

The Phylogeny of the Bethyloid Wasp Subfamily Pristocerinae (Hymenoptera, Bethyridae)

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Abstract The bethyloid wasp subfamily Pristocerinae is revised and its possible phylogenetic relationships are discussed. The cladistic analysis indicated that 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*) + *Diepyris*) and the rest. Subgenus *Acrepyris* of the genus *Pristocera* is raised to the generic state. A key to the genera of the world is presented.

Key words: Hymenoptera; Bethyridae; Pristocerinae; cladistics; phylogeny.

Introduction

The subfamily Pristocerinae, belonging to the family Bethyridae, is widely distributed from the tropics to the temperate regions of the world. The name, subfamily Pristocerinae was used by DALLA TORRE (1898) for the first time. Recently BENOIT (1963, 1981) established 3 tribes, Pristocerini, Dicrogeniini and Usakosiini, in this subfamily. In 1988, ARGAMAN established the subfamily Afgoiogfinae which consisted of genera *Afgoiogfa* and *Parascleroderma*. However, GORDH & MÓCZÁR (1990) and FINNAMORE & BROTHERS (1993) rejected the segregation of subfamily Afgoiogfinae from Pristocerinae. Up to the present, some 440 nominal species are known in the subfamily including 21 genera and 3 tribes.

The internal phylogeny of Pristocerinae remains unsolved. Only a systematic work at genus level is presented by EVANS (1963). Unfortunately few apomorphic characters were indicated to explain the relationships, and no phylogenetic study using the cladistic method has been made on this subfamily.

The present study aims to clarify the internal relationships of Pristocerinae at genus level and to contribute to the taxonomy of this taxa.

Materials and Methods

Taxa applied to the analysis

All the possible genera are treated. Out of 21 valid genera, *Parapenesia* is

excluded since this genus should be removed to the other subfamily (TERAYAMA, in prep.). Four genera, *Anisobrachium*, *Apristocera*, *Usakosia*, and *Parapristocera* (fossil), are excluded from the present analysis because of not only lack of the types or voucher specimens, most of which were presumably lost during the World Wars, but also insufficient information due to the poor original descriptions. The genus *Pristocera* consists of two subgenera, *Pristocera* and *Acrepyris*, which are separately used in this analysis. The female characters are omitted, because up to the present only 7 genera have been known of their females. Thus, in total 17 supraspecific taxa are used in this analysis.

The specimens examined in this study are listed as follows together with the institutions preserving the materials.

- BMNH: British Museum, Natural History, London, U.K.
 CNC: Canadian National Collection, Agriculture Canada, Ottawa, Canada
 EUM: Entomological Laboratory, Ehime University, Matsuyama, Japan
 HUS: Entomological Institute, Hokkaido University, Sapporo, Japan
 KU-K: KUSIGEMATI collection, Entomological Laboratory, Kagoshima University, Kagoshima, Japan
 KUF: Entomological Laboratory, Kyushu University, Fukuoka, Japan
 MCSN: Museo Civico di Storia Naturale, Genova, Italy
 MNHN: Muséum National d'Histoire Naturelle, Paris, France
 MU-Y: YAMAGISHI collection, Entomological Laboratory, Meijyo University, Nagoya, Japan
 MRAC: Musée Royal de l'Afrique Centrale, Tervuren, Belgium
 NSMT: National Science Museum, Tokyo, Japan
 NIAES: National Institute of Agro-Environmental Sciences, Tsukuba, Japan
 PMA: Provincial Museum of Alberta, Alberta, Canada
 TARI: Taiwan Agricultural Research Institute, Taichung, Taiwan
 TE: TERAYAMA collection, Department of Biology, University of Tokyo, Tokyo, Japan
 ZMC: Zoologisk Museum, Copenhagen, Denmark
 ZMHU: Zoologisches Museum an der Humboldt-Universität zu Berlin, Berlin, Germany

(T): holotype, paratypes or syntypes examined.

