

Phylogenetic Systematics of the Family Bethylidae (Insecta: Hymenoptera) Part II. Keys to subfamilies, tribes and genera in the world

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Abstract Keys to the 64 world genera in 6 subfamilies are provided. Genera *Homoglenus* and *Procaryoza* are synonymized with genera *Epyris* and *Anisepyris*, respectively. Genus *Bradepyrus* in the subfamily Epyrinae is transferred to the subfamily Mesitiinae.

Introduction

Following the new format of higher classification of the Family Bethylidae as shown in the part I, keys to the subfamilies, tribes, and genera of world Bethylidae are provided.

The style of keys follow that of Goulet and Huber (1993). Each set of entries is called a couplet. One to several characters are used separately in each couplet; opposing conditions for each character are given as 1a versus 1aa, b versus bb, and so on.

The zoogeographical distribution for each genus is shown in parentheses. Ambiguous genera are excluded in the keys to avoid the unnecessary confusions. The reasons for exclusion from the keys are, 1) lack of the types or voucher specimens, most of which were presumably lost, 2) insufficient information due to the poor original descriptions. The abbreviations of zoogeographic regions as follows: PAL, Palearctic Region; ORI, Oriental Region; AUS, Australian Region; ETH, Ethiopian Region; Nea, Nearctic; NET, Neotropical Region.

New synonymies and genus transferred

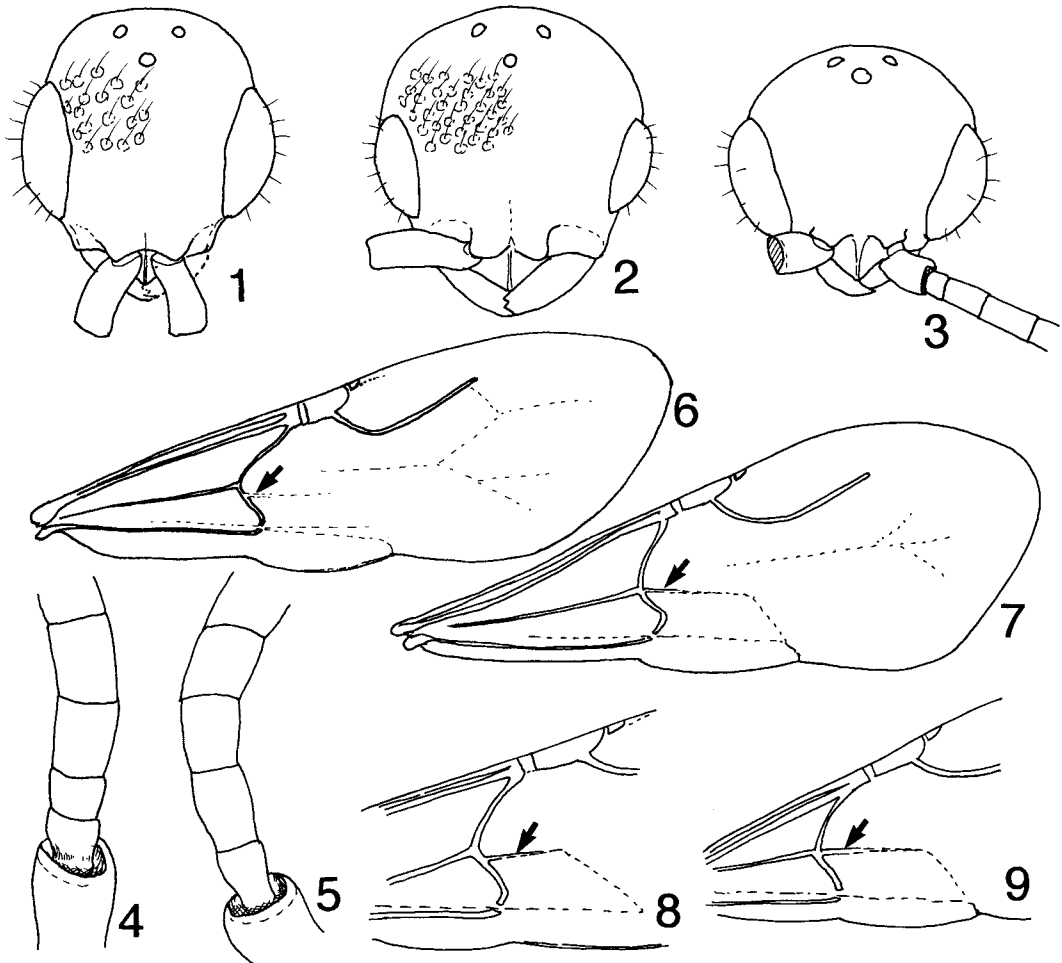
1. Genus *Epyris* Westwood, 1832. Genus *Homoglenus* Kieffer, 1905. **Syn. nov.**

The generic character of *Homoglenus* is the presence of nebulous m-cu vein of forewings (Figs. 7-9) and no other distinct character to separate it from *Epyris* is known. This condition should not be useful to separate the genera, since the vein is completely absent to weakly recognizable (Fig. 6) 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 seven species including a fossil 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.

