905. Syn. nov. (Provisional)

Remarks. The genus Procalyoza is distinguished from Anisepyris by ramose antennae (Fig. 67) and glabrous eyes. However, these should not be reliable generic characters to define the genus as Krombein (1992) synonymized Calyoza, Calyozell, and Paracalyoza with Epyris and also Evans suggested (1964). P. westwoodi (Figs. 66-68) is provisionally transfferred to the genus Anisepyris: A. westwoodi (Cameron) comb. nov.

Genus Disepyris Kieffer

Disepyris Kieffer, 1905.

Type species: Disepyris rufipes Kieffer

Lytepyris Kieffer, 1913. Syn. nov.

Remarks. A direct comparision between Disepyris rufipes and Lytepyris biscrensis (both are type species of respective genera) indicated no generic level difference. Two species, L. afer (Magretti) and L. biscrensis (Kieffer) which is originally described as a Epyris, are moved to the genus Disepyris: D. afer (Magretti) comb. nov., D. biscrensis (Kieffer) comb. nov.

Genus Allobethylus Kieffer

Allobethylus Kieffer, 1906.

Type species: Allobethylus multicolor Kieffer

Nesepyris Bridwell, 1920. Syn. nov.

The genus Allobethylus which consists of a single species, A. multicolor, is recorded from Papua New Guinea, and genus Nesepyris, consisting of 4 species, from the North to Central Americas and the Hawaii Islands. In his 1920 paper, Bridwell indicated that the characters that separate Nesepyris from Allobethylus as follows: 1) eyes with hairs, 2) submedian cell closed, 3) stigma weakly developed, 4) fossae of scutellum different, and 5) propodeum with a single imperfect median carina.

However, characters 1), 4) and 5) are only species level differences in the Epyrinae, character 2 is errounesuly cited, and the submedian cells are opened at the tip of anal vein in both genera. The character 3) is constitunious; 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 Nesepyris 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.

Type species: Bethylopsis fullawayi Fouts

Remarks. 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 closely related to the genus Allobethylus, but is separated from the latter by the reduction in wing size and absence of natauli (Figs. 85-88).

The measurements of the type (female) are as followes: HL 0.37 mm; HW 0.65 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.

Genus Odontepyris Kieffer

Odontepyris Kieffer, 1904

Type species: Odontepyris flavinervus Kieffer

Remarks. Although Gordh & Moczar (1990) included this genus in the subfamily Epyrinae, I followed Kieffer (1914) and Evans (1964) who assigned it to the subfamily Bethylinae.

Genus Bradepyris Kieffer

Bradepyris Kieffer, 1905

Type species: Bradepyris apterus Kieffer

Remark. This genus consists of 5 species, of which a single species B. inermis is examined (Figs 89-96). The following characters suggest that this species belongs to the subfamily Mesitiinae though this has few punctures on the surface of head and alitrunk: 1) posterolateral corners of propodeum with a short, but distinct spine; 2) 2nd gastral tergite large; 3) basal median portion of propodeum with a carina which extends to the metanotum; 4) eyes strongly convex and with erect hairs; 5) notauli large and strongly curved outward.

As I could not examine the type species, B. apterus, of which the place of type deposition is not known, I provisionally treat this genus as a member of Mesitiinae.

Results and discussions

Analysis of relationships among tribes

Table 8 shows chatacters used in this analysis and Table 9 character matrix. The single most parsimonious tree was found (length = 16, consistency

index 1.000, retention index 1.000) (Fig. 97). The tree indicated Epyrinae as the sister-group of (Sclerodermini + Cephalonomiini). This phylogenetic relationship essentially supports the tribal phylogeny proposed by Evans (1964); he divided Epyrinae into 3 tribes, Epyrini as a generalized element and both Scleroderminin and Cephalonomiini as specialized stocks. The clade (Sclerodermini + Cephalonomiini) is supported by 2 synapomorphic character states: trancate median lobe of clypeus (character 2) and loss of occipital carina (character 4). Sclerodermini and Cephalonomiini were each found to possess uniquely derived character states, demonstrating that each is monophyletic. Character 3 (position of eyes) supports the monophyly of the tribe Sclerodermini. Two autoapomorphic states support the monophyly of Cephalonomiini: reduction of antennal segments (character 1) and reduction of segments of labial palpi (character 6). The monophyly of Epyrinae is supported by the presence of fovea at the posterolateral corners of propodeum (character 8).

The autoapomorhic states for Sclerodermini (character 3) and Epyrinae (character 8) are relatively weak. Chatacter 3 is also seen in some apterous females of the genus Cephalonomia, though this is thought to be convergently developed. Some species of Epyrinae have the propodeal foveae that are secondarily reduced. The average size reduces from Epyrini through Sclerodermini to Cephalonomini, and such a size reduction should be related to the degenerative specialization in external morphology. Observed specialization are: 1) size reduction; 2) reduction in wing veenation; 3) reduction of the number of antennal and palpal segments; and 4) loss of wings, notauli and propodeal sculpture.

Analysis of relationships among genera in Epyrini

Thirteen genera are used for the analysis. Table 10 lists characters and their states and Table 11 presents data matrix used in the analysis.

The analysis results in 11 equally parsimonious trees (tree length = 44, consistency index = 0.750, retention index = 0.593). These data provide supports for several competing hypotheses about phylogenetic relationships within the Epyrinae. Figs. 98 c-e, show the strict, Adams, and 50% majority consensus trees of 11 equally parsimonious trees. Despite the competing hypotheses that merit consideration, the following conclusions are consistent for all cases: 1) Holepyris and Laelius constitute a monophyletic assemblage by characters 24 (weakly concave anterior margin of forewings) and 25 (position of pterostigma); 2) ((Aspidepyris + Bakereilla) + Calyozina) constitutes a monophyletic assemblage by character 20 (large scutellar pits); 3) Aspidepyris and Bakeriella constitute a monophyletic assemblage by character 22 (presence of a blunt short tooth at posterolateral corners of propodeum). As for the Adams consensus tree, the clade (Epyris + Isobrachium + Trachepyris) is characterized by the apomorphic condition of character 11 (long pronotal disc in the females). This clade and the clade ((Aspidepyris + Bakeriella) + Calyozina) each form a monophyletic group supported by character 20 (presence

of the scutellar pits).

Analysis of relationships among genera in Sclerodermini

Nine genera in the tribe are used for the analysis. Table 12 lists characters and their polalities and Table 13 presents data matrix. Exact analysis of the matrix in Table 13 resulted in one cladogram (Fig. 99). Tree length is 36, with a consistency index of 0.778 and a retention index of 0.692. The Nothepyris, Chilepyris, and (Thlastepyris + Alongatepyris) 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 autoapomorphy 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.

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

Analysis of relationship among genera in Chephalonomiini

Five genera are used for the analysis. The characters and their polarities, and data matrix are shown in Tables 14 and 15, respectively. Two most parsimonious trees were found (tree length = 17, consistency index = 1.000, retention index = 1.000) (Fig. 100-a, -b). Fig. 100-c shows the strict consensus tree from these 2 most parsimonious trees. The genus Islaelius is positioned basally, and after that there is a basal polytomy involving Plastanoxus, Prolops, and the clade (Cephalonomia + Acephalonomia). Islaelius was found to posess one autoapomorphic character, broad basal vein (character 12). Character 14 (the shape of paramere) supports the monophyly of Plastanoxus. Six autoapomorhies also support the monophyly of Prolops: 3 segmented maxillary palpi (character 1); the shape of front of head (character 4); moderately convex eyes (character 5); absence of parapsidal lines (character 6); the shape of scutellum (character 7); absence of scutellar pits nor groove (character 8). Two synapomorphic conditions support the clade (Cephalonomia + Acephalonomia): the position of pterostigma (character 9) and absence of radial vein (character 11). Genus Acephalonomia has an autoapomorphic character state, 9-segmented antennae, while no unequivocal autoapomorphies were obtained in Cephalonomia. Genus Islaelius seems to occupy an intermediate position between Sclerodermini and Cephalonomiini. The Prolops is the most specialized genus in Epyrinae since this has much more

apomorphic character states.

iii) Subfamily Mesitiinae

The subfamily Mesitiinae is a compact and less diverse group, including 12 genera, restricted to the Ethiopian, Palaearctic and Oriental regions. The genus Codorcas is excluded in this analysis, since it is regarded as a provisional synonym of Heterocoelia. The monotypic genus Codorcas (type: C. cursor) is separated from Heterocoelia by the reduction of median and discal carinae of Propodeum. There is, however, a possibility that this is not genus level but only species-specific characteristic.

The genus Bradepyris is transeferred subfamily Epyrinae.

Results and discussions

Characters refferred to in the generic diagnoses for the genera are summarized in Tables 16 and 17. Six equally most parsimonious trees, of which one had a zero length internode by ACCTRAN (tree 6 in Fig. 101), were obtained from the data; tree length is 21, consistency index 0.905 and retention index 0.889 (Fig. 101). Fig. 102 shows the strict consensus of all 5 trees. The following conclusions are consistent: 1) The cladogram has a polytomy involving (Anaylax + Pseudomesitius), Bradepyris, and the remaining 9 genera; 2) Anaylax and Pseudomesitius constitute a monophyletic assemblage by character 11 (parapsidal furrows absent or indistinct); 3) Parvoculus and Pilomesitius constitute a monophyletic assemblage by character 12 (scutellum extremelly convex dorsally); 4) The presence of longitudinal furrow of propodeum (character 13) support the monophyly of Bradepyris, although the phylogenetic position is ambiguous; 5) Nine genera excluding Anaylax, Pseudomesitius, and Bradepyris were found to possess 2 synapomorphies: head strongly punctate (character 2), median longitudinal furrow on pronotum completely developed (character 8). However, further studies are needed to determine the phylogenetic relationship in detail and reexamine the complete framework of genera.

iv) Subfamily Bethylinae

Nine genera have been known in this subfamily. In this paper, however,

genera Anoxus and Eupsenella are synonymized with Bethylus and Lytopsenella respectively. The genus Trissomalus which is included in the subfamily Epyrinae in the list by Gordh & Moczar (1990) is presumably a synonym of the genus Odontepyris.

Bethylus Latreille

Bethylus Latreille, 1802.

Type species: Omalus fuscicornis Jurine

Perisemus Foerster, 1856. [Synonymized by Kieffer, 1905.]

Episemus Thomson, 1862. [Synonymized with Perisemus by Ashmead, 1893.]

Digoniozus Kieffer, 1905. [Synonymized by Evans, 1962.]

Anoxus Thomson, 1862. Syn. nov.

Anoxys Dalla Torre, 1898. [Unjustified emendation.]

Remarks. Anoxus (Figs. 103-105, 108) differs from Bethylus only in haired eyes and relatively more produced antennal sockets. These conditions, however, indicate only species level diferences within genus in the taxonomy of Bethylidae. The following 3 species are moved to the genus Bethylus: B. boops (Thomson) comb. nov., B. coniceps (Kieffer) comb. nov, and B. pilosus (Kieffer) comb. nov.

Genus Eupsenella Westwood

Eupsenella Westwood, 1874.

Type species: Eupsenella agilis Westwood

Lytopsenella Kieffer, 1911. Syn. nov.

Remarks. Differences between genera Eupsenella and Lytopsenella are slight; only the shape of marginal cell of forewings is different but this has no significance in separating the genera. The marginal cells of E. agilis (type species of Eupsenella) are variable in shape, presenting intermediate conditions between them. Kieffer's explanation and Figure 193 for Lytopsenella in "Das Tierreich" is incorrect as Evans pointed out (1964). The following 5 species of which 3 are fossil species preserved in the Baltic amber are transeferred to the genus Eupsenella: E. crastina (Brues) comb. nov., E. herbsti (Kieffer) comb. nov, E. setigera (Brues) comb. nov., E. simplex (Brues) comb. nov., and E. testaceicornis (Kieffer) comb. nov.

Three fossil species designated by Brues (1923) were originally placed in the genus Sierola, and were later transferred to the genus Eupsenella by him in 1933. In 1958, however, Evans placed them in the genus Lytopsenella.

Results and discussions

Characters reffered to in the generic diagnoses are included in the lists comprising Tables 17 and 18. Cladistic analysis using the data matrix yielded 8 equally most parsimonious trees (Fig. 113), of length 36, consistency index 0.861, and retention index 0.615. One of the 8 trees (tree 8 in Fig. 113) had a zero length internode by ACCTRAN. Fig. 114 gave the strict consensus of all 8 trees. The Eupsenella is placed basally, and after that there is a basal polytomy involving Bethylus, Sielora, Goniozus, Prosierola, and Odontepyris. These 5 genera were found to possess 4 synapomorphies: maxillary palpi with 5 segments (character 2), notauli absent (character 3), pterostigma broad (character 15), and marginal cell opened (character 20), while there is only one autoapomorphy (hind trochanthers with spine; character 24) in Eupsenella.