Afroceras: *A. bamboutoana* [Cameroon, MNHN(T)]

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

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

- Dicrogenium*: *D. rosmarum* [Cameroon, ZMHU(T)]; *D. alberti* [Zaire, MRAC(T)]
- Diepyris*: *D. brunneus* [Zaire, MRAC(T)]
- Dissomphalus*: *D. kinabarensis* [Indonesia, NIAES(T)]; *D. khaoyaiensis* [Thailand, PMA(T)]; *D. chipenensis* [Taiwan, NSMT(T)]; *D. luteus* [Italy, MCSN(T)]; *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]; *D. sp.* [Malaysia, TE]
- Kathepyris*: *K. basutoensis* [Lesotho, MRAC(T)]; *K. uelensis* [Zaire, MRAC(T)]
- Neodicrogenium*: *N. sampwense* [Zaire, RMAC(T)]
- Neoapenesia*: *N. leytensis* [Philippines, CNC(T)]
- Parapenesia*: *P. unicolor* [Republic of South Africa, ZMHU(T)]
- Parascleroderma*: *P. spp.* [Taiwan, NIAES, TE]; *P. spp.* [Thailand, PMA]; *P. sp.* [Malaysia, PMA]
- Pristocera* (s. str.): *P. formosana* [Taiwan & Korea, TARI(T), KUF, NSMT, TE]; *P. carinata* [Myanmar, 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*): *P. japonica* [Japan, KUF(T), HUS, NIAES]; *P. japonica ishigakiensis* [Japan, KUF(T)]; *P. minuta* [Japan, KUF(T)]; *P. mieae* [Taiwan, NIAES, NSMT(T)]; *P. tainanensis* [Taiwan, HUS, NIAES(T)]; *P. takasago* [Taiwan, HUS, NSMT(T)]; *P. antennata* [Myanmar, MCSN(T)]; *P. spp.* [Japan, KUF, KU-K, NIAES]; *P. spp.* [Taiwan, NSMT, TARI, KUF, HUS, CNC, TE]; *P. spp.* [Nepal, CNC]; *P. spp.* [Indonesia, CNC]; *P. spp.* [India, PMA, CNC]
- Prosapenesia*: *P. lacteipennis* [Botswana, ZMHU(T)]; *P. schoutedeni* [S. W. Africa, MRAC(T)]; *P. spp.* [S. W. Africa, BMNH]
- Protisobrachium*: *P. gracile* [Zaire, MRAC(T)]; *P. asianum* [Thailand, PMA(T)]; *P. sp.* [Thailand, PMA]
- Pseudisobrachium*: *P. sp.* [Colombia, NSMT]; *P. spp.* [Japan, KUF]; *P. sp.* [Hong Kong, TE]; *P. spp.* [Thailand, PMA]; *P. spp.* [Nepal, CNC]
- Trichiscus*: *T. wittei* [Zaire, MRAC(T)]

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 which guarantees to find all optimal trees. The accelerated transformation (ACCTRAN) option, which minimizes the ratio of parallelism to reversal, was used. This minimizes the length of all subtrees in the multiple most parsimonious reconstructions (MPRs) (MINAKA, 1993). I also

used MacClade Ver. 2.1 drawn by MADDISON & MADDISON (1987) for graphic display of the number of synapomorphies on different branches of the cladogram and for tracing of selected characters.

The character state definitions and polarities largely followed prevailing theories of evolutionary change within the aculeate Hymenoptera (BROTHERS, 1975; BROTHERS & CARPENTER, 1993; CARPENTER, 1986; KÖNIGSMANN, 1978). Since the phylogenetic relationships between the bethylids and other wasps have not been fully resolved, I used hypothetical ancestor of aculeate Hymenoptera which had the plesiomorphic state in every character as an outgroup.

I have not made use of the fossil subfamily Protopristocerinae established by NAGY (1974) as an outgroup since many of the characters of interest in my data matrix cannot be tested in the subfamily and monophyly of Protopristocerinae is not confirmed.

Results and Discussions

Tables 1 and 2 show the characters used in this analysis and the character matrix respectively. Cladistic analysis led 3 equally most parsimonious trees (Fig. 1): the length is 75, with a consistency index (KLUGE & FARRIS, 1969) of 0.747 and a retention index (FARRIS, 1989) of 0.716. One of the 3 trees (tree C in Fig. 1) has a zero length internode by ACCTRAN. Fig. 2 show the strict consensus tree from these 3 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 rest. The former group (*(Afgoiogfa + Parascleroderma) + Prosapenesia + Diepyris*) constitutes a monophyletic assemblage defined by the absence of the metacarpus vein of forewings (character 30); while the latter, which is characterized by the clypeus well produced anteriorly (character 3), has 4 unresolved dichotomies.

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

Parascleroderma may be the sister-group of *Afgoiogfa*, but no autoapomorphy has been revealed for this genus in the present analysis.

BENOIT (1963, 1981) divided Pristocerinae into three tribes, Dicrogeniini, Pristocerini and Usakosiini, based mainly on the African material. But I can not

Table 1. The Characters and their states used in the cladistic analysis. Zero indicates plesiomorphic state and number greater than 0 indicates progressive and more apomorphic states.