2. Genus *Anisepyris* Kieffer, 1905. Genus *Procaryoza* Kieffer, 1905. **Syn. nov.**

The genus *Procaryoza* is distinguished from *Anisepyris* by the ramose antennae and the glabrous eyes (Figs. 10-12). However, there should not be reliable generic characters to define the genus as Krombein (1992) synonymized *Calyoza*, *Calyozella*, and *Paracalyoza* with *Epyris* and also Evans suggested (1964). *Procaryoza westwoodi* is transferred to the genus *Anisepyris*: *A. westwoodi* (Cameron) comb. nov.

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Received. Aug. 20, 2003



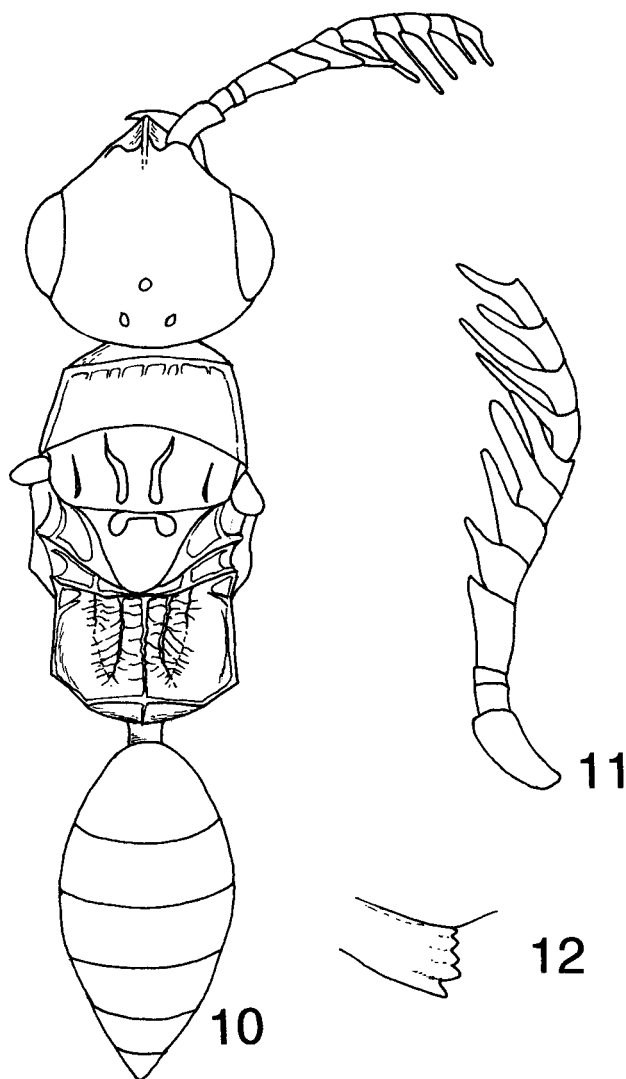
Figs. 1-9. *Homoglenus* spp. (1-5, 7-9) and *Epyris* sp. from Indonesia (6). 1, 4, 7, *H. punctatus* Kieffer (drawn from holotype); 2, 5, 8, *H. montanus* (Kieffer) (drawn from holotype); 3, 9, *H. indicus* (Kieffer) (drawn from holotype). 1-3, head, full face view; 4, 5, 2nd to 5th segments of antenna; 6-9, forewing, arrows indicate m-cu vein.

3. Genus *Bradepyrus* Kieffer, 1905

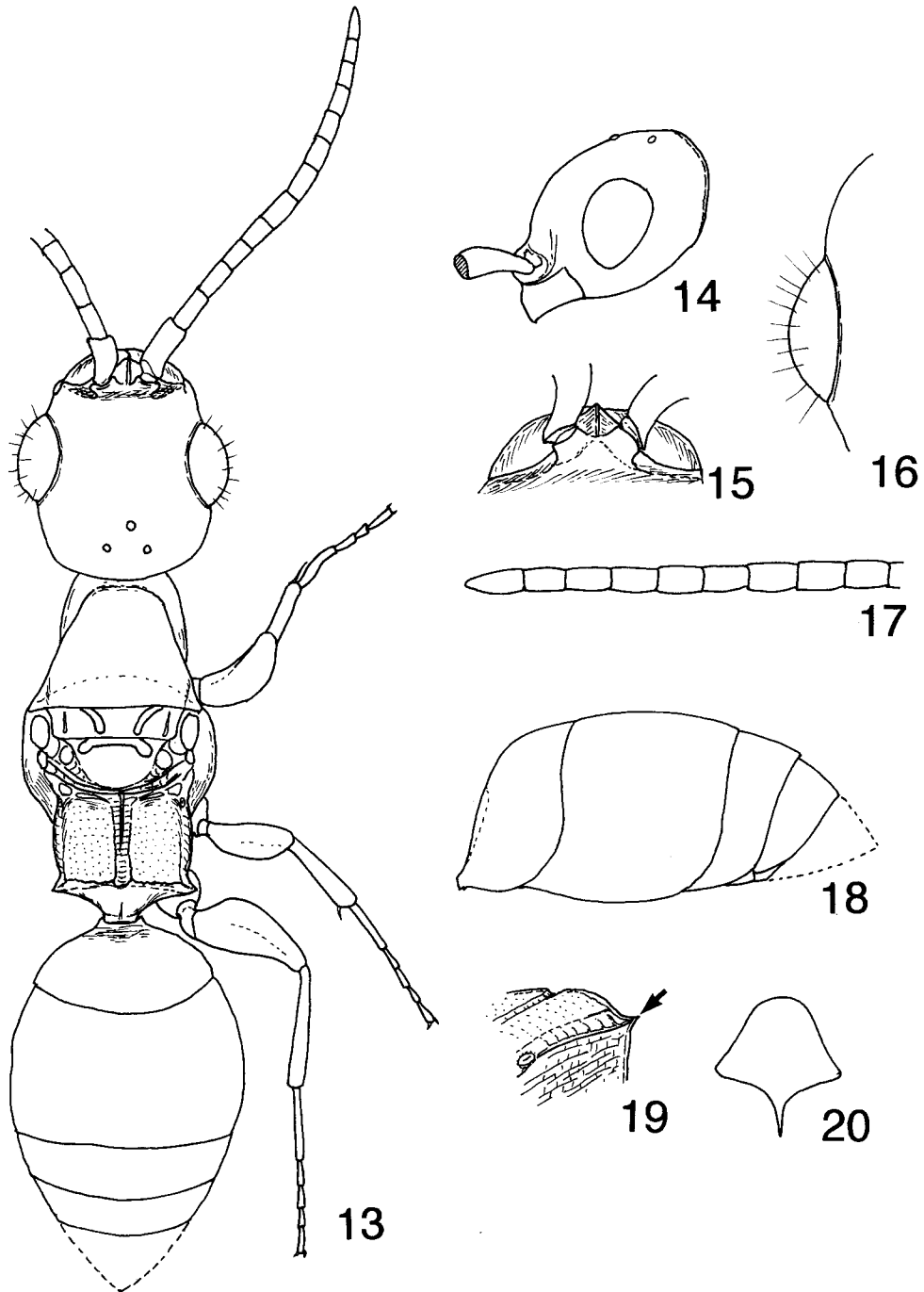
This genus consists of 5 species, of which a single species *B. inermis* Kieffer is examined (Figs. 13-20). The following characters suggest that this species belongs to the subfamily Mesitiinae though this has few punctures on the surfaces of head and mesosoma: 1) posterolateral corner of propodeum with a short, but distinct spine; 2) second gastral tergite large; 3) basal median portion of propodeum with a carina