The shape of basal vein (character 18) is another possible apomorphic character for the genus, but this may have convergently occurred in Bethylus.

It is highly possible that Prosielora is the sister-group of Odontepyris since 5 of the 7 trees indicate the clade (Prosierola + Odontepyris). The long median carina of head (character 6) is a possible synapomorphy for these genera. The geographical distribution of these genera is allopatric; Prosielara is distributed in the New World, while Odontepyris in the Ethiopian, Oriental, and southern Palaearctic Regions. Judging from the original description, Prosierola mordavica Nagy, 1976 from Mordavia, East Europe, should be synonymous with Odontepyris.

The following characters support the monophyly of the genus Bethylus: antennae with 12 segments (character 1), labial palpi with 2 segments (character 3), head rather flat and rectangular (character 4), anterior border of clypeus broadly rounded (character 5), basal vein meeting subcosta based of stigma by about length of stigma (character 17), and anal and transverse median veins angulate (characters 19).

Odontepyris, Prosierola and Goniozus were each found to possess uniquely derived character conditions demonstrating that each genus is monophyly. The autoapomorphy for Odontepyris is character 11 (presence of a pair of pits in basal outer portion of propodeum), that for Prosielora is character 10 (presence of a pair of pits of basal inner portion of propodeum), and that for Goniozus is character 16 (large and triangular prostigma). However, the present analysis did not reveal any unequivocal apomorphic character condition for Sielora.

Evans (1978) established 2 tribes, Bethylini and Sielonini, in this subfamily. However, the present results did not support his system. The genus Bethylus, although having much more apomorphic characters, is not clearly separated as the sister-group of all the other genera combined. On the other hand, Eupsenella is separated from the other 5 genera. But I did not establish a new tribe for this genus since this subfamily consists of compact genera in morphology. Eupsenella is the most primitive of the Bethylinae with respect to the wing venation, palpal formula, and presence of notauli.

Zoogeographical synopsis

The number of described species in each genus is shown in Appendix II in this part. The number of genera in each subfamily is presented in Table 18.

The subfamily Pristocerinae has the highest genus number (16 genera) in the Ethiopian region, followed by 9 genera in Oriental region. The Ethiopian region has also abundant endemic genera; the following 11 genera are restricted to this region: Afgoiogfa, Afrocera, Apristocera, Dicrogenium, Diepyris, Kathepyris, Neodicrogenium, Paraprístocera, Prosapenesia, Trichiscus and Usakosia. Apenesia, Dissomphalus, Parascleroderma and Pseudisobrachium are widely distibuted in the world. The distribution pattern of Pristocera and Acrepyris is principally allopatric; Acrepyris is mostly distributed in the New World and a few species in the Oriental and southeast Palaearctic regions, while Pristocera occurs in the Ethiopian and Oriental regions.

The Oriental region has the highest genus number in Epyrinae. In the tribe Epyrini, the Oriental region is richest in gunus number (16 genera), and the Ethiopian region is second richest (13 genera). However, not a few genera have been left without taxonomic revisions. The Sclerodermini is distributed evenly at generic level in the world. In specific level, however, the genus Sclerodermus has abundant in the Palaearctic region and the Oceania. Chilepyris is restricted to the Australian (New Zealand) and the southern

Neotropical (Chile) regions. No record for the tribe Cephalonomiini has been known in the Australian and the Ethiopian regions.

The distribution pattern of the Mesitiinae is unique in Bethylidae: 1) It has not been found in the New World and the Australian region; 2) The largest generic diversity is seen in the Palaearctic region.

The subfamily Bethylinae has been recorded from all zoogeographical regions. The genus Bethylus is principally distributed in the Palaearctic and Nearctic regions. Two closely related genera Prosierola and Odontepyris show allopatric distribution pattern; Prosierola is distributed in the New World and Odontepyris in the Ethiopian, Oriental and southern Palaearctic regions. The genus Eupsenalla is restricted to the Australian and southern Neotropical regions. This distribution pattern seems to indicate the AS groups firstly designated by Hennig (1960). However fossil species were found in the Eurasia in the Oligocene (Brues, 1923).

The New World has a few endemic genera, only three (Thlastepyris, Alongatepyris and Nothepyris) in the Neotropical region and no endemism is known for the Nearctic region. On the other hand, the Ethiopian and Oriental regions have many endemic genera, 16 and 5 respectively. Thirteen genera occur in the Australian region. However, fewer faunal surveys may have been carried out in the tropics such as the Australian, Oriental and Ethiopian regions compared with the Palaearctic and Nearctic regions. Intensive studies in the tropics will give us much more exact information about diversities at species and genus level.

Relationships between phylogeny and hosts

Little has been known about the hosts of Bethylidae except for few special genera which seem especially useful for biological controls. However, it is known that pristocerine and epyrine species are parasitic on the larvae or pupae of Coleoptera, and Bethylinae on the larvae of Lepidoptera. The remaining subfamilies have not been known for their hosts. The host-parasite associations are presented in Table 19 mainly based on Tachikawa (1980, 1985) and Evans (1978). Some possible assosiations are omitted in this table. For example, Holepyris and Goniozus can lay eggs to other orders of insects under experimental conditions, but this is not cited because incompletenessof information.

The present results suggest the relationship (Pristocerinae + (Epyrinae + Bethylinae)). As mentioned above, both Pristocerinae and Epyrinae parasitize coleopteran larvae, and Bethylinae as lepidopteran larvae. Therefore, given the present phylogenetic analysis may be correct then it is suggested that the host preference by Pristoceriae and Epyrinae is plesiomorphic and that by Bethylidae is apomorphic (Fig. 115).

New format keys to the subfamilies and genera in the world

No taxonomic key has been published in Bethylidae of the world since Kieffer (1914). Unfortunately, Kieffer's key includes inadequate and erroneous descriptions, and some of his genera actually belong to other families or inadequate subfamilies, and many generic names have proved to be synonyms. Therefore I present here new format keys of Bethylidae for testing and critical comments.

The zoogeographical distribution for each genus is shown in parentheses. The abbreviations of zoogeographic regions are as follows: PAL, Palaearctic region; ORI, Oriental region; AUS, Australian region; ETH, Ethopian region; NEA, Nearctic region; NET, Neotropical region. Ambiguousgenera, for most of which the types were lost, are excluded in the keys to avoid the unnecessary confusions.

Key to subfamilies of Bethylidae

1. Propodeum with distinct spines at dorsal posterolateral corners; 2nd gastral segment large, accounting for considerably more than half the length of the gaster in dorsal view (Figs. 118, 119)··························Mesitiinae
- Propodeum without spine at dorsal posterolateral corners; 2nd gastral segment much smaller, accounting for much less than half the length of the gaster in dorsal view ··································2
2. Fifth gastral sternite with a pair of large cornicles (Figs. 136, 137) ··································Galodoxinae [known from female only]
- Fifth gastral sternite simple, without modification····················3
3. Propodeum oval in dorsal view, distincly wider than long; mesonotum and mesopleuron also fused (Fig. 120)·································· ····················Parapenesiinae subfam. nov.[known from female only]
- Propodeum more or lee rectangular, longer than wide; mesonotum and mesopleuron not fused··································4
4. Metanotum of male well developed; scutellum and propodeum not nearly in contact medially; metanotum with a small fovea at middle; females completely apterous, with the eyes small to absent; eye height at most 0.25 x head width (Fig. 117)····························Pristocerinae
- Metanotum much reduced in both sexes; the scutellum in contact with the propodeum medially or nearly so; metanotum without fovea medially;

females alate, brachypterous, or apterous; eyes large, eye height more than 0.30 x head width (Figs. 123-126)··························5

5. Basal vein simple, not giving rise to a vein or stub (Fig. 123; with few exception); claws weakly to moderately curved; frons without longitudinal median carina or polished streak extending from clypeus ··Epyrinae

- Basal vein giving rise to a vein (Fig. 127); claws strongly curved; frons usually with a longitudinal median carina or polished streak extending for a short distance from clypeus·················Bethylinae

Key to the genera of Pristocerinae

(Male)

1. Subgenital plate deeply divided into two lobes······················2

- Subgenital plate simple, posterior border at most weakly concave, and never deeply divided into two lobes·································6

2. An acute spine present at gena of head in lateral view·············3

- Genal area without spine··4

3. Mandibles sickle-shaped···························Dicrogenium [ETH]

- Mandibles more or less triangular with teeth on masticately margin··· ··Neodicrogenium [ETH]

4. Mandibles sickle-shaped, with only 2 apical teeth·····Diepyris [ETH]

- Mandibles triangular with 3-6 teeth·································5

5. Cubital and subdiscoidal veins reaching the wing margin············· ··Kathepyris [EYH]

- Cubital and subdiscoidal veins not reaching the wing margin······· ···Pristocera [ETH, ORI, PAL]

6. Head truncated anteriorly; pterostigma exceptionally large; posterior border of subgenital plate with a tergum······Prosapenesia [ETH]

- Head not truncated anteriorly; pterostigma moderate in size or absent; posterior border of subgenital plate simple, without a tergum···7

7. Pterostigma absent·································Calopenesia [ORI]

- Pterostigma present··8

8. Second gastral tergite with a pair of spots, pits or depressions ; posterior border of 2nd gastral tergite without modification; 3rd tergite simple························Dissomphalus [PAL, ORI, ETH, NEA, NET]

- Second gastral tergite without modification, but posterolateral border strongly concave; 3rd tergite with a pair of spots ··Trichiscus [ETH]

- Both of 2nd and 3rd abdminal tergites simple, without modification····9

9. Propodeum long, more than twice as long as wide; scutellar disc elongate, more than twice as long as wide···························Afrocera [ETH]

- Propodeum much less than twice as long as wide; scutellar disc shorter, less than twice as long as wide·····································10

10. Anterior border of clypeus trapezoidal and truncate apically ; eyes densely covered with hairs; genitalia with the parameres deeply divided into two lobes·········· Pseudisobrachium [PAL, ORI, ETH, NEA, NET]

-- Clypeus not trapezoidal nor truncate apically; eyes glabrous, or only scattered with short hairs; genitalia with parameres not deeply divided into two lobes (except for Neopenesia)·····························11

11. Notauli absent or nearly so··12

-- Notauli complete or nearly so···13

12. Clypeus produced; head longer than wide; pronotum usual in size; paramere simple, not divided into two lobes························· ··Protisobrachium [ETH, ORI]

-- Lateral borders of anterior margin of clypeus not remarkably produced; head wider than long; pronotum extremely short; genitalia with paramere deeply divided into two lobes·············· Neopenesia [ORI]

13. Ocelli small, forming a flat triangle, situated almost near the occipital border; metacarpus vein absent·····································14

-- Ocelli larger, more or less forming a right triangle, situated far from the occipital border; metacarpus vein present·····················15

14. Anterior border of clypeus with a single median projections··········· ·······························Parascleroderma [PAL, ORI, ETH, NEA, NET]

-- Anterior border of clypeus with 3 small projection·····Afgoiogfa [ETH]

15. Median lobe of clypeus depressed near the antennal insertions; cuspis simple, not divided or setose; paramere consisting of 3 valves······· ··Acrepyris [PAL, ORI, NEA, NET]

-- Median lobe of clypeus not depressed near the antennal insertions; cuspis divided into a simple dorsal and a setose ventral arm (except in a few species); paramere simple, not consisting of 3 valves········ ·····································Apenesia [PAL, ORI, AUS, ETH, NEA, NET]

(Female; known in 8 genera only)

1. Body extremelly flat dorsoventrally ··································2

- Body at most only weakly flattened····································3

2. Base of pronotum in contact with base of scutellum in dorsal view·····

································Parascleroderma [PAL, ORL, ETH, NEA, NET]

- Pronotum not in contact with scutellum in dorsal view·················
 ···Afgoiogfa [ETH]

3. Propodeum strongly constricted at its anterior end, where it forms a pair of small processes which embrace the apex of the elongate mesonotum ···4

- Propodeum not constricted at anterior end, broadly in contact with the mesonotum ··5

4. Tip of median lobe of clypeus truncate and thickened; eyes absent·····
 ··Prosapenesia [ETH]

- Tip of median lobe of clypeus not thickened; eyes present·············
 ····························Pseudisobrachium [PAL, ORI, ETH, NEA, NET]

5. Mesopleura very small in dorsal view; propodeum nearly parallel-sided, at most weakly constricted····························
 ··································Dissomphalus [PAL, ORI, ETH, NEA, NET]