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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 in lateral view. Not obliquely truncated [0]; obliquely 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 triangle. Forming regular triangle and situated far from occipital border [0]; flat and situated well near occipital border [1].
 10. Posterior border of head in frontal view. Straight to moderately convex [0]; strongly convex [1].
 11. Occipital 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, less than 1.3× as long as wide [0]; longer, more than 1.4× as long as wide [1].
 20. Propodeum. Not produced [0]; produced dorsally [1].
 21. 1st gastral tergite. Shorter, less than 1.2× as long as wide [0]; longer, more than 1.5× as long as wide [1].
 22. Gaster in dorsal view. Slender [0]; oval [1].
 23. 2nd gastral tergite. Simple, without modification [0]; with a pair of spots, pits or depressions [1].
 24. Posterior border of 2nd gastral tergite. Without modification [0]; strongly concave laterally [1].
 25. 3rd gastral tergite. Simple, without modification [0]; with a pair of pits [1].
 26. Middle tibiae. Without spine [0]; with strong spines at outer margin [1].
 27. Middle tibial spurs. Same length [0]; unequal 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].
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Table 1. (continued)

37. Cubital vein. Weak but distinct and reaching the wing margin [0]; indistinct or not reaching the wing margin [1].
38. Subdiscoidal vein. Weak but distinct and reaching the wing margin [0]; indistinct or not reaching the wing margin [1].
39. Median vein of hindwing. Weak but distinct and reaching the wing margin [0]; obsolete or absent [1].
40. Anterior border of 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 lobe [0]; with a lamellar lobe [1].
44. Parameres. Broad [0]; long and thin, bearing a shaft at the middle [1].
45. Parameres. With a single lobe [0]; divided into two 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. Aedeagus. Simple [0]; consisting of three distinct sets of valves [1].
49. Cusps. Simple [0]; divided into two separate arms [1].

Table 2. Character coding for the analysis of the generic relationships in the subfamily *Pristocerinae*. 0 = plesiomorphic state, 1 & 2 = apomorphic states.
 ? = states unknown. P = polymorphic condition.

Taxon	123456789	1111111111 0123456789	2222222222 0123456789	3333333333 0123456789	4444444444 0123456789
<i>Afgoiogfa</i>	001000001	0000110010	0000000000	1000?00111	1000001000
<i>Parascleroderma</i>	001000001	0000110010	0000000000	1000P00111	1000000000
<i>Dicrogenium</i>	100000000	0110110010	0000000000	0000000000	0100100000
<i>Neodicrogenium</i>	010000000	00101?0010	0000000000	0000000000	0100100000
<i>Diepyris</i>	100000100	0000100010	0000000000	1000000111	0100100000
<i>Kathepyris</i>	010000000	0000100010	0010100000	1000000000	0100100000
<i>Acrepyris</i>	010000000	0000100010	0010000000	00001001P1	0000000010
<i>Pristocera</i>	010000100	0000100010	0000000000	0000100001	0100P00000
<i>Afrocera</i>	001000000	10001?0111	0100000000	0000100111	??00000100
<i>Apenesia</i>	001000000	0000100010	0010000000	00001P0111	0000000001
<i>Protisobrachium</i>	001100010	1000101011	0000000100	0000110111	?000000000
<i>Pseudisobrachium</i>	002000010	P100101011	0000000100	0000100111	1000010000
<i>Prosapenesia</i>	000011000	0000100010	0000001000	101110P111	1001000000
<i>Dissomphalus</i>	001000000	0000100010	0011000110	0000111111	0000000000
<i>Trichiscus</i>	001000000	0000100010	0010110110	0000111111	0000000000
<i>Caloapenesia</i>	001000010	0000100010	0000000001	0100110111	0000010000
<i>Neoapenesia</i>	001000000	0001101010	0000000100	1000110111	1010000000
Outgroup	000000000	0000000000	0000000000	0000000000	0000000000

consent to these tribes in the subfamily for two reasons: first, there has been found no informative character to separate tribes in this analysis; second, some genera have intermediate characteristics defining the tribes.