which extends to the metanotum; 4) eye strongly convex and with erect hairs; 5) notauli large and strongly curved outward.

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



Figs. 10-12. *Procalyzoa westwoodi* (Cameron), drawn from holotype. 10, Body, dorsal view; 11, right antenna (apical segment missing); 12, right mandible.



Figs. 13-20. *Bradepyrus inermis* Kieffer, drawn from holotype. 13, Body, dorsal view; 14, head, lateral view; 15, clypeus; 16, eye; 17, antenna; 18, gaster, lateral view; 19, propodeal spine (arrow); 20, subgenital plate.

Outline of distribution pattern

Table 1 indicated the number of extant genera arranged by subfamily in six zoogeographical regions. The geographic distribution pattern of the Mesitiinae is unique in Bethyridae: 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. On the other hand, the subfamilies Bethylinae, Epyrinae and Pristocerinae have been recorded from all zoogeographical regions. Morphologically, Mesitiinae is compact and not diverse. These distributional and morphological features suggest that Mesitiinae is recently developed among the bethyrid subfamilies. It is interesting that this subfamily has the highest genus number in the Palaearctic Region, while the other subfamilies are prospering in the tropics.

Table 1. Number of genera in each subfamily by zoogeographical regions.

Figures in parentheses are endemic genera. In case where no published record is available but the author has reliable information, those are included in this table.

PAL: Palaearctic Region, ORI: Oriental Region, AUS: Australian Region, ETH, Ethiopian Region, NEA: Nearctic Region, NET: Neotropical Region.

Subfamilies	Region						Total
	PAL	ORI	AUS	ETH	NEA	NET	
Pristocerinae	6(1)	9(2)	1(0)	16(10)	5(0)	5(0)	20
Parapenesiinae				1(1)			1
Epyrinae	15(3)	23(6)	8(0)	15(0)	17(0)	19(2)	39
Galodoxinae		1(1)					1
Mesitiinae	10(6)	5(0)		6(2)			13
Bethylinae	5(0)	4(0)	4(1)	2(0)	3(0)	3(1)	7
Total	36(10)	43(9)	13(1)	40(13)	25(0)	27(3)	82

Key to subfamilies of Bethyridae

1a, Propodeum with distinct spines at dorsal posterolateral corners; b, second metasomal segment large, accounting for considerably more than half the length of the metasoma in dorsal view..... Mesitiinae

1aa, Propodeum without spine at dorsal posterolateral corners; bb, second metasomal segment much smaller, accounting for much less than half the metasoma in dorsal view 2

2a, Fifth metasomal sternite with a pair of large cornicles Galodoxinae [It contains a single genus *Galodoxa* Nagy [ORI; the Philippines] and is known from female only]

2aa, Fifth metasomal sternite simple, without modification 3

3a, Propodeum oval in dorsal view, distinctly wider than long; b, mesonotum and mesopleuron fused; c, mesonotum remarkably broaden, larger than pronotum Parapenesiinae [It contains a

single genus *Parapenesia* Kieffer [ETH; South Africa] and is known from female only]

3aa, Propodeum more or less rectangular; bb, mesonotum and mesopleuron not fused; cc, mesonotum not modified, smaller than pronotum 4