- Mesopleura strongly developed in dorsal view; propodeum with a distinct constriction at the spiracles····························6

6. Propodeal constriction strong; maximum width of propodeum at least twise at constriction; eyes large, consisting of more than 15 facets·········
 ·············Pristocera [PAL, ORI, ETH] or Acrepyris [PAL, ORI, NEA, NET]

- Propodeal constriction less strong, maximum width of propodeum less than twice that at constriction; eyes small, consisting of less than 15 facets
 ····································Apenesia [PAL, ORI, AUS, ETH, NEA, NET]

1. Antennae with 13 segments (3rd segment very small but visible in some species); clypeus with a projecting median lobe; eyes situated laterally on head; PF= 6-5, 3-2·················2. (Tribe Epyrini)

- Antennae with 13 segments; clypeus short, truncate; eyes situated forward on head; PF= 6-5, 3-2···········13 (Tribe Sclerodermini)

- Antennae with 12 segments or less; clypeus short, truncate; eyes situated laterally on head (with few exceptions of apterous females) ; PF= 5-3, 2-1·························21 (Tribe Cephalonomiini)

2. Scutellum with a pair of basal pits, either completely separate or connected by a very thin and shallow line························3

- Scutellum basally with a transverse, undivided groove, that is straight or deflected backward at each end, sometimes broadened at each end, but in this case the termini still connected by a deep groove······8

3. Antennal scapes with strong setae; mandibles long, forming a straight shaft with apical blunt tooth··············Trachepyris [ETH, ORI]

- Antennal scapes without distinct large setae; mandibles shorter, more or less triangular··4

4. Pronotal disc transversely carinate in front; scutellar pits large

··Bakeriella [NEA, NET]

- Pronotal disc simple without a transverse carina anteriorly·········5

5. Pronotum with strong anterior and lateral emarginations; anterolateral corners strongly angulate···························Calyozina [ORI]

- Propodeum not distinctly emarginate anteriorly and laterally; antero-lateral corners rounded, not forming an angle in lateral view······6

6. Pronotum with its posterior part elevated and prolonged arcuately backward so as to overlie the base of the mesoscutum················ ···Aspidepyris

- Pronotum with its posterior margin simple, not prolonged backward so as to overlie the base of the mesoscutum····························7

7. Notauli absent··························Isobrachium [PAL, ORI, ETH]

- Notauli present·························Epyris [PAL, ORI, AUS, ETH, NEA, NET]

8. Clypeus with 3 prominent lobes; basal vein reaching subcosta based of stigma by approximately the length of pterostigma; notauli weak and incomplete (with few exception)··Holepyris [PAL, ORI, AUS, ETH, NEA, NET]

-. Clypeus with only the median lobe developed; basal vein reaching subcosta close to base of pterostigma·······························9

9. Radial vein very short, at most slightly longer than basal vein·····10

- Radial vein long, distinctly longer than basal vein·················11

10. Pterosigma present; wing veins without distinct setae··············· ··Disepyris [PAL, ORI, ETH]

-- Pterostigma absent; wing veins with large distinct setae···········

··Laelius [PAL, ORI, ETH]

11. Pronotal disc with a transverse carina in front; its sides sharply set off and also carinate··························Anisepyris [NEA, NET]

-- Pronotal disc rounded off anteriorly and laterally; its sides not sharp or carinate··12

12. Transverse foveae present in posterior portion of pronotum; mesonotum also with a transverse foveae in midlength; transverse groove of scutellum broad···································Asianepyris [ORI]

-- Transverse carina absent in posterior portion of pronotum and mesonotum; transvers groove of scutellum thin, but forming a deep groove······ ·····························Rhabdepyris [PAL, ORI, AUS, ETH, NEA, NET]

(Tribe Sclerodermini)

13. Mandibles thin and elongate, terminating in 2-3 teeth; head quadrate, distinctly longer than wide in frontal view·····················14

-- Mandibles thick and broad; head at most weakly longer than wide in frontal view···15

14. Wings fully developed; notauli distinct···························· ···································Allobethylus [PAL, ORI, AUS, NEA]

-- Wings reduced, not reaching the posterior border of propodeum; notauli indistinct·······Bethylopsis [Marquas Isls., known from female only]

15. Mandibles with 7 small teeth, upper margin denticulate; wings fully developed or brachypterous············Glenosema [PAL, ORI, AUS, ETH, NEA]

-- Mandibles with less than 6 teeth, upper margin without denticule····16

16. 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, known female only]

-- Gastral sternites 4-6 simple or their margins shallowly sinuate······17

17. Body extremely depressed dorsoventrally······························18

-- Body at most weakly depressed dorsoventrally·························19

18. 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 cell not separated by median vein·······································Thlastepyris [NET]

19. Radial vein present·································Nothepyris [NEA]

-- Radial vein absent, at most indicated by a very faint line; apterous female present in some species·································20

20. Pterostigma large and almost circular; head very large, wider than long, much wider than maximum width of alitrunk in dorsal view··············Chilepyris [NET, known male only]

-- Pterostigma smaller and longer than wide; head slightly wider than long, almost as long as wide or only slightly wider than maximum width of alitrunk; winged and apterous forms bresent in both sexes and much common in apterous female·······································Sclerodermus [PAL, ORI, AUS, ETH, NEA, NET]

(Tribe Cephalonomiini)

21. Antennae with 10 segments; winged and brachypterous forms present in both sexes·····································Acephalonomia [PAL]

-- Antennae with 12 segments·······································22

22. Median vein broader in the midlength·············Israelius [PAL, ORI]

-- Median vein almost with the same width from anterior to posterior ends, not broaded in the midlength···································23

23. Radial vein absent; wings frequently absent or much reduced···Cephalonomia [PAL, ORI, NEA, NET]

-- Radial vein present at least in part; wings always fully developed··24

24. Frons produced below a nasus which overlies the antennal insertions and clypeus······································Prorops [NEA, NET]

-- Frons simple, not produced below··············Plastanoxus [PAL, ORI, NEA]

Key to genera of Mesitiinae

1. Pronotum with a distinct longitudinal furrow which is at least partly developed··2

- Pronotum without distinct longitudinal furrow··························9
2. Propodeum without sublateral carinae in both sexes and discal carinae in the female···Clytrovorus [PAL]
- Propodeum with sublateral and discal carinae··························3
3. Median carina of clypeus dilated and spoon-like anteriorly···Mesitius [PAL]
- Median carina of clypeus simple, not dilated anteriorly················4
4. Gastral tergites 1-2 covered with pale yellowish gold and black hairs ··Pilomesitius [ETH]
- Gastral tergites with scattered hairs································5
5. Head much longer than wide; lateral borders of pronotum strongly concave ; eyes small···Parvoculus [ETH]
- Head almost slightly longer than wide; lateral borders of pronotum straight or weakly concave; eyes larger···························6
6. Median furrow of mesonotum distinct·································7
- Median furrow of mesonotum indistinct or absent······················ ··Heterocoelia [PAL, ETH, ORI]
7. Head, pronotum only superficially punctate, usually alitaceous-microreticulate·······································Metrionotus [PAL, ETH, PAI]
- Head, pronotum deeply, densely or coarsely rugose, punctate and extremely densely··8
8. Gastral 2nd tergite deeply punctate·········Pycnomesitius [ETH, ORI]
- Gastral 2nd tergite moderately to coarsely punctate····················

······································Sulcomesitius [PAL, ETH, ORI]
9. Lateral carina of propodeum absent····················Bradepyris [PAL]
- Lateral carinae of propodeum present································10
10. Median carina and inner lateral carinae parallel, outer lateral carinae present only basally···························Pseudomesitius [PAL]
-- Median carina and inner lateral carinae not parallel, outer lateral carinae complete, reaching the transverse carina···················11
11. Pronotum with punctures; mesonotum with a short langitudinal furrow ··Incertosulcus [PAL, ORI]
-- Pronotum smooth, without distinct punctures; mesonotum without longitudinal furrow·····································Anaylax [PAL]

Key to the genera of Bethylinae

1. Fore wing with 6 closed cells, marginal and submarginal cell closed; notauli present·······························Eupsenella [AUS, NET]
- Fore wing with at most 4 closed cells; notauli absent·············2
2. Marginal cell closed····················Sierola [PAL, ORI, AUS, NEA; abundant on the Hawaiian Islands]
- Marginal cell open apically··3
3. Antennae with 12 segments; head flat and rectangular; basal vein forming almost a right angle; its basal 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; head more or less rounded (few exceptions in Goniozus); basal vein oblique, only slightly angled, leaving median vein at about the same point as the transverse median vein; always fully winged··4

4. Prostigma large, forming 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·······························5

5. Complete median carina of propodeum present; base of propodeal disc with a pair of small pits at the outermost part of basal triangle········· ·································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]

Conclusion

The cladistic analysis at the subfamily level in Bethylidae results in a single most parsimonious tree. The following conclusion has been reached: 1) 6 subfamilies are recognized; 2) Afgoioginae is included in the Pristocerinae; 3) a new subfamily, Parapenesiinae, is proposed; 4) Epyrinae, Mesitiinae, and Galodoxinae are marked as sister-groups each other, and Galodoxinae should be raised to subfamily rank; 5) 3 tribes, Epyrini, Sclerodermini, and Cephalonomiini, are considered to hold within the current position.

Subfamily Pristocerinae

(Figs. 116-117)

Pristocerinae Dalla Torre, 1897.

Type genus: Pristocera Klug, 1808.

Pristoceriini; Kieffer, 1914 [As a tribe.]

Pristocerinae; Berland, 1928 [Rasised to subfamily status.]; Evans, 1964.

Afgoioginae Argaman, 1988. Type genus: Afgoiogfa Argaman, 1988. Syn. nov.

Subfamily Parapenesiinae nov.

Type genus: Parapenesia Kieffer, 1910.

(Figs. 120-121)

Diagnosis. Small apterous wasps (female) with the following combination of characters.

1. Antennae with 13 segments.
2. Clypeus with a median carina; anterior border truncate.
3. Eyes medium sized, situated forward on head.
4. Mesoscutum and mesopleura fused, but the mesopleura produced laterally in dorsal view.
5. Mesoscutum broaden.
6. Notauli present but shallow.
7. Parapsidal lines absent.
8. Teglae absent.
9. Metanotum reduced.
10. Propodeum oval, wider than long.
11. Middle tiviae spinose.
12. Gaster dipressed dorsoventraly.

Remarks. The caracters 4, 5, and 10 are autoapomorphic of Parapenesiinae.

Male. Not known.

Parapenesia unicolor Kieffer

Parapenesia unicolor Kieffer, 1910.

Redescription of type. Female. HL 0.77 mm; HW 0.68 mm; LA 1.31 mm; LP 0.45 mm; WPD 0.56 mm; TL 3.8 mm.

Body yellowish brown; tip of mandibles reddish brown.

Head longer than wide, with gently convex occipital border in frontal view; posterolateral corners not forming an angle; surface smooth and shining. Mandibles with 3 teeth, apical most projecting and basal 2 dull. Eyes 0.19 mm in length. Antennae short; scapes robsut and short; 2nd to 5th segments each as long as wide; 6th to 13th segments each slightly longer than wide.

Alitrunk smooth and shining; pronotum 0.5 x as long as wide, anterior border semicircular, posterior border straight in dorsal view; mesothorax including mesopleura 0.71 mm in maximum width; propodeum 1.25 x as long as wide.

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

Gaster rather smooth but weakly microreticulate.

Holotype. Female, Cap. Sre'ge (Africa).

Type depository, Zoological Museum, Berlin.

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

Subfamily Epyrinae

(Figs. 123-126)

Epyrini Kieffer, 1914. [As a tribe].

Type genus: Epyris Westwood, 1832.

Epyrinae; Berland, 1928, [Raised to subfamily status.]; Evans, 1964.

Subfamily Mesitiinae

(Figs. 118-119)

Mesitinae [sic.] Berland, 1928.

Type genus: Mesitius Spinola, 1851.

Mesitiinae; Kurian, 1954.

Remarks. The name Mesitinae was given initialy by Berlands (1928), and then, Nagy (1969) or Moczer (1970 a, b; 1971) employed it. However, Mesitinae should be corrected as Mesitiinae, according to the International Code of Zoological Nomenclature (1985) by Articles 32(b), (c) and (d).

Subfamily Galodoxinae

(Figs. 128-137)

Galodoxinae Nagy, 1988.

Type genus: Galodoxa Nagy, 1988.

Subfamily Bethylinae

(Fig. 127)

Bethylini Kieffer, 1914 [As a tribe.]