The single diagnostic characteristics of *Dicrogeniini* proposed by BENOIT is

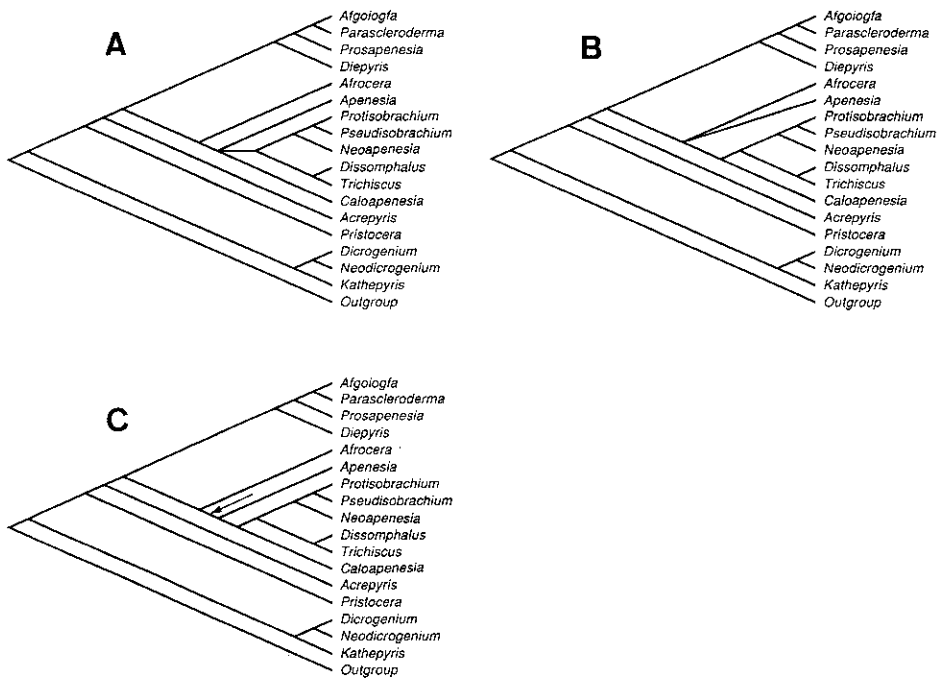


Fig. 1. Most parsimonious cladograms of subfamily Pristocerinae. Tree C has a zero length internode (arrow) by ACCTRAN.

merely a synapomorphy for *Dicrogenium* and *Neodicrogenium* (character 12 in this analysis). In this analysis, the group (*(Dicrogenium + Neodicrogenium) + Kathepyris*) constitutes a monophyletic assemblage by the shape of parameres (character 44), which, however, also occurs in some species of the genus *Pristocera*.

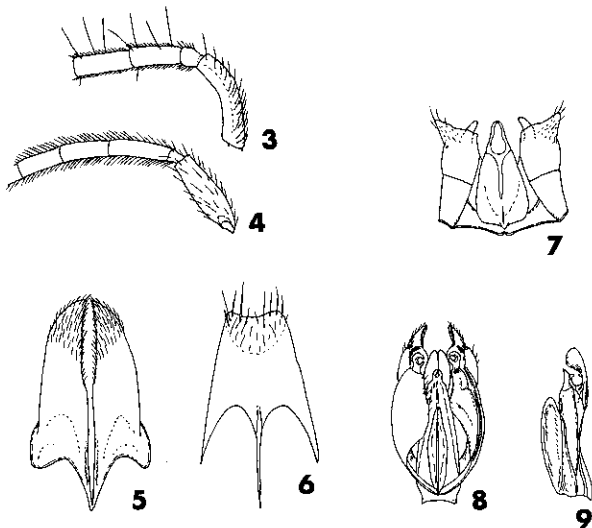
Pristocera and *Acrepyris* present some difficulty in attempting to separate them to the different tribes, because they include some species in character composition between the clade (*(Dicrogenium + Neodicrogenium) + Kathepyris*) and the rest.

I cannot agree with BENOIT (1981) that the genus *Prosapenesia* put into his Usakosiini, because the present analysis did not indicate it as an independent taxon at tribal level. This genus has 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 lamellar lobe (character 43).

EVANS (1963) presented relationships among the 8 New World species groups of *Apenesia* and 3 genera, *Pristocera*, *Dissomphalus* and *Pseudisobrachium*. He assumed that the latter 3 genera each may have arisen from a different species group of *Apenesia*. However, the present analysis did not support his assumption,

This genus is distinguished from *Pristocera* by the following combinations of characters in the male: (1) Antennae long, extending to or beyond the posterior border of propodeum (short, not reaching the anterior border of propodeum in *Pristocera*); (2) Antennal funicular segments without distinct long erect hairs (Fig. 4) (with distinct long erect hairs in *Pristocera* (Fig. 3)); (3) Subgenital plate simple (Fig. 6) (deeply divided into two lobes in *Pristocera* (Fig. 5)); (4) Aedoeagus of genitalia consisting of 3 sets of valves (Figs. 8 & 9) (simple in *Pristocera* (Fig. 7)); (5) Digni of genitalia forming slender, curved rods (forming broad, truncate plates in *Pristocera*).