4a, Metanotum of male developed, scutellum and propodeum not nearly contact medially; b, metanotum with a small fovea at middle; c, females completely apterous; d, eye of females small to absent, eye height at most 0.25 times head width Pristocerinae

4aa, Metanotum much reduced in both sexes, the scutellum in contact with the propodeum medially or nearly so; bb, metanotum without fovea medially; cc, females fully winged, brachypterous, or apterous; dd, eye of females large; eye height more than 0.30 times head width..... 5

5a, Basal vein of forewing simple, not giving rise to a vein or stub; b, tarsal claws weakly to moderately curved; c, frons without longitudinal median carina or polished streak extending from clypeus.... Epyrinae

5aa, Basal vein of forewing giving rise to a vein; bb, tarsal claws strongly curved; cc, frons usually with a longitudinal median or polished streak extending for a short distance from clypeus..... Bethylinae

Key to genera of subfamily Pristocerinae

1a, Male; fully winged, tegla present..... 2

1aa, Female; apterous, tegla absent..... 18

(Male)

2a, Subgenital plate deeply divided into two lobes..... 3

2aa, Subgenital plate simple, posterior margin at most weakly concave, and never deeply divided into two lobes..... 7

3a, Head in lateral view with an acute spine at gena 4

3aa, Genal area without spine..... 5

4a, Mandible sickle-shaped *Dicrogenium* Stadelmann

[ETH]

4aa, Mandible more or less triangular with several teeth on masticatory margin; basalmost tooth directed inward *Neodicrogenium* Benoit [ETH]

5a, Mandible sickle-shaped, with 2 apical teeth only..... *Diepyris* Benoit [ETH]

5aa, Mandible triangular with 3-6 teeth; basalmost tooth directed inward 6

6a, Cubital and subdiscoidal veins of forewing reaching the wing margin; b, median vein of hindwing weak but distinct and reaching the wing margin..... *Kathepyris* Kieffer [ETH]

6aa, Cubital and subdiscoidal veins of forewing barely visible, not reaching the wing margin; bb, median vein of hindwing obscure to absent and not reaching the wing margin *Pristocera* Klug [ETH, ORI, PAL]

7a, Head truncated anteriorly; b, pterostigma exceptionally large; c, posterior margin of subgenital plate with a lamellar lobe *Prosapenesia* Kieffer [ETH]

7aa, Head not truncated anteriorly; bb, pterostigma moderate in size or absent; cc, posterior margin of subgenital plate simple, without a lamellar lobe 8

8a, Pterostigma obscure *Caloapenesia* Terayama [ORI]

8aa, Pterostigma distinct 9

9a, Second gastral tergite with a pair of spots, pits or depressions *Dissomphalus* Ashmead

[PAL, ORI, ETH, NEA, NET]

- 9aa, Second gastral tergite without modification 10
- 10a, Posterolateral margin of 2nd gastral tergite strongly concave; b, 3rd gastral tergite with a pair of spots *Trichiscus* Benoit [ETH]
- 10aa, Psterior margin of 2nd gastral tergite without modification; bb, 3rd gastral tergite simple, without spots..... 11
- 11a, Propodeum long, more than twice as long as wide; b, scutellar disc elongate, more than twice as long as wide; c, 1st gastral tergite long, more than 1.5 times as long as wide in dorsal view..... *Afroceras* Benoit [ETH]
- 11aa, Propodeum less than twice as long as wide; bb, scutellar disc shorter, less than twice as long as wide; cc, 1st gastral tergite less than 1.3 times as long as wide in dorsal view 12
- 12a, Anterior margin of clypeus trapezoidal and truncate apically; b, eye densely covered with hairs; c, genitalia with the parameres deeply divided into two lobes *Pseudisobranchium* Kieffer [PAL, ORI, ETH, NEA, NET]
- 12aa, Anterior margin of clypeus various, but not trapezoidal; bb, eye glabrous, or only scattered with short hairs; cc, genitalia with parameres not deeply divided into two lobes 13
- 13a, Notauli absent or nearly so 14
- 13aa, Notauli complete or nearly so 15
- 14a, Clypeus strongly produced; b, head longer than wide; c, pronotum usual in size *Protisobranchium* Benoit [ETH, ORI]
- 14aa, Anterior margin of clypeus not remarkably produced; bb, head wider than long; cc, pronotum extremely short *Neoapenesia* Terayama [ORI]
- 15a, Ocelli forming a flat triangle and situated almost near the occipital margin; b, postmarginal vein absent 16
- 15aa, Ocelli more or less forming a right triangle, situated far from the occipital margin; bb, postmarginal vein present 17
- 16a, Anterior margin of clypeus with a single median projection *Parascleroderma* Kieffer [PAL, ORI, ETH, NEA, NET]
- 16aa, Anterior margin of clypeus with 3 small projections *Afgoiogfa* Argaman [ETH]
- 17a, Median lobe of clypeus depressed near antennal insertion; b, basalmost tooth of mandible directed inward; c, cuspis simple, not divided nor setose; d, paramere consisting of 3 valves..... *Acrepyris* Kieffer [PAL, ORI, NEA, NET]
- 17aa, Median lobe of clypeus not depressed near antennal insertions; bb, basalmost tooth of mandible triangular, not directed inward, or mandible with an apical tooth only; cc, cuspis divided into two arms, dorsal arm simple and ventral one setose (except in a few species); dd, paramere simple, not consisting of 3 valves *Apenesia* Westwood [PAL, ORI, AUS, ETH, NEA, NET]
- (Female; known in 8 genera only)**
- 18a, Body extremely flat dorsoventrally 19
- 18aa, Body at most only weakly flattened 20
- 19a, Base of pronotum in contact with base of scutellum in dorsal view *Parascleroderma* Kieffer [PAL, ORI, ETH, NEA, NET]
- 19aa, pronotum not in contact with scutellum in dorsal view *Afgoiogfa* Argaman [ETH]
- 20a, Propodeum strongly constricted at its anterior end, where it forms a pair of small processes