Type genus: Bethylus Latreille, 1802.

Bethylinae; Berland, 1928, [Raised tosubfamily status]; Evans, 1964.

Subfamily Pristocerinae comprises 20 genera, but I did not establish any tribe within it. This subfamily prospers in the Ethiopian region at the genus level. In Epyrinae, which is most diverse group in external morphology, 3 tribes are recognized. Bethylinae comprises 6 genera and I did not recognize any tribe within it because of compact, less diverse morphology among genera. The subfamily Mesitiinae is phylogenetically most related to the Epyrinae or Galodoxinae. The range of this subfamily is restricted to the Ethiopian, Oriental and Palaearctic regions, although Pristocerinae, Epyrinae and Bethylinae all occur over the world. Morphologically, Mesitiinae is compact and not diverse. These distributional and morphological features suggest that this is most recently developed among the bethylid subfamilies. It is interesting that this subfamily has the highest genus number in the Palaearctic region, while the other subfamilies are thriving in the tropics. The taxonomic history of Bethylidae is summarized in Table 20, and the taxonomic system, which includes all the genera in the world, proposed by the present study is presented in Appendix III.

In the cladistic analysis with the external morphologies, there have been found many homoplasious character states. The following evolutionary trends associated with the reduction in body size are observed among different phylogenetic lines: 1) Wing reduction; 2) simplification of the body sculpture; and 3) transformation to ant-like body forms in the females. The ant-like body form in the female may be related to the ecological resemblance, especially to host search behavior. It is sometimes claimed that such a specialization may prevent to find synapomorphies in phylogenetic analyses. However, to analyze such phenomena is very important to understand the evolution of ecology and morphology of wasps and their diversities. So we must pay attention to morphologically and functionally similar character conditions frequently developed in phylogenetically different lines.

In the sense that the more characters employed assure more reliable phylogenies, one could except to have a higher confidence to the family to genus level phylogenies given in this paper than previously published schemes. This means, naturally, that additions of new characters will lead to further changes and improved resolutions. Especially, the molecular sequence data will contribute in improving the inconclusive or weakly supported parts of the phylogenetic hypothesis here proposed.

Appendix I. Specimens examined.

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, Honolulu, 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

HNM: Hungarian Natural History Museum, Budapest, Hungary

HUS: Entomological Institute, Hokkaido University, Sapporo, Japan

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

KUF: Entomological Laboratory, Kyushu University, Fukuoka, Japan

MCSN: Museo Civico di Storia Naturale, Genova, Italy

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

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

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

NASM: National Science Museum, Tokyo, Japan

NHMC: Natural History Museum and Institute, Chiba, Japan

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

OMNH: Osaka Museum of Natural History, Japan

PMA: Provintial Museum of Alberta, Alberta, Canada

SAM: South Australian Museum, Adelaide, Australia

SMNH: Swedish Museum of Natural History, Stockholm, Sweden

TARI: Taiwan Agricultural Research Institute, Taichung, Taiwan

TE: Terayama collection, Department of Biology, 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-Universitat zu Berlin, Berlin, Germany

Specimen code:

(T): holotype, paratypes or syntypes examined.

List of species examined

Subfamily Pristocerinae

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

Apenesia: A. spp. [Japan, NIAES, NASM, KUF, KU-K, HUS, MU-Y, EUM]; Apenesia spp. [Taiwan, NASM, NIAES, TE]; A. spp. [Thailand, PMA]; A. spp. [Nepal; CNC]; A. sp. [Philippines, PMA]

Calopenesia: C. philippinensis [Philippines, ZMC(T)]; C. thailandensis [Phillipine, CNC(T)].

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

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

Dissomphalus: D. sp. [Japan, KUF]; D. spp. [Taiwan, NIAES, PMA]; D. sp. [Philippines, CNC]; D. sp. [Indonesia, NIAES]; D. spp. [Thailand, PMA]; D. sp. [Nepal, CNC];

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

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

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

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

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

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

Pristocera (Acrepyris): A. japonica [Japan, KUF(T), HUS, NIAES]; P. ishigakiensis [Japan, KUF(T)]; P. minuta [Japan, KUF(T)]; P. antennata [Myanmar, MCSN(T)]; P. spp. [Japan, KUF, KU-K, NIAES]; P. spp. [Taiwan, NASM, TARI, KUF, HUS, CNC, TE]; 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. sp. [Thailand, PMA]

Pseudisobrachium: P. sp. [Colombia, NASM]; P. spp. [Japan, KUF]; P. sp. [Hong Kong, TE]; P. spp. [Thailand, PMA]; P. spp. [Nepal, CNC]

Psilobethylus: P. luteus [Italy, MCSN(T)]

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

Subfamily Afgoioginae

Parascleroderma: P. spp. [Taiwan, NIAES, TE]; P. spp. [Thailand, PMA]; P. sp. [Malaysia, PMA]

Subfamily Epyrinae

Tribe Epyrini

Bradepyris: B. inermis [Morocco, HNM(T)]

Calyozina: C. ramicornis [Taiwan, ZMHU(T)]; C. sp. [Thialand, 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. 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. [Philippines, CNC, MU-Y]; E. spp. [Thailand, PMA, CNC, TE]; E. spp. [Malaysia, PMA, CNC]; E. spp. [Nepal, CNC]; E. spp. [India, PMA, CNC]; E. spp. [Sri Lanka, CNC]

Holopyris: H. atamiensis [Japan & Taiwan, USNM(T), NASM, NIAES, 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: 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. microneurus [France, MNHN(T)]; L. spp. [Japan, HUS, NIAES, NASM, MU-Y, EUM, KUF, KU-K, TE]

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

Orientepyris: A. thailandensis [Thailand, PMA(T)]; A. thormini [Thailand, PMA(T)]; A. indicus [India, CNC]

Procalyoza: P. westwoodi [Panama, BMNH(T)]

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

Trachepyris: T. sp. [Indonesia, TE]

Tribe Sclerodermini

Allobethylus: A. multicolor [New Guinea, HNHM(T)]

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

Glenosema: G. spp. [Thailand, PMA]

Nesepyris: N. sp. [Japan, TE, NIAES, KUF]

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

Tribe Cephalonomiini

Cephalonomia: C. gallicola [Japan, EUM, KUF, NIAES, TE]; C. tarsalis [Japan, EUM, TE]; C. sp. [Japan, KUF]

Islaelius: I. sp. [Thailand, PMA]

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

Subfamily Mesitiinae

Heterocoelia: H. vietnamensis [Thailand, PMA]; H. spp. [Japan, TE]; H. sp. [Thailand, PMA]

Sulcomesitius: S. haemorrhoidalis [Taiwan, NASM, MU-Y]; S. thailandensis

[Thailand, NASM, PMA]; S. spp. [India, PMA]; S. spp. [Nepal, CNC, PMA]

Metrionotus: 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

Anoxus: A. boops [Sweden, SMNH]

Bethylus: B. spp. [Japan, HUS, TE]; B. sp. [Nepal, CNC]; G. sp. [Korea, NASM]

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

Goniozus: G. japonicus [Japan & Korea, USNM(T), HUS, NIAES, NASM, MU-Y, EUM, KUF, KU-K, TE]; G. marianensis [Mariana Isls., NHMC(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. sp. [Japan, HUS, NIAES, NASM, TE]; O. spp. [Taiwan, NASM, TE]; O. sp. [Korea, MU-Y, PMA]; O. sp. [Hong Kong, NASM]; O. spp. [Thailand, PMA]; O. spp. [India, PMA, Polaszek collection]; O. sp. [Nepal, CNC]

Prosierola: P. sp. [Trinidad, Polaszek collection]

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

[Thailand, PMA]; S. sp. [India, PMA]

Trissomalus: T. sp. [India, PMA]; T. sp. [Thailand, PMA]

Appendix II. Zoogeographical synopsis of Bethylidae.

The number of currently recognized species-level taxa (until 1992) in each genus is shown by zoogeographical region. In case where no published recoed is available but the author has reliable information. currenty recognized species-level taxa until 1992. The cases undescribed "X" is applied there. The Hawaiian subdivision is separately shown but the Maragacy 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.

Region	PAL	ORI	AUS	ETH	NEA	NET	HAW	Total
Pristocerinae								
Acrepyris	2	1			5	6		24
Afgoiogfa				1				1
Afrocera				1				1
Anisobrachium	1							1
Apenesia	X	18	3	17	17	71		123
Apristocera				1				1
Calopenesia		2						2
Dicrogenium				23				23
Diepyris				6				6
Dissomphalus	5	3		12	8	51		80
Kathepyris				4				4
Neodicrogenium				6				6
Neopenesia		1						1
Parascleroderma	15	X		2	4	1		21
Pristocera	6	10	1	58				72
Prosapenesia				4				4
Protisobrachium		X		2				2
Pseudisobrachium	8	2		9	42	76		136
Trichiscus				2				2
Usakosia				1				1
Parapenesiinae								
Parapenesia				1				1
Epyrinae								
Epyriini								
Anisepyris		1			21	52		68
Orientepyris		3						3
Aspidepyris						2		2
Bakeriella					1	19		20
Calyozina		1		1	1	3		6

Disepyris	1	2		1				4
Epyris	40	44	4	38	30	50	1	201
Holepyris	36	12	2	18	21	20	2	98
Isobrachium	4	2		1				7
Laelius	15	2			5	1		20
Leptepyris		1						1
Melanepyris		1		1				2
Neodisepyris		5						5
Neurepyris		1		1				2
Planepyris				1				1
Pristepyris		2		2				4
Prolaelius				2				2
Rhabdepyris	13	17	19	6	21	36		106
Trachepyris	2	1		6				11
Triglenus	1							1
Trissepyris				1				1
Xenepyris		2						2
Sclerodermini								
Allobethylus	X	X	1		2	1	1	5
Alongatepyris						1		1
Ateleopterus								
Bethylopsis							1	1
Chilepyris			1	2		1		2
Discleroderma		1						1
Glenosema	5	X	1	2	1			9
Lepidosternopsis			2			1		3
Nothepyris						1		1
Scaphepyris		1						1
Sclerodermus	25	9	2	3	2	5	17	68
Thlastepyris						1		1
Cephalonomiini								
Acephalonomia	1							1
Cephalonomia	19	4	2		9	3	2	33
Israelius	1	X						1
Plastanoxus	6	X	1	1	5	3		8
Prorops					2	3		3
Galodoxinae								
Galodoxa		1						1
Mesitiinae								
Anaylax	9							9
Bradepyris	5							5
Clytrovorus	6							6
Codorcas	1							1
Heterocoelia	17	5		7				29
Incertosulcus	2	1						3
Mesitius	15							15
Metrionotus	6	5		18				28
Parvoculus				1				1
Pilomesitius				1				1
Pseudomesitius	1							1
Pycnomesitius		3		3				6
Sulcomesitius	3	52		25				78
Bethylinae								
Eupsenella			3			2		5
Bethylus	29	1			3			33
Goniozus	13	36	12	11	41	40	1	140
Odontepyris	1	5	2	3				11
Prosierola					1	8		8
Sierola	1	x	4		1		190	196
[Subfamily incertae sedis]								
Foenobethylus		1						1

Appendix III. Taxonomic list of the Family Bethylidae.

The genera of living bethylid wasps are listed alphabetically under tribes or subfamilies. Six subfamilies including 82 genera are recognized. The genera transferred to the other families are also given.