The following 27 species are moved from the genus *Pristocera* to the genus *Acrepyris*: *A. antennatus* (MAGRETTI) comb. nov., *A. armiferus* (SAY) comb. nov., *A. atrus* (KLUG) comb. nov., *A. bridwelli* (EVANS) comb. nov., *A. californicus* (EVANS) comb. nov., *A. chihuahuus* (EVANS) comb. nov., *A. cockerelli* (EVANS) comb. nov., *A. dreisbachi* (EVANS) comb. nov., *A. fraternus* (EVANS) comb. nov., *A. hyalinus* (BRUES) comb. nov., *A. intermedius* (EVANS) comb. nov., *A. japonicus* (YASUMATSU) comb. nov., *A. japonicus ishigakiensis* (YASUMATSU) comb. nov., *A. mieae* (TERAYAMA) comb. nov., *A. minutus* (YASUMATSU) comb. nov., *A. nebulosus* (EVANS) comb. nov., *A. otomi* (EVANS) comb. nov., *A. palliditarsis* (CAMERON) comb. nov., *A. parkeri* (EVANS) comb. nov., *A. porteri* (EVANS) comb. nov., *A. quirogus* (EVANS) comb. nov., *A. sinalous* (EVANS) comb. nov., *A. tainanensis* (TERAYAMA) comb. nov., *A. takasago*



Figs. 3-9. Genera *Pristocera* and *Acrepyris*. — 3, 5, 7, *Pristocera formosana* MIWA & SONAN, 1935; 4, 6, 8, 9, *Acrepyris japonicus* (YASUMATSU, 1955). — 3, 4, First 4 segments of antenna; 5, 6, subgenital plate; 7, 8, male genitalia; 9, aedoeagus of genitalia, lateral view.

(TERAYAMA) comb. nov., *A. tenochcus* (EVANS) comb. nov., and *A. varidens* (CAMERON) comb. nov.

Zoogeographical distribution

The number of described species in each genus is shown in Table 3. This subfamily has the highest genus number (15 genera) in the Ethiopian Region, followed by 9 genera in the Oriental Region. The Ethiopian region has also abundant endemic genera; the following 10 genera are restricted to this region: *Afgoiogfa*, *Afrodera*, *Apristocera*, *Dicrogenium*, *Diepyris*, *Kathepyris*, *Neodicrogenium*, *Prosapenesia*, *Trichiscus* and *Usakosia*. Genera *Apenesia*, *Dissomphalus*, *Parascleroderma* and *Pseudisobrachium* are widely distributed in the world.

The distribution pattern of *Pristocera* and *Acropyris* is principally allopatric; *Acropyris* is mostly distributed in the New World with a few species in the Oriental and southeast Palaearctic Regions, while *Pristocera* occurs in the Ethiopian and the Oriental Regions.

Table 3. Zoogeographical synopsis of subfamily Pristocerinae. The number is represented the species-level taxa currently recognized in each genus by respective region. The Maragacy Region is included in the Ethiopian Region in this table. "X" means unpublished data. The zoogeographic regions are abbreviated as follows: PAL, Palaearctic; ORI, Oriental; AUS, Australian; ETH, Ethiopian; NEA, Nearctic; NET, Neotropical.

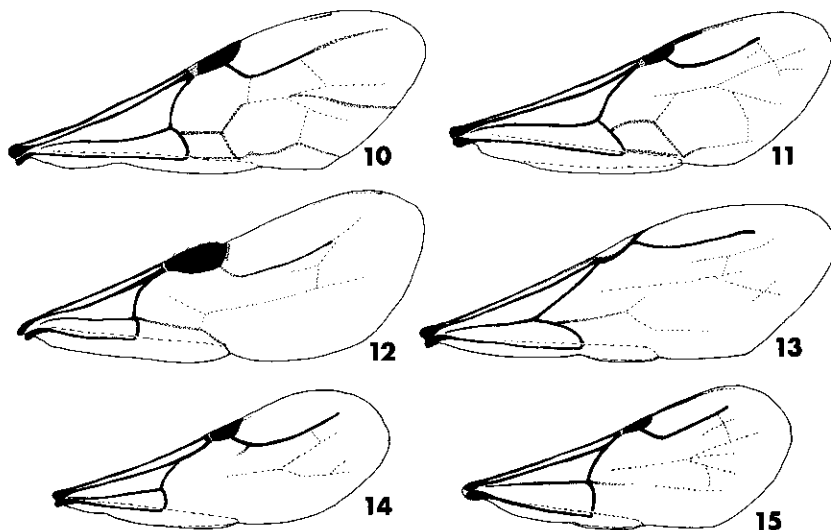
Genera	Region						No. of described species
	PAL	ORI	AUS	ETH	NEA	NET	
<i>Acropyris</i>	2	4			5	6	17
<i>Afgoiogfa</i>				1			1
<i>Afrodera</i>				1			1
<i>Anisobrachium</i>	1						1
<i>Apenesia</i>	X	18	3	17	17	71	123
<i>Apristocera</i>				1			1
<i>Caloapenesia</i>		2					2
<i>Dicrogenium</i>				23			23
<i>Diepyris</i>				6			6
<i>Dissomphalus</i>	5	6		12	8	51	83
<i>Kathepyris</i>				4			4
<i>Neodicrogenium</i>				6			6
<i>Neoapenesia</i>		1					1
<i>Parascleroderma</i>	15	X		2	4	1	21
<i>Pristocera</i>	6	10	1	58			72
<i>Prosapenesia</i>				4			4
<i>Protisobrachium</i>		1	2				3
<i>Pseudisobrachium</i>	8	2		9	46	76	136
<i>Trichiscus</i>				2			2
<i>Usakosia</i>				1			1