- which embrace the apex of the elongate mesonotum. 21
- 20aa, Propodeum not constricted at anterior end, broadly in contact with the mesonotum. 22
- 21a, Tip of median lobe of clypeus truncate and thickened; b, eye absent *Prosapenesia* Kieffer [ETH]
- 21aa, Tip of median lobe of clypeus not thickened; bb, eye present *Pseudisobrachium* Kieffer [PAL, ORI, ETH, NEA, NET]
- 22a, Mesopleura very small in dorsal view; b, propodeum nearly parallel-sided, at most weakly constricted *Dissomphalus* Ashmead [PAL, ORI, ETH, NEA, NET]
- 22aa, Mesopleura developed; bb, propodeum with a distinct constriction at the spiracle 23
- 23a, Propodeal constriction strong; maximum width of propodeum at least twice at constriction; b, eye large, consisting of more than 15 facets (with a few exception) *Pristocera* Klug [PAL, ORI, ETH]/ *Acrepyris* Kieffer [PAL, ORI, NEA, NET]
- 23aa, Propodeal constriction less strong, maximum width of propodeum less than twice that at constriction; bb, eye small, consisting of less than 15 facets *Apenesia* Westwood [PAL, ORI, AUS, ETH, NEA, NET]

Genera excluded in this key: *Anisobrachiium* Kieffer, *Apristocera* Kieffer, *Usakosia* Kieffer.

Key to tribes and genera of Subfamily Epyrinae

- 1a, Antenna with 13 segments (2nd or 3rd segment very small but visible in some species); b, clypeus with a projecting median lobe; c, eye situated laterally on head; d, PF = 6-5, 3-2 .. 2 (Tribe Epyrini)
- 1aa, Antenna with 13 segments; bb, clypeus short, truncate apically; cc, eye situated forward on head; dd, PF = 6-5, 3-2 13 (Tribe Sclerodermini)
- 1aaa, Antenna with 12 segments or less; bbb, clypeus short, truncate apically; ccc, eye situated laterally on head (with a few exception in apterous females) 20 (Tribe Cephalonomiini)

(Tribe Epyrini)

- 2a, Scutellum with a pair of basal pits, either completely separate or connected by a very thin and shallow line 3
- 2aa, 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
- 3a, Antennal scape with strong setae; b, mandible long, forming a straight shaft with apical blunt tooth *Trachepyrus* Kieffer [ETH, ORI]
- 3aa, Antennal scape without distinct large seta; bb, mandible shorter, more or less triangular 4
- 4a, Pronotal disc transversely carinate in front; b, scutellar pit large *Bakeriella* Kieffer [NEA, NET]
- 4aa, Pronotal disc simple without a transverse carina anteriorly; bb, scutellar pit various 5
- 5a, Pronotum with strong anterior and lateral emarginations; b anterolateral corner of pronotum strongly angulate in dorsal view *Calyozina* Enderlein [ORI]
- 5aa, Pronotum not distinctly emarginate anteriorly and laterally; bb, anterolateral corner of pronotum rounded, not forming an angle in dorsal view 6
- 6a, Pronotum with its posterior margin simple, not prolonged backward so as to overlie the base of the mesoscutum 7
- 6aa, Pronotum with its posterior part elevated and prolonged arcuately backward so as to overlie the

base of the mesoscutum	<i>Aspidepyris</i> Evans [NET]
7a, Notauli absent	<i>Isobrachium</i> Förster [PAL, ORI, ETH]
7aa, Notauli present	<i>Epyris</i> Westwood [PAL, ORI, AUS, ETH, NEA, NET]
8a, Clypeus with 3 prominent lobes; b, basal vein reaching subcosta based of pterostigma by approximately the length of pterostigma	<i>Holepyris</i> Kieffer [PAL, ORI, AUS, ETH, NEA, NET]
8aa, Clypeus with only a median lobe developed; bb, basal vein reaching subcosta close to base of pterostigma	9
9a, Radial vein very short, at most slightly longer than basal vein	10
9aa, Radial vein long, distinctly longer than basal vein	11
10a, Large pterostigma present; b, prostigma present; c, fore tarsus with a lake	<i>Disepyris</i> Kieffer [PAL, ORI, ETH]
10aa, Pterostigma usual in size to small; bb, prostigma absent; cc, fore tarsus without lake	<i>Laelius</i> Ashmead [PAL, ORI, ETH]
11a, Pronotal disc without transverse carina in front, its sides not sharp or carinate	12
11aa, Pronotal disc with a transverse carina in front, its sides sharply set off and also carinate	<i>Anisepyris</i> Kieffer [NEA, NET]
12a, Transverse foveae present on posterior portion of pronotum; b, mesonotum with a transverse foveae at midlength; c, transverse groove of scutellum broad .. Undescribed genus [ORI; Terayama, in prep.]	
12aa, Transverse foveae absent on posterior portion of pronotum; bb, mesonotum without transverse foveae; cc, transverse groove of scutellum thin, but forming a deep groove	<i>Rhabdepyris</i> Kieffer [PAL, ORI, AUS, ETH, NEA, NET]