Family Bethylidae

Subfamily Pristocerinae
= Afgoiogfinae

Acrepyris Kieffer 1905 = Neopristocera Yasumatsu 1955
Afgoiogfa Argaman 1988
Afrocera Benoit 1983
Anisobrachium Kieffer 1905
Apenesia Westwood, 1874 = Propristocera Kieffer, 1905 = Aeluroides Tullgren 1904 = Cleistepyris Kieffer 1910, = Dipristocera Kieffer 1914 = Neopristocera Benoit 1957
Apristocera Kieffer 1914
Calopenesia Terayama 1994
Dicrogenium Stadelmann 1894 = Nomineia Kieffer 1911
Diepyris Benoit 1957
Dissomphalus Ashmead 1893 = Ecitopria Wasmann 1899 = Thaumatepyris Kieffer 1910 = Glenobethylus Kieffer 1910 = Parecitopria Ogloblin 1930 = Psilobethylus Kieffer 1906
Kathepyris Kieffer 1907
Neodicrogenium Benoit 1957
Neopenesia Terayama 1994
Parascleroderma Kieffer 1904 = Ceratepyris Kieffer 1905
Pristobrachium Benoit 1957
Pristocera Klug 1808 = Mangesia Kieffer, 1911 = Trichelobrachium Kieffer, 1914
Pseudisobrachium Kieffer 1904 = Monepyris Kieffer 1905 = Xestobethylus Cameron 1909 = Plutobethylus Kieffer 1910 = Lyssepyris Kieffer 1913 = Afrisobrachium Benoit 1957 = Xantepyris Kieffer 1913 = Xanthepyris Kieffer 1914(emendation) = Parisobrachium Kieffer 1914 = Pseudoisobrachium Ogloblin 1925 (Unjustified emendation) = Edapholigon Ogloblin 1963
Prosapenesia Kieffer 1910 = Neusakosia Benoit 1981
Protisobrachium Benoit 1957
Trichiscus Benoit 1956
Usakosia Kieffer 1914

Subfamily Parapenesiinae

Parapenesia Kieffer 1910

Subfamily Epyrinae

Tribe Epyrini

Anisepyris Kieffer 1905 = Lophepyris Evans 1959 = Procalyoza Kieffer 1905 (Provisional)
Aspidepyris Evans 1964
Bakeriella Kieffer 1910
Calyozina Enderlein 1912
Disepyris Kieffer 1905 = Lytepyris Kieffer 1913
Epyris Westwood 1832 = Muellerella Saussure 1892 = Parepyris Kieffer 1913 = Psilepyris Kieffer 1913 = Dolus Motschulsky 1863 = Calyoza Westwood 1837 = Paracalyoza Cameron 1909 = Artiepyris Kieffer 1913) = Calyozella Enderlein 1920 = Callioza Agassiz 1846 (Unjustified Emendation) = Pseudocalyoza Turner 1915 = Homoglenus Kieffer 1904
Holepyris Kieffer 1905 =Rysepyris Kieffer 1906 = Misepyris Kieffer 1913 = Parepyris Brethes 1913
Isobrachium Foerster 1856
Laelius Ashmead 1893 = Allepyris 1905 = Paralaelius Kieffer 1905
Leptepyris Kieffer 1914
Neodisepyris Kurian 1955
Orientepyris Terayama 1994
Planepyris Kieffer 1905
Prolaelius Kieffer 1905
Neurepyris Kieffer 1905
Melanepyris Kieffer 1913
Pristepyris Kieffer 1905
Rhabdepyris Kieffer 1904
Subgenus Rhabdepyris s. str. Kieffer 1904
Subgenus Trichotepyris Kieffer 1906
Subgenus Chlorepyris Kieffer 1913
Trachepyris Kieffer 1905 = Pristobethylus Kieffer 1905 = Acanthepyris Kieffer 1912
Triglenus Marshall 1905
Trissepyris Kieffer 1905
Xenepyris Kieffer 1913

Tribe Cephalonomiini

Acephalonomia Sterjcek 1991
Cephalonomia Westwood 1833 = Holopedina Foerster 1850 = Cephaloderma Hoffer 1936 = Cephalomia Kirchner 1867 (Unjustified Emendation)
Islaelius Richards 1952

Plastanoxus Kieffer 1905 = Snappania Hedqvist 1975
Prorops Waterston 1923

Tribe Sclerodermini

Allobethylus Kieffer 1905 = Nesepyris Bridwell 1920
Alongatepyris Azevedo 1992
Bethylopsis Fouts 1939
Chilepyris Evans 1964
Glenosema Kieffer 1905 = Arysepyris Kieffer 1905 = Rysepyris Kieffer 1906
Lepidosternopsis Ogloblin 1954
Sclerodermus Latreille 1809 = Scleroderma Oken 1817 (Unjustified emendation) = Sclerochroa Foerster 1850 = Neoscreroderma Kieffer 1905
Discleroderma Kieffer 1904
Ateleopterus Foerster 1856
Thlastepyris Evans 1973
Nothepyris Evans 1973
Scaphepyris Kieffer 1905

Subfamily Mesitiinae
= Subfamily Mesitinae (Unjustified Emendation)

Anaylax Moczar 1970
Bradepyris Kieffer 1905
Clytrovorus Nagy 1972
Codorcas Nagy 1972
Heterocoelia Dahlbom 1854
Incertosulcus Moczar 1970
Mesitius Spinola 1851
Metrionotus Moczar 1970
Pilomesitius Moczar 1970
Parvoculus Moczar 1970
Pseudomesitius Duchaussoy 1916
Pycnomesitius Moczar 1971
Sulcomesitius Moczar 1970 = Topcobius Nagy 1972

Subfamily Galodoxinae

Galodoxa Nagy 1974

Subfamily Bethylinae

Bethylus Latreille 1802 = Perisemus Foerster 1856 = Episemus Thomson 1862 = Anoxus Thomson 1862 = Anoxys Dalla Torre 1898 (Unjustified Emendation) = Digoniozus Kieffer 1905
Eupsenella Westwood 1874 = Lytopsenella Kieffer 1911
Goniozus Foerster 1856 = Parasierola Cameron 1883 = Progoniozus Kieffer 1905 = Perisierola Kieffer 1914
Odontepyris Kieffer 1904 = Trissomalus Kieffer 1905 (Provisional)
Prosierola Kieffer 1905
Sierola Cameron 1881

Subfamily incertae sedis

Foenobethylus Kieffer 1913

Genera transferred to the Tiphiidae
Bruesiella Mann 1914 [Evans 1964]
Dryinopsis Brues 1910 [Reid 1941, Evans 1964]

Genera transferred to the Rhopalosomatidae
Saphobethylus Kieffer 1911 [Turner & Waterston 1917]
Algoella Kieffer 1914 [= Algoa Brues 1910, nec Castelnau 1961; Brues 1922]
Harpagocryptus Perkins 1908 [Brues 1922, Reid 1941]

Genera transferred to the Chrysididae
Godfrinia Kieffer 1911 [Reid 1941]
Promesitius Kieffer 1905 [Reid 1941]
Lustrina Kurian 1955 [Kimsey & Bohart 1990]
Laccomerista Cameron 1910 [Evans 1910, Kimsey & Bohart 1990]

Genus transferred to the Scolebytidae
Clystopsenella Kieffer 1911 [Evans 1963]

Genus transferred to the Scelionidae
Mantibaria Kirby 1900

Genus transferred to the Sierolomorphidae
Proscleroderma Kieffer 1905 [Nagy 1990]

Genus transferred to the Formicidae
Neoclystopsenella Kurian 1955 [Brown 1987]

Genera which cannot be recognized
Omaloderus Walker 1843 = Homaloderus (laspus) Dalla Torre 1898 [Evans 1964]
Xestobethylus Cameron 1909 [Evans 1964]

Appendix IV. Fossil records of Bethylidae.

#Subfamily Pritopristocerinae	
#Archaepyris minutus Evans 1973	Upper Cretaceous
#Bethylitella cylidrella Brues 1933	Miocene
#Bethylopteron ambignum Brues 1933	Lower Oligocene
#Palaeobethyloides longiceps Breus 1933	Lower Oligocene
#Protopristocera sucini Breuse 1923	Lower Oligocene
Subfamily Pristocerinae	
Apenesia electriphila Cockerell, 1917	
#Parapristocera skwarrae Breus 1933	Lower Oligocene
#Pristapenesia primaeva Breus 1933	Lower Oligocene
Pseudisobrachium oligocenicum Theobald 1937	Oligocene
Subfamily Epyrinae	
#Celonophamia taimyria Evans 1973	Upper Cretaceous
#Ctenobethylus succinalis Breus 1939	Oligocene
Epyris kiefferi (Brues 1933)	Oligocene
E. atavellus Cockerell 1920	Miocene
E. deletus Breus 1910	Miocene
E. inhabilis (Breus 1923)	Oligocene
E. longipes (Breus 1923)	Oligocene
E. bifossatus (Breus 1939)	Lower Oligocene
E. rectinervis (Cockerell 1921)	Oligocene
E. tenellus Stotz 1938	Oligocene

Holepyris dubius (Breus 1933)	Lower Oligocene
H. minor (Breus 1933)	Lower Oligocene
H. planiceps Breus 1933	Lower Oligocene
H. precursor Breus 1933	Lower Oligocene
H. robustus (Breus 1933)	Lower Oligocene
Isobrachium concaptum Breus 1933	Lower Oligocene
I. invelatum Breus 1933	Lower Oligocene
Laelius nudipennis Brues 1933	Lower Oligocene
L. pallidus Breus 1933	Lower Oligocene
#Messoria copalina Menuier 1916	
Rhabdepyris elatus Breus 1933	Lower Oligocene
R. setosus Breus 1933	Lower Oligocene
Sclerodermus quadridentatus Cockerell 1917	Miocene
Subfamily Mesitiinae	
Uromesitius caudatus Breus 1933	Lower Oligocene
Subfamily Bethylinae	
Goniozus contracta Breus 1933	Lower Oligocene
Prosierola submersa Breus 1933	Lower Oligocene
Eupsenella crastina (Breus 1923)	Oligocene
E. setigera (Breus 1923)	Oligocene
E. simplex (Breus 1923)	Oligocene
Genera of Uncertain Placement	
#Palaeobethylus brevicollis Breus 1933	Lower Oligocene

#P. politus Breus 1923 Lower Oligocene

#P. longicollis Breus 1923 Lower Oligocene

#: Genus or subfamily is known from fossil only.

Appendix V. Results of the bootstrap analysis.

In order to assess the robustness of my results, I conducted a bootstrap analysis of my data, using the procedure available in PAUP. This was carried out using the mathematically approximate, but much faster, default option of heuristic search. One thousand (1,500 in the data matrix of Pristocerinae) bootstrap replicates using the 50% majority rule were performed. The results are summarized in Figs. A-J.

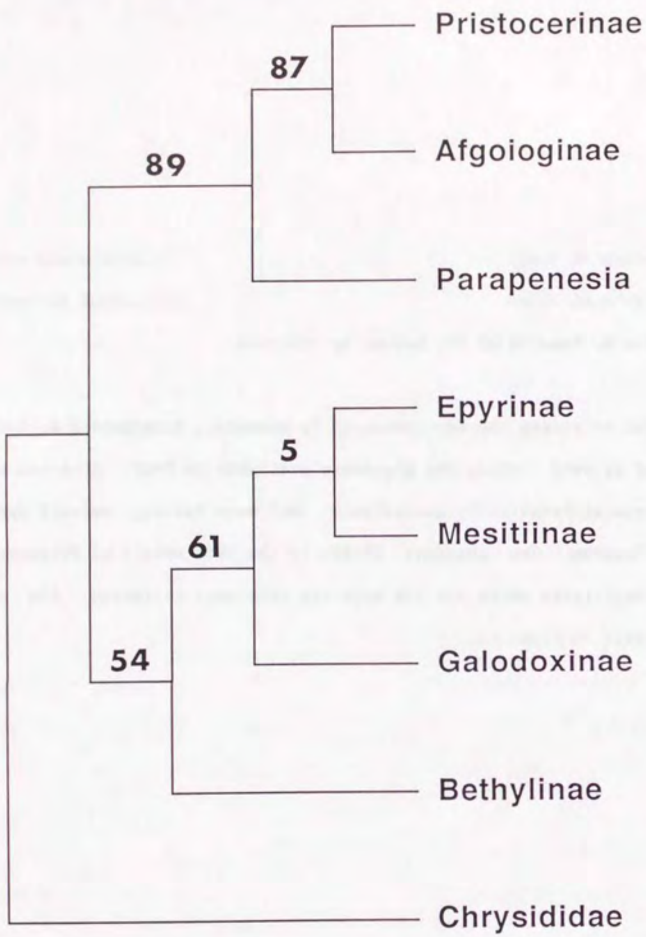

Fig. A. The bootstrap tree using the data matrix of 1st subfamily level analysis.

Outgroup: Chrysididae.