Key to genera of Pristocerinae (male)

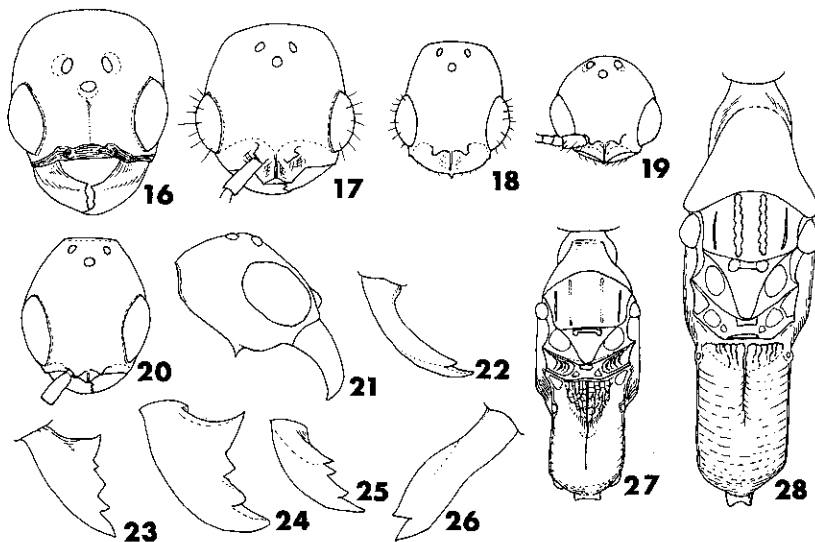
The zoogeographical distribution for each genus is shown in parentheses. For the abbreviations of zoogeographic regions, see Table 3. Ambiguous genera are excluded in the key to avoid the unnecessary confusions.

1. Subgenital plate deeply divided into two lobe (Figs. 5 & 34)2
- Subgenital plate simple, posterior border at most weakly concave, and never deeply divided into two lobe (Figs. 6, 32, 33 & 35)6
2. Head in lateral view with acute spine at gena (Fig. 21)3
- Genal area without spine4
3. Mandibles sickle-shaped (Fig. 22) ... *Dicrogenium* STADELMANN [ETH]
- Mandibles more or less triangular with teeth on masticately margin (Fig. 23); basalmost tooth directed inward .. *Neodicrogenium* BENOIT [ETH]
4. Mandibles sickle-shaped, with 2 apical teeth only (Fig. 26)
..... *Diepyris* BENOIT [ETH]
- Mandibles triangular with 3–6 teeth5
5. Cubital and subdiscoidal veins reaching wing margin (Fig. 10)
..... *Kathepyris* KIEFFER [ETH]
- Cubital and subdiscoidal veins barely visible, not reaching wing margin (Fig. 11) *Pristocera* KLUG [ETH, ORI, PAL]
6. Head truncated anteriorly (Fig. 16); pterostigma exceptionally large (Fig. 12); posterior border of subgenital plate with a lamellar lobe (Fig. 33)
..... *Prosapenesia* KIEFFER [ETH]
- Head not truncated anteriorly; pterostigma moderate in size or absent; posterior border of subgenital plate simple, without a lamellar lobe....7
7. Pterostigma absent (Fig. 13) *Caloapenesia* TERAYAMA [ORI]
- Pterostigma present8
8. Second gastral tergite with a pair of spots, pits or depressions (Fig. 30) ..
..... *Dissomphalus* ASHMEAD [PAL, ORI, ETH, NEA, NET]
- Second gastral tergite without modification9
9. Posterolateral borders of 2nd gastral tergite strongly concave; 3rd gastral tergite with a pair of spots (Fig. 31) *Trichiscus* BENOIT [ETH]
- Psterior border of 2nd gastral tergite without modification; 3rd gastral tergite simple, without spots10
10. Propodeum long, more than twice as long as wide; scutellar disc elongate, more than twice as long as wide (Fig. 28); 1st gastral tergite long, more than 1.5× as long as wide in dorsal view (Fig. 29)
..... *Afroceras* BENOIT [ETH]
- Propodeum less than twice as long as wide; scutellar disc shorter, less than twice as long as wide; 1st gastral tergite less than 1.3× as long as wide in dorsal view11