(Tribe Sclerodermini)

13a, Mandible thin and elongate, terminating in 2-3 teeth; b, head rectangular, with parallel sides in full face view	14
13aa, Mandible thick and broad; bb, head with more or less convex sides in full face view	15
14a, Wings fully developed; b, notauli distinct	<i>Allobethylus</i> Kieffer [PAL, ORI, AUS, NEA, NET]
14aa, Wings reduced, not reaching the posterior margin of propodeum; bb, notauli obscure	<i>Bethylopsis</i> Fouts [Marquesas Isls.; known from a female only]
14a, Gastral sternites 4-6 deeply bimarginate, with broad median apical plates and narrower lateral plates	<i>Lepidosternopsis</i> Ogloblin [NET, AUS]
14aa, Gastral sternites 4-6 simple or their margins shallowly sinuate	15
15a, Body extremely depressed dorsoventrally	16
15aa, Body at most weakly depressed dorsoventrally	17
16a, Costal vein and costal cell present; b, median vein dividing median and submedian cells; c, radial vein long	<i>Alongatepyris</i> Azevedo [NET]
16aa, Costal vein and costal cell obscure; bb, median vein short, median and submedian cells not completely separated by a median vein; cc, radial vein short	<i>Thlastepyris</i> Evans [NET]
17a, Mandible with 7 small teeth, upper margin denticulate in female; b, mandible with 5 teeth in male	<i>Glenosema</i> Kieffer [PAL, ORI, AUA, ETH, NEA]
17aa, Mandible with 2-3 teeth, upper margin without denticule in female; bb, mandible with 2-3 teeth in male	18
18a, Pterostigma large and circular; b, head very large, wider than long, much wider than maximum width of mesosoma in dorsal view; c, fully winged in both sexes	<i>Chilepyris</i> Evans [NET, AUS]

18aa, Pterostigma smaller and longer than wide; bb, head slightly wider than long, almost as long as wide or only slightly wider than maximum width of thorax; cc, winged and apterous forms present in both sexes but female usually apterous 19

19a, 4th and 5th gastral terga each with a pair of blunt teeth; b, parapsidal furrows well developed
Discleroderma Kieffer [ORI]

19aa, Gasteral terga simple, without tooth; bb, parapsidal furrows absent or only weakly indicated *Sclerodermus* Latreille [PAL, ORI, AUS, ETH, NEA, NET]

(Tribe Cephalonomiini)

20a, Antenna with 10 segments; b, winged and brachypterous forms present in both sexes
Acephalonomia Strejcek [PAL]

20aa, Antenna with 12 segments; bb, wings various 21

21a, Notauli present; b, anal vein present Undescribed genus [PAL; Terayama, in prep.]

21aa, Notauli absent; bb, anal vein various, absent to distinct 22

22a, Median vein broadest at the midlength; b, anal vein present *Israelius* Richards [PAL, ORI]

22aa, Median vein almost with the same width from anterior to posterior end, not broaden at the midlength, or median vein obscure; bb, anal vein obscure to absent 23

23a, Radial vein absent; b, wings frequently absent or much reduced *Cephalonomia* Westwood [PAL, ORI, NEA, NET]

23aa, Radial vein present at least in part; bb, wings always fully developed 24

24a, Frons produced below a nasus which overlies the antennal insertions and clypeus *Prorops* Waterston [PAL, ORI, NEA, NET]

24aa, Frons simple, not produced below *Plastanoxus* Kieffer [PAL, ORI, NEA]

Genera excluded in this key:

Tribe Epyrini; *Leptepyrus* Kieffer, *Neodisepyris* Kurian (Provisional; possible junior synonym of *Holepyris* Kieffer), *Planepyrus* Kieffer, *Neurepyris* Kieffer, *Melanepyrus* Kieffer (Provisional; possible junior synonym of *Epyris* Westwood), *Pristepyrus* Kieffer, *Triglenus* Marshall, *Trissepyris* Kieffer, *Xenepyrus* Kieffer.

Tribe Sclerodermini; *Ateleoapterus* Fouts, *Pararhabdepyris* Gorbatovsky.

Key to genera of subfamily Mesitiinae

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

1aa, Pronotum without longitudinal furrow 9

2a, Propodeum without sublateral carinae in both sexes and discal carinae in the female
Clytrovorus Nagy [PAL]

2aa, Propodeum with sublateral and discal carinae 3

3a, Median carina of clypeus dilated and spoon-like anteriorly *Mesitius* Spinola [PAL]

3aa, Median carina of clypeus simple, not dilated anteriorly 4

4a, First and 2nd gastral terga covered with pale yellowish gold and black hairs abundantly
Pilomesitius Móczár [ETH]

4aa, Gasteral terga with hairs sparsely to moderately 5

5a, Head much longer than wide; b, lateral margin of pronotum strongly concave in dorsal view; c, eye relatively small *Parvoculus* Móczár [ETH]