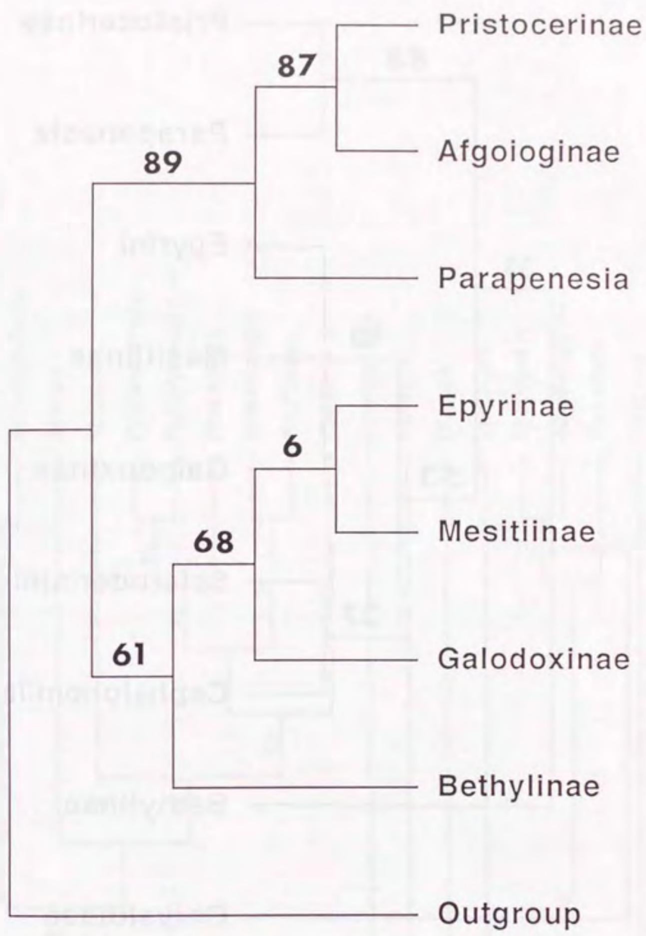

Fig. B. The bootstrap tree using the data matrix of 1st subfamnily level analysis.

Outgroup: hypothetical ansestor.

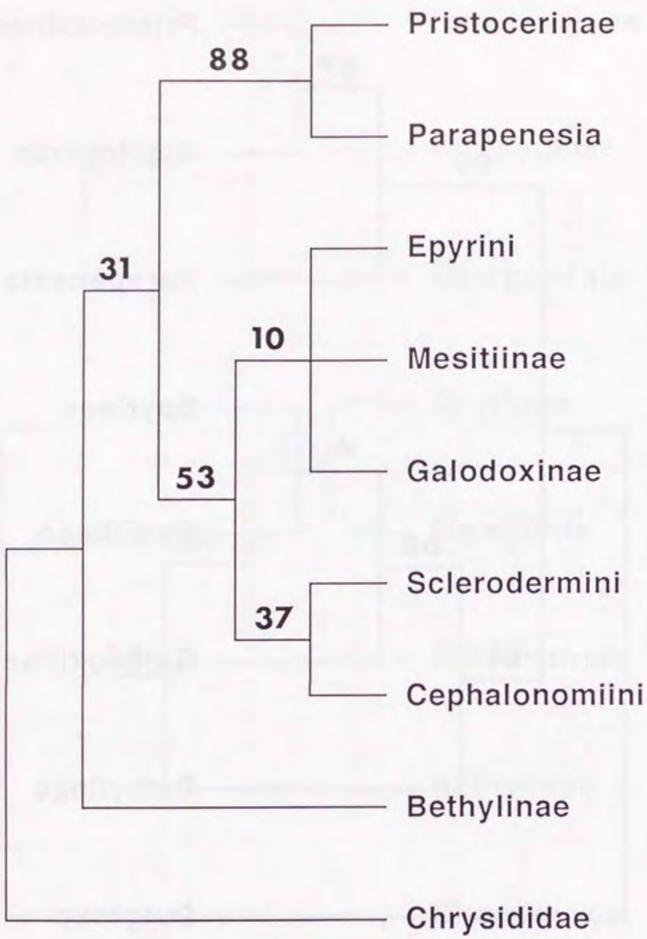

Fig. C. The bootstrap tree using the data matrix of 2nd subfamily level analysis.

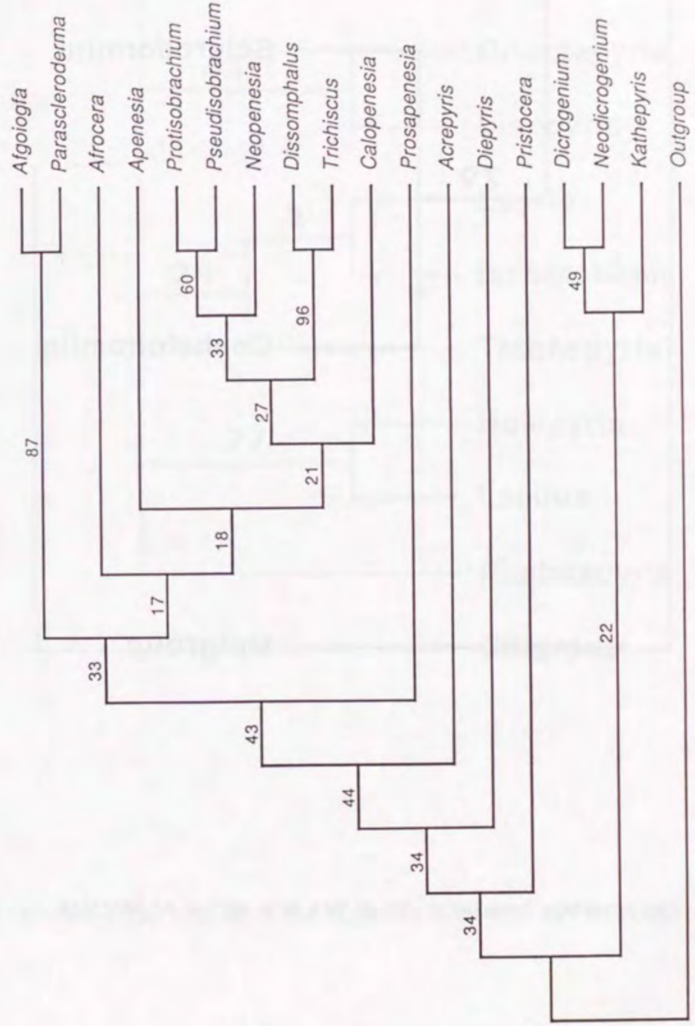

Fig. D. The bootstrap tree using the 18 genera data matrix of Pristocerinae.

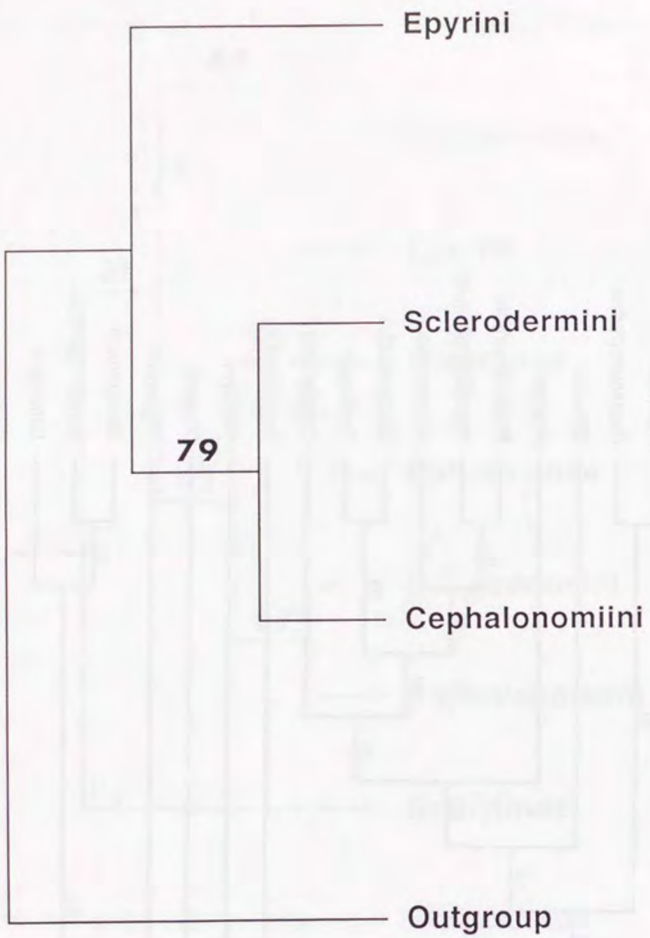

Fig. E. The bootstrap tree using the tribes data matrix of Epyrinae.

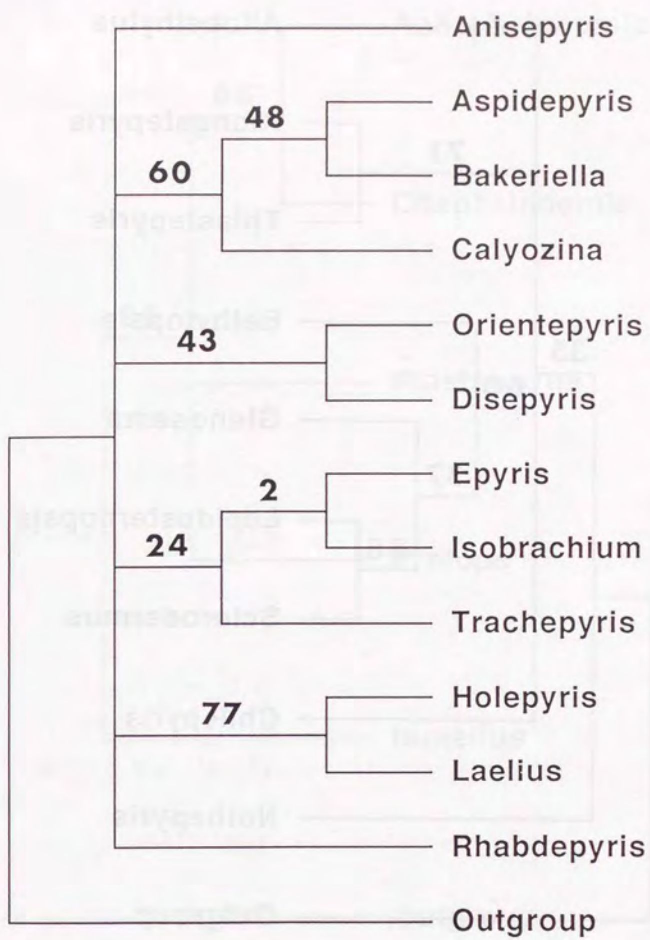

Fig. F. The bootstrap tree using the 12 genera data matrix of Epyrini.

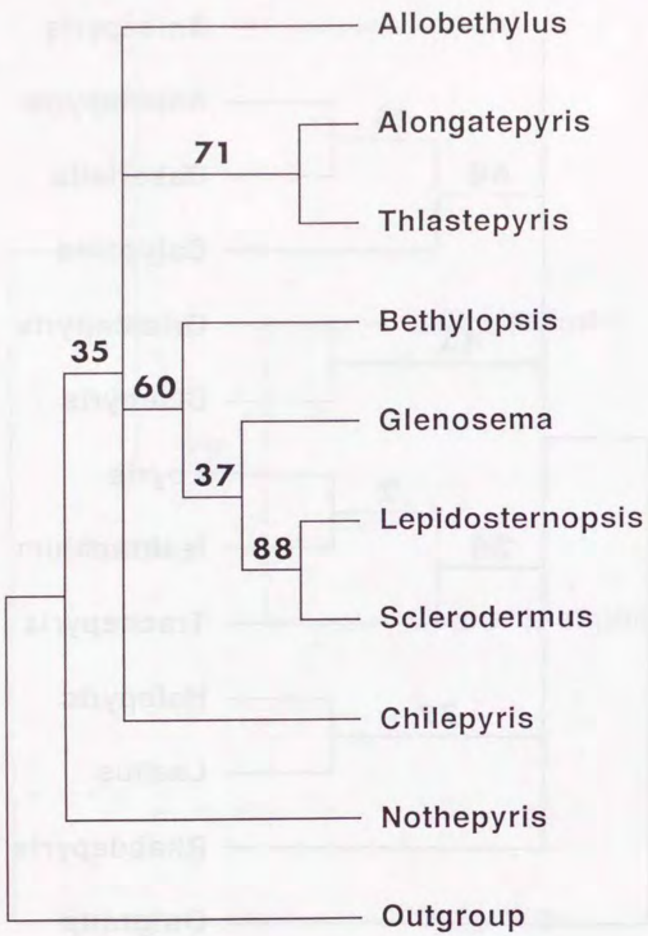

Fig. G. The bootstrap tree using the 9 genera data matrix of Sclerodermini.