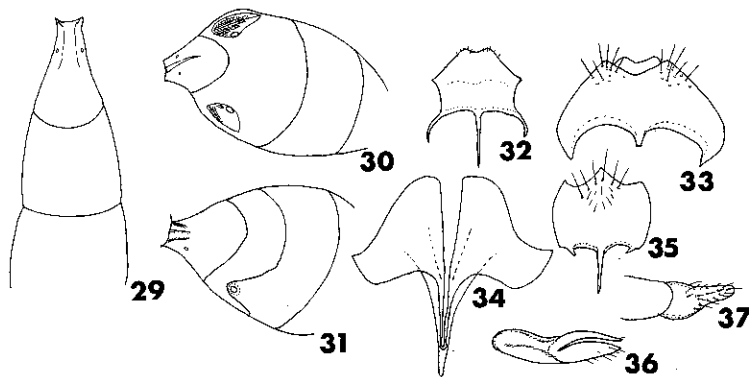
11. Anterior border of clypeus trapezoidal and truncate apically (Fig. 17); eyes densely covered with hairs; genitalia with the parameres deeply divided into two lobes (Fig. 36)
 *Pseudisobrachium* KIEFFER [PAL, ORI, ETH, NEA, NET]
 — Clypeus not trapezoidal nor truncate apically; eyes glabrous, or only scattered with short hairs; genitalia with parameres not deeply divided into two lobes (Fig. 37) 12
12. Notauli absent or nearly so (Fig. 27) 13
 — Notauli complete or nearly so 14
13. Clypeus strongly produced; head longer than wide (Fig. 18); pronotum usual in size *Protisobrachium* BENOIT [ETH, ORI]
 — Lateral borders of anterior margin of clypeus not remarkably produced; head wider than long (Fig. 19); pronotum extremely short
 *Neoapenesia* TERAYAMA [ORI]
14. Ocelli forming a flat triangle and situated almost near the occipital border (Fig. 20); metacarpus vein absent (Fig. 14) 15
 — Ocelli more or less forming a right triangle, situated far from the occipital border; metacarpus vein present (Fig. 15) 16
15. Anterior border of clypeus with a single median projection (Fig. 20)
 *Parascleroderma* KIEFFER [PAL, ORI, ETH, NEA, NET]
 — Anterior border of clypeus with 3 small projections



Figs. 10–15. Forewings of *Pristocerinae*. — 10, *Kathepyris uelensis*, drawn from holotype; 11, *Pristocera* sp.; 12, *Prosapenesia* sp.; 13, *Caloapenesia thailandiana*, drawn from holotype; 14, *Parascleroderma* sp.; 15, *Apenesia* sp.



Figs. 16-28. Head, mandible and mesosoma of Pristocerinae. — 16, *Prosapenesia* sp.; 17, *Pseudisobrachium* sp.; 18, 27, *Protisobrachium asianum*, drawn from holotype; 19, *Neoapenesia leytensis*, drawn from holotype; 20, *Parascleroderma* sp.; 21, 22, *Dicrogenium alberti*, drawn from holotype; 23, *Neodicrogenium sampwense*, drawn from holotype; 24, *Acrepyris japonicus*, drawn from paratype; 25, *Apenesia* sp.; 26, *Diepyris brunneus*, drawn from holotype; 28, *Afrodera bamboutoana*, drawn from holotype. — 16-20, head, frontal view; 21, head, lateral view; 22-26, mandible; 27, 28, mesosoma, dorsal view.