- 5aa, Head slightly longer than wide; bb, lateral margin of pronotum straight or at most weakly concave in dorsal view; cc, eye larger 6
- 6a, Median furrow of mesonotum indistinct or absent *Heterocoelia* Dahlbom [PAL, ETH, ORI]
- 6aa, Median furrow of mesonotum distinct, at least on the posterior portion 7
- 7a, Head and pronotum only superficially punctate, usually alitaceous-microreticulate ... *Metrionotus* Móczár [AL, ETH, PAL]
- 7aa, Head and pronotum deeply, densely or coarsely rugose, and extremely densely punctate 8
- 8a, Second gastral tergite deeply and densely punctate; interspaces narrower than punctures at the densest part *Pycnomesitius* Móczár [ETH, ORI]
- 8aa, Punctures on the 2nd gastral tergite much shallower; interspaces everywhere larger than punctures *Sulcomesitius* Móczár [PAL, ETH, ORI]
- 9a, Median carina and inner lateral carinae of propodeum parallel; b, outer lateral carina present only basally on propodeal disc *Pseudomesitius* Duchaussoy [PAL]
- 9aa, Median carina and inner lateral carinae of propodeum not parallel; bb, outer lateral carina of propodeal disc complete, reaching transverse carina 10
- 10a, Pronotum with punctures; b, mesonotum with a short longitudinal furrow *Incertosulcus* Móczár [PAL, ORI]
- 10aa, Pronotum smooth, without distinct punctures; bb, mesonotum without longitudinal furrow ...
....11
- 11a, Propodeal disc without lateral carinae *Bradepyrus* Kieffer [PAL]
- 11aa, Propodeal disc with distinct lateral carinae *Anaylax* Móczár [PAL]

Genus excluded in this key: *Codorcas* Nagy

Key to genera of subfamily Bethylinae

- 1a, Forewing with 6 closed cells; marginal and submarginal cells closed; b, notauli present 2
- 1aa, Forewing with at most 5 closed cells; closed marginal and submarginal cells absent; bb, notauli absent 3
- 2a, Propodeum with a median longitudinal carina; b, pterostigma broad; c, marginal cell shorter *Eupsenella* Westwood [AUS]
- 2aa, Propodeum without median longitudinal carina; bb, pterostigma thin; cc, marginal cell longer, the length more than 1.5 times its width *Lytopsenella* Kieffer [NET]
- 3a, Marginal cell closed *Sierola* Cameron [PAL, ORI, AUS, NEA; abundant on the Hawaiian Islands]
- 3bb, Marginal cell open apically 4
- 4a, Antenna with 12 segments; b, basal vein forming almost a right angle, its portion appearing as a continuation of the median vein; c, transverse median vein far basaed of the apparent basal vein; d, fully winged, but brachypterous or micropterous in a few species *Bethylus* Latreille [PAL, ORI, NEA]
- 4aa, Antenna with 13 segments; bb, basal vein oblique, only slightly angled, leaving median vein at about the same point as the transverse median vein; cc, transverse median vein near based of the apparent basal vein; dd, always fully winged 5
- 5a, Prostigma large, forming a subtriangle; b, median carina of clypeus short, extending up to the frons at most for short distance; c, Rs + m vein shorter than rs vein *Goniozus* Förster

[PAL, ORI, AUS, ETH, NEA, NET]

5aa, Prostigma small, not forming a triangle; bb, median carina of clypeus long, continueing on well up to the frons; cc, Rs + m vein shorter than rs 6

6a, Complete median carina of propodeum present; b, base of propodeal disc with a pair of small pits at the outer portion *Odontepyris* Kieffer [PAL, ETH, ORI, AUS]

6aa, Median carina of propodeum absent; bb, base of propodeal disc with a pair of pits at the extreme base medially *Prosierola* Kieffer [NEA, NET]

Acknowledgments

I wish to express my cordial thanks to M. C. Day, T. Huddleston & B. Bolton (Natural History Museum, London), I. Löbl (Muséum d'Historie Naturelle, Geneve), J. Papp (Hungarian Natural History Museum), E. De Conick (Musée Royal de l'Afrique Centrale, Tervuren), V. Raineri (Museo Civico di Storia Naturale, Genova), for lending the types and/or valuable specimens or giving useful information about types. My thanks are extended to Dr. T. Matsumoto (University of Tokyo) for his kind guidances and constant encouragements.

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Appendix. List of genera on the subfamily Bethylidae.

#: genera lack of the types or voucher specimens, most of which were presumably lost.

Family Bethylidae

Subfamily Pristocerinae = Subfamily Afoiogfinae

Afoiogfa 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#; Caloapenesia Terayama 1995; Dicrogenium Stadelmann 1894 = Nomineia Kieffer 1911; Diepyris Benoit 1957; Dissomphalus Ashmead 1893 = Ecitopria Wasmann 1899 = Thaumatepyris Kieffer 1919 = Glenobethylus 1910 = Parecitopria Oglöblin 1930 = Psilobethylus Kieffer 1906; Kathepyris Kieffer 1907; Neodicrogenium Benoit 1957; Neoapenesia Terayama 1995;