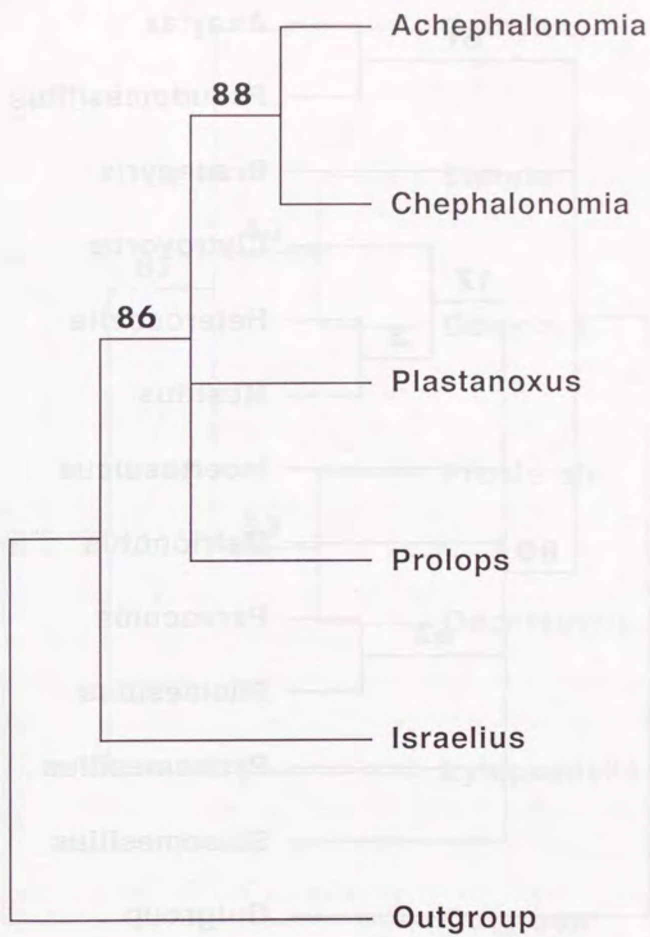

Fig. H. The bootstrap tree using the 5 genera data matrix of Cephalonomiini.

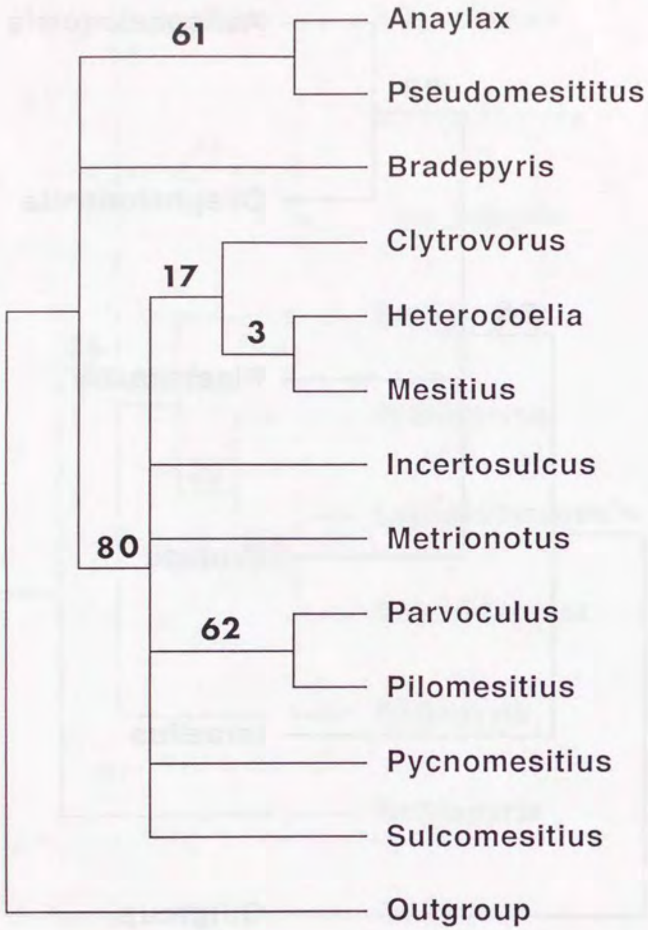

Fig. I. The bootstrap tree using the 12 genera data matrix of Mesitiinae.

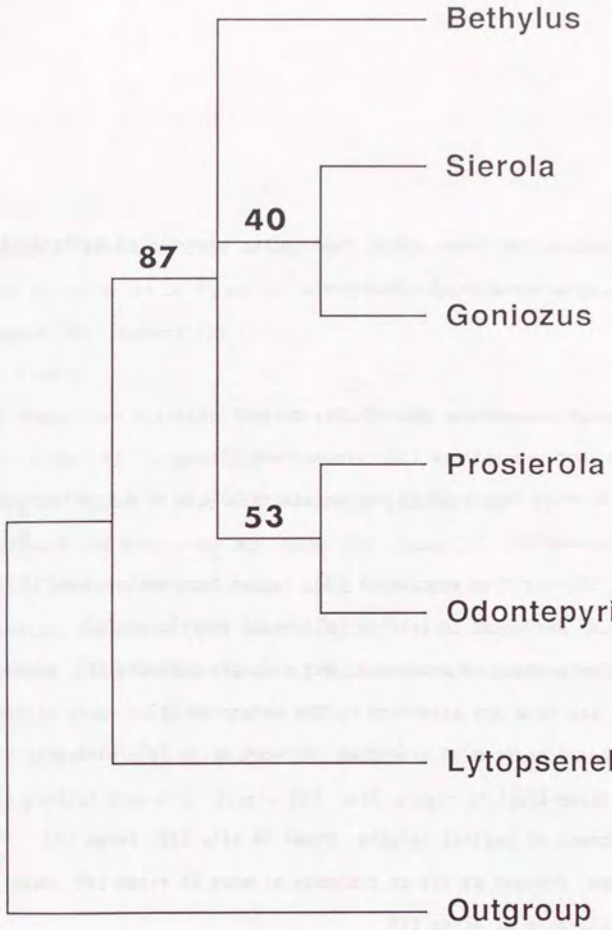

Fig. J. The bootstrap tree using the 6 genera data matrix of Bethylinae.

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

1. Strong sexual dimorphism. Absent [0]; present [1].
2. Head form. Not prognathous [0]; prognathous [1].
3. Clypeus. Without longitudinal median carina [0]; with a longitudinal median carina [1].
4. Pronotum. Shorter than mesoscutum [0]; longer than mesoscutum [1].
5. Metasternum. Not broad anteriorly [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 segment of gastral tergite. 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 margin near the base of the hind wings. Absent [0]; present [1].
12. Claws. Weakly to moderately curved [0]; strongly curved [1].

Male

13. Anterior portion of propoleuron. Short [0]; elongate [1].

14. Metanotum. Developed [0]; reduced [1].
15. Small emargination or fovea on the anterior portinn of metanotum. Absent [0]; present [1].

Female

16. Body shape. Not flattened [0]; extremely flat dorsolaterally [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. Lateral portions of mesoscutum. Large [0]; reduced [1].
21. Metanotum. Developed [0]; reduced [1].
22. Propodeum. Long, lateral sides at most moderately convex [0]; broad, lateral sides strongly convex [1].
23. Forth gastral sternite. Simple [0]; with a pair of large cornicles [1].
24. Fifth gastral sternite. Simple [0]; with a pair of large cornicles [1].

Table 2. Character coding for the analysis of the subfamilial relationships.

? = states unknown, P = polymorphic.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24
Pristocerinae	1	1	1	0	1	0	0	0	0	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	0	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	1	0	1	1	0	1	0	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	1	0	0	0	?	?	?	0	?	?	?	0	0	1	1	1	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

Table 3. Character coding for the 2nd analysis of the subfamilial relationships.

? = states unknown, P = polymorphic.

As for characters 1-24, see Table 1. Character 25: Eyes with lateral sides on head in male [0], forward in male [1]. Character 26: Propodeal fovea absent [0], present [1]. Character 27: Median carina of clypeus of male produced [0], truncated [1]. Character 28: Submedian cell of fore wings fully formed [0], obsolute or absent [1]. Character 29: Prostigma absent or smaller than the pterostigma [0], prostigma developed and larger than the pterostogma, pterostigma small, obsolute or absent [1].

Taxon	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
Pristocerinae	1	1	1	0	1	0	0	0	0	1	0	0	1	0	1	P	1	0	0	1	1	0	0	0	0	0	P	0	0
Epyrini	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Sclerodermini	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	P	0	0	0	0	0	0	0	0	1	0	1	P	0
Cephalonomiini	0	1	1	1	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	P	P
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	0	0	0	0	0
Bethylinae	0	1	1	0	1	0	0	0	1	0	1	1	0	1	0	0	0	0	0	0	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	0	0	0	0	0
Parapenesia	?	1	1	0	1	0	0	0	?	?	?	0	?	?	?	0	0	1	1	1	1	1	0	0	?	0	1	?	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	0	0	0	0	0

Table 4. Remarkable characters and their states in the 26 genera of Epyrinae.

1. Propodeal fovea. Absent [0]; present [1].
2. Position of eyes. Lateral [0]; forward [1].
3. Number of antennal segments. 13[0]; 12[1]; 10[2].
4. Median lobe of clypeus. Projecting [0]; truncate [1].
5. Occipital carina. Present [0]; absent [1].
6. Number of labial palpal segments. 3[0]; 2[1]; 1[2].
7. Number of maxillary palpi segments. 6[0]; 5-4[1]; 3[2].
8. Notauli. Present [0]; absent [1].
9. Transverse carina of propodeum in female. Present [0]; absent [1].
10. Lateral carinae of propodeum. Present [0]; absent [1].
11. Median carina of propodeum. Present [0]; absent [1].
12. Pterostigma. Large [0]; obsolete or absent [1].
13. Median vein. Present [0]; absent [1].
14. Anal vein. Present [0]; absent [1].
15. Costa of forewing. Present [0]; absent [1].
16. Prostigma. Absent [0]; present [1].
17. Outer margin of forewing. Dully angulated [0]; rounded [1].
18. Anterior margin of forewing. Straight [0]; weakly concave near the pterostigma [1].
19. Position of pterostigma. Almost at middle from the base [0]; near the base [1].
20. Radial vein. Long [0]; short [1]; absent [2].
21. Condition of wings in female. Fully winged [0]; brachypterous [1]; apterous [2].
22. Two different wing forms in female within a species. Absent [0]; present (fully winged and apterous or brachypterous) [1].

Table 5. Character matrix among the 26 genera of Epyrinae.

			1				2		
	12	3456	78901	23	4	5678	90	1	2
Epyrini									
Anisepyris	10	0000	00000	00	0	0000	00	0	0
Aspidepyris	10	0000	00000	00	0	0000	00	0	0
Bakeriella	10	0000	00000	00	0	0000	00	0	0
Caliozina	10	0000	00000	00	0	0000	00	0	0
Orientepyris	10	0000	00000	00	0	0000	00	0	0
Rhabdepyris	10	0000	00000	00	0	0000	00	0/10	
Epyris	10	0000	00000	00	0	0000	00	0/10	
Isobrachium	10	000?	?1000	00	0	0000	00	0	0
Trachepyris	10	0000	00000	00	0	0000	01	0	0
Disepyris	10	0000	00000	00	0	0100	01	0	0
Holepyris	10	0000	01000	00	0	0001	10	0/10	
Laelius	10	0000	01000	00	0	0011	11	0	0
Sclerodermini									
Nothepyris	01	1100	00000	00	0	?010	00	0	0
Allobethylus	01	1101	00000	00	0	0010/100		0	0
Bethylopsis	01	1100	01001	??	?	????	??	1	0
Chilepyris	01	1100	01000	00	0	0000	12	0	0
Glenosema	01	100?	?1001	10	0	1011	10	0/10	
Thlastepyris	01	1100	01000	10	1	1111	11	0	0
Alongatepyris	01	1100	01000	10	1	1111	11	0	0
Lepdosternopsis	01	1100	11111	??	?	????	??	1	0
Sclerodermus	01	1100	11111	00	0/11010		12	2	1
Chephalanomiini									
Islaelius	00	1111	10000	00	0	1011	10/1	0	0
Plastanoxus	00	1111	10000/100/11			1111	10	0	0
Chephalonomia	00/1111/210000/111				1	1011	22	2	1
Achephalonomia	00	112?	?0000	11	1	1011	22	0/11	
Prorops	00	1112	21111	01	1	1111	10	0	0

Table 6. Characters and their states used in the analysis of Pristocerinae.

0, plesiomorphic; 1 & 2, apomorphic.

1. Mandibles. More or less triangular [0]; sickle-shaped [1].
2. Basal tooth of mandibles. Simple [0]; directed inward [1].
3. Anterior border of clypeus. Truncate [0]; produced and mostly triangular [1]; strongly produced and trapezoidal [2].
4. Lateral borders of anterior clypeal margin. Not remarkably produced [0]; strongly produced [1].
5. Frontal portion of head. Not obliquely truncated [0]; obliqueuly truncated [1].
6. Antennal sockets: Developed [0]; reduced [1].
7. Antennal funicular segments. Without long erect hairs [0]; with long erect hairs [1].
8. Eyes. Hairless or only with short hairs [0]; with long erect hairs [1].
9. Ocellar triangule. Forming a regular triangle and situated far from the occipital border [0]; flat and situated well near the occipital border [1].
10. Occipit. Shorter [0], remarkably elongate [1].
11. Occitital carina. Complete [0]; obsolete dorsally [1].
12. Genal areas. Simple [0]; with a pair of spines [1].
13. Head. Longer than wide [0]; remarkably wider than long [1].

14. Anterior portion of propleuron. Shorter [0]; elongate [1].
15. Acetabular carina of mesonotum. Present [0]; absent [1].
16. Notauli. Present and distinct [0]; absent or obsolete [1].
17. Scutellar disc. Moderate in size [0]; elongate [1].
18. Anteromedian portion of Metanotum. Without small emargination or fovea [0]; with a small emargination or fovea [1].
19. Propodeum. Shorter [0]; elongate [1].
20. Propodeum. Not produced [0]; produced dorsally [1].
21. Gaster. Usual [0]; elongate [1].
22. Gaster. Usual [0]; broaden [1].
23. 2nd gastral tergite. Simple [0]; structured [1].
24. Posterior border of 2nd gastral tergite. Without modification [0]; strongly concave leterally [1].
25. 3rd gastral tergite. Simple [0]; structured [1].
26. Middle tibiae. Without spine [0]; with strong spines at outer margin [1].
27. Middle tibial spures: Same length [0]; short and long respectively [1].
28. Outer margin of forewings. More or less dully angulate [0]; rounded [1].
29. Costa. Present [0]; obsolete [1].
30. Metacarpus vein. Present [0]; absent [1].
31. Pterostigma. Present [0]; absent [1].
32. Pterostigma. Usual in size [0]; remarkably large and broad [1].
33. Radial vein. Distinct [0]; thin and weak [1].
34. Transverse cubital vein arising from the radial vein. Present [0]; absent

[1].

35. Basal vein. Arising near pterostigma [0]; far from the level of pterostigma [1].

36. Transverse median vein. Simple [0]; strongly curved to the base [1].

37. Cubital vein. Indistinct or not reaching the wing margin [0]; weak but distinct and reaching the wing margin [1].

38. Subdiscoidal vein. Indistinct or not reaching the wing margin [0]; weak but distinct and reaching the wing margin [1].

39. Median vein of hind wing. Obsolete or absent [0]; weak but distinct and reaching the wing margin [1].

40. Subgenital plate. With a single stalk [0]; with three stalks [1].

41. Subgenital plate. Simple [0]; deeply divided into two parts [1].

42. Lateral borders of subgenital plate. Convex or straight [0]; concave [1].

43. Posterior border of subgenital plate. Without process [0]; with a process [1].

44. Parameres. Broad [0]; long and thin, forming a shaft at the middle [1].

45. Parameres. With a single lobe [0]; divided into 2 separate arms [1].

46. A lobe at inner part of parameres. Absent [0]; present [1].

47. A lobe at posterior part of parameres. Absent [0]; Present [1].

48. Aedoeagus. Simple [0]; consisting of 3 distinct sets of valves [1].

49. Cuspis. Simple [0]; divided into two separate armes [1].

Table 7. Character coding for the analysis of the generic relationships in the subfamily Pristocerinae.

? = states unknown, P = polymorphic.

Taxon	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
Afgoiogfa	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
Parascleroderma	0	0	1	0	0	0	0	0	1	0	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0
Dicrogenium	1	0	0	0	0	0	0	0	0	0	1	1	0	1	1	0	0	1	0	0	0	0	0	0	0
Neodicrogenium	0	1	0	0	0	0	0	0	0	0	0	1	0	1	?	0	0	1	0	0	0	0	0	0	0
Diepyris	1	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Kathepyris	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	1	0	0	0	0	0
Acrepyris	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Pristocera	0	1	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Afrocera	0	0	1	0	0	0	0	0	0	1	0	0	0	1	?	0	1	1	1	0	1	0	0	0	0
Apenesia	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Protisobrachium	0	0	1	1	0	0	0	1	0	1	0	0	0	1	0	1	0	1	1	0	0	0	0	0	0
Pseudisobrachium	0	0	2	0	0	0	0	1	0	P	1	0	0	1	0	1	0	1	1	0	0	0	0	0	0
Prosapenesia	0	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Dissomphalus	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	1	0	0
Trichiscus	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	1	1
Calopenesia	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0
Neopenesia	0	0	1	0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	0
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

Taxon	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49
Afgoiogfa	0	0	0	0	1	0	0	0	?	0	0	1	1	1	1	0	0	0	0	0	1	0	0	0
Parascleroderma	0	0	0	0	1	0	0	0	P	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0
Dicrogenium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Neodicrogenium	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Diepyris	0	0	0	0	1	0	0	0	0	0	0	1	1	1	0	1	0	0	1	0	0	0	0	0
Kathepyris	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0
Acrepyris	0	0	0	0	0	0	0	0	1	0	0	1	P	1	0	0	0	0	0	0	0	0	1	0
Pristocera	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	1	0	0	P	0	0	0	0	0
Afrocera	0	0	0	0	0	0	0	0	1	0	0	1	1	1	?	?	0	0	0	0	0	1	0	0
Apenesia	0	0	0	0	0	0	0	0	1	P	0	1	1	1	0	0	0	0	0	0	0	0	0	1
Protisobrachium	0	1	0	0	0	0	0	0	1	1	0	1	1	1	?	0	0	0	0	0	0	0	0	0
Pseudisobrachium	0	1	0	0	0	0	0	0	1	0	0	1	1	1	1	0	0	0	0	1	0	0	0	0
Prosapenesia	1	0	0	0	1	0	1	1	1	0	P	1	1	1	1	0	0	1	0	0	0	0	0	0
Dissomphalus	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Trichiscus	0	1	1	0	0	0	0	0	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
Calopenesia	0	0	0	1	0	1	0	0	1	1	0	1	1	1	0	0	0	0	0	1	0	0	0	0
Neopenesia	0	1	0	0	1	0	0	0	1	1	0	1	1	1	1	0	1	0	0	0	0	0	0	0
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

Table 8. Characters and their states used at the tribe level analysis of Subfamily Epyrinae.

0, plesiomorphic; 1, apomorphic.

1. Antennal segments. 13 [0]; 12 or less [1].
2. Median lobe of clypeus. Projecting [0]; truncate [1].
3. Position of eyes in frontal view. Lateral sides [0]; forward [1].
4. Occipital carina. Present [0]; absent [1].
5. Maxillary palpi. With 6 segments [0]; less than 6 [1].
6. Labial palpi. With 3 segments [0]; less than 3 [1].
7. Notauli. Present [0]; absent [1].
8. Fovea of posterolateral corners of propodeum. Absent [0]; present [1].
9. Pterostigma. Developed [0]; obsolete or absent [1].
10. Annal vein. Present [0]; indistinct or absent [1].
11. Costa. Present [0], absent [1].
12. Transverse carina of propodeum. Present in female [0]; absent in female [1].

Table 9. Character coding for the analysis of the tribal relationships in the subfamily Epyrinae.

"P" indicates polymorphic.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12
Epyrini	0	0	0	0	0	0	0	1	0	0	0	0
Sclerodermini	0	1	1	P	P	0	P	0	0	0	P	P
Cephalonomiini	1	1	0	1	1	1	1	0	1	P	1	1
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0

Table 10. Characters and their states used in the analysis of tribe Epyrinae.

0, plesiomorphic, 1 & 2, apomorphic.

1. Mandibles. Short [0]; elongate with a shaft [1].
2. Lateral lobes of clypeus. Not developed [0]; developed [1].
3. Antennal scapes. Without strong setae [0]; setose [1].
4. Eyes. Smaller, less than 0.8 x head length [0]; larger, more than 1.0 x head length [1].
5. Occipit. Without strong setae [0]; with strong setae [1].
6. Carinae around eyes. Absent [0]; present [1].
7. Base of clypeus. Not overhung by the antennal socket [0]; overhung [1].
8. Posterolateral borders of head. Not broaden [0]; broaden [1].
9. Occipital border of head. More or less with angles [0]; round, not forming an angle [1].
10. Pronotum. longer than wide [0]; distinctly wider than long [1].
11. Pronotum. Less than 1.3 x wider than long [0]; more than 1.4 x wider than long [1].
12. Anterodorsal border of pronotum in lateral view. Roundly sloped [0]; forming right angle [1].
13. Pronotal disc. Widest at posterior most [0]; widest at anterior most [1].

14. Posterior border of pronotal disc. Almost straoght to weakly concave [0]; U-shaped [1].
15. Pronotal disc. Without emargination [0]; with a emargination [1].
16. Longitudinal median carina on pronotal disc. Absent [0]; present [1].
17. Posterior portion of pronotal disc. Without transverse furrow [0]; with a transverse furrow [1].
18. Mesoscutum. Without transverse furrow at middle [0]; with a transverse furrow [1].
19. Notauli. Present [0]; obsolete or absent [1].
20. Scutellar pits. Absent, but with a groove at anterior portion of scutellum [0]; present [1].
21. Propodeal fovea of posterolateral corners. Absent [0]; present [1].
22. Posterolateral corners of propodeum. Only angulated [0]; with a blunt short tooth [1].
23. Anterior potion of fovea. Simple [0]; with a dull tooth [1].
24. Anterior margin of forewings. Straight [0]; weakly concave at pterostigma [1].
25. Pterostigma. Present at almost middle of wings [0]; situated near the base [1].
26. Radial vein. Long [0]; short [1].
27. Prostigma. Absent [0]; present [1].
28. Median vein. Arising from subcosta near pterostigma [0]; arising to sepatate to pterostigma [1].

29. Fore tarsus. Simple [0]. With a rake of stout bristle [1].

Table 11. Character coding for the analysis of the generic relationships in the tribe Epyrini.

"P" indicates polymorphic.

Taxon	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
Anisepyris	0	0	0	1	0	0	0	1	1	1	0	0	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Aspidepyris	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	1	1	0	0	0	0	0	0	0
Orientepyris	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	0	0	0	0	0
Bakeriella	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	2	1	1	0	0	0	0	0	0	0
Calyozina	0	0	0	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0
Disepyris	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	1	1	0	1
Epyris	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	P	P	0	1	1	0	0	0	0	0	0	0	0
Holepyris	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	p	1	0	1	0	0	1	1	0	0	1	0
Isobrachium	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	0	0	0
Laelius	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	1	1	1	1	0	0	0
Rhabdepyris	0	0	0	0	P	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0
Trachepyris	1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0	0	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	0

Table 12. Characters and their states used in the analysis of tribe Sclerodermini (based on the female).

0, plesiomorphic; 1, apomorphic.

1. Occiput of head. Shorter [0]; elongate [1].
2. Size of head. Smaller [0]; much wider than maximum width of alitrunk [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 intercaraly border of mandibles. Less than 7 [0]; 7 [1].
6. Inner 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].

Table 13. Character coding for the analysis of the generic relationships in the tribe Sclerodermini.

Taxon	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
Allobethylus	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
Alongatepyris	0	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1
Bethylopsis	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0
Chilepyris	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
Glenosema	1	0	0	1	1	1	1	0	0	0	1	1	0	0	0	0	0	0	0	1	0	0	2	0	0	0	0
Lepidosternopsis	0	0	0	0	0	0	1	0	1	1	1	1	1	0	1	1	0	1	1	1	1	1	2	0	0	0	0
Nothepyris	0	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Sclerodermus	0	0	0	0	0	0	1	0	0	1	1	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0
Thlastepyris	1	0	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	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

Table 14. Characters and their states used in the analysis of tribe Chephalonomiini.

1. Maxillary palpi. with 6 segments [0]; with 5 or 4 segments [1]; with 3 segments [2].
2. Labial palpi. With 3 segments [0]; 2 segments [1]; with 1 segment [2].
3. Antennal segments. 13 [0]; 12 [1]; 10 [2].
4. Frons of head. Simple [0]; produced below into bifid process [1].
5. Eyes. Flat to weakly convex [0]; moderately convex [1].
6. Parapsidal fullows. Present [0]; absent [1].
7. Scutellum. Not separated from scutum by a thin line [0]; separated from scutum by a thin line [1].
8. Scutellum. With a pair of pits or a transverse groove [0]; Without pits nor groove [1].
9. Pterostigma. Situated more than 1/3 of distance from the base [0]; situated near to the base of wing [1].
10. Prostigma. Relatively small [0]; large [1].
11. Radial vein. Present [0]; absent [1].
12. Basal vein. Narrow [0]; broad at midlength[1].
13. Anal vein. Present [0]; absent [1].
14. Paramere. Simple [0]; deeply divided into two arms [1].