Parascleroderma Kieffer 1904 = Ceratepyris Kieffer 1905; Pristocera Klug 1808 = Mangesia Kieffer 1911 = Trichelobrachium Kieffer 1914; Acrepyris Kieffer 1905 = Neopristocera Yasumatsu 1955; Pseudisobrachium Kieffer 1904 = Monepyris Kieffer 1905 = Xestobethylus Cameron 1909 = Plutobethylus Kieffer 1910 = Lyssepyris Kieffer 1913 = Afrisobrachium Benoit 1957 = Xantepyris Kieffer 1913 = Xanthepeyris Kieffer 1914 (Unjustified 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 = Procalyzoa Kieffer 1905; Aspidepyris Evans 1964; Bakeriella Kieffer 1910; Calyozina Enderlein 1912; Disepyrus Kieffer 1905 = Lytepyris Kieffer 1913; Epyris Westwood 1832 = Muellerella Saussure 1892 = Parepyris Kieffer 1913 = Psilepyris Kieffer 1913 = Dolus Motschulsky 1863 = Calyzoa Westwood 1837 = Paracalyzoa Cameron 1909 = Artiepyris Kieffer 1913 = Calyozella Enderlein 1920 = Callioza Agassiz 1846 (Unjustified emendation) = Pseudocalyzoa Turner 1915 = Homoglenus Kieffer 1904; Holepyris Kieffer 1905 = Rysepyris Kieffer 1906 = Misespyris Kieffer 1913 = Parepyris Brethes 1913; Isobrachium Förster 1856; Laelius Ashmead 1893 = Allepyris Kieffer 1905 (Provisional) = Paralaelius Kieffer 1905; Leptepyrus Kieffer 1914#; Neodisepyris Kurian 1955#; Planepyrus Kieffer 1905#; Prolaelius Kieffer 1905; Neurepyris Kieffer 1905; Melanepyrus Kieffer 1913#; Pristepyrus Kieffer 1905#; Rhabdepyris Kieffer 1904 (Subgenus Rhabdepyris s. str. Kieffer 1904, Subgenus Trichotepeyris Kieffer 1906, Subgenus Chlorepyris Kieffer 1913); Trachepeyris Kieffer 1905 = Pristobethylus Kieffer 1905 = Acanthepeyris Kieffer 1912; Triglenus Marshall 1905#; Trissepyris Kieffer 1905#; Xenepyrus Kieffer 1913#

Tribe Sclerodermini

Allobethylus Kieffer 1905 = Nesepeyris Bridwell 1920; Alongatepyris Azevedo 1992; Ateleoapterus Förster 1856#; Bethyloopsis Fouts 1939; Chilepeyris Evans 1964; Discleroderma Kieffer 1904; Glenosema Kieffer 1905 = Arysepyris Kieffer 1905; Lepidosternopsis Ogloblin 1954 = Nothepeyris Evans 1973; Sclerodermus Latreille 1890 = Scleroderma Oken 1817 (Unjustified emendation) = Sclerochroa Förster 1850 = Neoscleroderma Kieffer 1905; Scaphepyris Kieffer 1905; Thlastepyrus Evans 1973

Tribe Cephalonomiini

Acephalonomia Strojcek 1990; Cephalonomia Westwood 1833 = Holopedina Förster 1850 = Cephaloderma Hoffer 1936 = Cephalomia Kirchner 1867 (Unjustified emendation); Islaelius Richards 1952; Platanoxus Kieffer 1905 = Snappania Hedqvist 1975; Prorops Waterston 1923

Subfamily Mesitiinae = Subfamily Mesitinae (Unjustified emendation)

Analyx Móczár 1970; Bradepyrus Kieffer 1905; Clytrovorus Nagy 1972; Codorcas Nagy 1972; Heterocoelia Dahlbom 1854; Incertusulcus Móczár 1970; Mesitius Spinola 1851; Metrionotus Móczár 1970; Pilomesitius Móczár 1970; Parvoculus Móczár 1970; Pseudomesitius Duchaussoy 1916#; Pycnomesitius Móczár 1971; Sulcomesitius Móczár 1970 = Topcobius Nagy 1972

Subfamily Galodoxinae

Galodoxa Nagy 1974

Subfamily Bethylinae

Bethylus Latrelle 1820 = Perisemus Förster 1856 = Episemus Thomson 1862 = Anoxus Thomson 1862 = Anoxys Dalla Torre 1898 (Unjustified emendation) = Digonozus Kieffer 1905; Eupsenella Westwood 1874; Goniozus Förster 1856 = Parasierola Cameron

1883 = Progoniozus Kieffer 1905 = Perisierola Kieffer 1914; Lytopsenella Kieffer 1911; Odontepyrus Kieffer 1904 = Trissomalus Kieffer 19065; Prosierola Kieffer 1905; Sierola Cameron 1881

Subfamily incertae sedis

Foenobethylus Kieffer 1913#

Genera transferred to the Tiphidae

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 [= Alogoa Brues 1910, nec Castelnau 1961; Brues 1922]; Harpagocrypus 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 Scolytidae

Clystostenella Kieffer 1911 [Evans 1963]

Genus transferred to the Scelionidae

Mantibaria Kirby 1900 [Masner 1976]

Genus transferred to the Sierolomorphidae

Proscleroderma Kieffer 1905 [Nagy 1990]

Genus transferred to the Formicidae

Neoclystostenella Kurian 1955 [Brown 1987]

Genera which cannot be recognized

Omaloderus Walker 1843 = Homaloderus (Laspus) Dalla Torre 1898 [Evans 1964; not a bethylid wasp.]