Figs. 29-37. Gaster, subgenital plate and paramere of genitalia of Pristocerinae. — 29, *Afrodera bamboutoana*, drawn from holotype; 30, *Dissomphalus* sp.; 31, *Trichiscus wittei*, drawn from holotype; 32, *Caloapenesia thailandiana*, drawn from holotype; 33, *Prosapenesia schoutedeni*, drawn from holotype; 34, *Kathepyris uelensis*, drawn from holotype; 35, *Neoapenesia leytensis*, drawn from holotype; 36, *Pseudisobrachium* sp.; 37, *Apenesia* sp. — 29, First 3 segments of gaster, dorsal view; 30, 31, ditto, dorsolateral view; 32-35, subgenital plate; 36, 37, paramere of genitalia.

-*Afgoiogfa* ARGAMAN [ETH]
 16. Median lobe of clypeus depressed near antennal insertions; basalmost tooth of mandibles directed inward (Fig. 24); cuspis simple, not divided nor setose; aedoeagus consisting of 3 valves (Figs. 8 & 9)
*Acrepyris* KIEFFER [PAL, ORI, NEA, NET]
 — Median lobe of clypeus not depressed near antennal insertions; basalmost tooth of mandibles triangular, not directed inward (Fig. 25), or mandibles with apical tooth only; cuspis divided into two arms, dorsal arm simple and ventral one setose (except in a few species); aedoeagus simple, not consisting of 3 valves
*Apenesia* WESTWOOD [PAL, ORI, AUS, ETH, NEA, NET]

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References

- ARGAMAN, Q., 1988. A new subfamily of Bethyloidea allied to Pristocerinae (Hymenoptera). *Bull. Soc. ent. Ital.*, **120**: 139–152.
- BENOIT, P. L. G., 1963. Monographie des Bethyloidea d'Afrique noire (Hymenoptera) I. Sous-famille Pristocerinae tribu Dicrogeniini tribu Pristocerini, gen. *Pristocera* KLUG. *Ann. Mus. R. Afr. Centr., Ser 8, Zool.*, (119): 1–95.
- 1981. Bethyloidea africains (Hymenoptera). La tribu Usakosiini. *Rev. de zool. Afr.*, **77**: 93–94.
- BROTHERS, D. J., 1975. Phylogeny and classification of the aculeate Hymenoptera, with special reference to Mutillidae. *Univ. Kansas Sci. Bull.*, **50**: 483–648.
- & J. M. CARPENTER, 1993. Phylogeny of Aculeata: Chrysidoidea and Vespoidea (Hymenoptera). *J. Hym. Res.*, **2**: 227–304.
- CARPENTER, J. M. 1986. Cladistics of the Chrysidoidea (Hymenoptera). *J. New York ent. Soc.*, **94**: 303–330.
- DALLA TORRE, C. G. DE, 1898. Bethyloidea, Pristocerinae. *Catalogus Hymenopterorum hucusque descriptorum systematicus et synonymicus*, **5**: 547–562.
- EVANS, H. E., 1963. A revision of the genus *Apenesia* in the Americas (Hymenoptera, Bethyloidea). *Bull. Mus. comp. Zool.*, **130**: 251–359.
- 1964. A synopsis of the American Bethyloidea (Hymenoptera, Aculeata). *Bull. Mus. comp. Zool.*, **132**: 1–222.
- FARRIS, J. S., 1989. The retention index and the rescaled consistency index. *Cladistics*, **5**: 417–419.
- FINNAMORE, A. T. & D. J. BROTHERS, 1993. Superfamily Chrysidoidea. In H. GOULET & J. T. HUBER (eds.), *Hymenoptera of the world: an identification guide to families*, Agriculture Canada, 130–160.
- GORDH, G. & L. MÓCZÁR, 1990. A catalog of the world Bethyloidea (Hymenoptera: Aculeata). *Mem. Amer. ent. Inst.*, **46**: 1–364.
- KIEFFER, J. J., 1905. Proctotrypidae. In E. ANDRÉ (ed.), *Species des Hyménoptères d'Europe & d'Algérie*, A. HERMANN, Paris, **9**: 65–288.
- KLUGE, A. G. & J. S. FARRIS, 1969. Quantitative phyletics and the evolution of anurans. *Syst. Zool.*, **18**: 1–32.
- KÖNIGSMANN, E., 1978. Das phylogenetische System der Hymenoptera Teil 4: Aculeata (Unterordnung Apocrita). *Deut. Ent. Zeitschr.*, (N. F.), **25**: 365–435.
- MADDISON, W. P. & D. R. MADDISON, 1987. MacClade, version 2.1. Cambridge, Massachusetts.
- MINAKA, N., 1933. Algebraic properties of the most parsimonious reconstructions of the hypothetical ancestors on given trees. *Forma*, **8**: 277–296.
- NAGY, C. G., 1974. A new bethyloid subfamily allied to Protopristocerinae. *Bull. Soc. ent. Ital.*, **106**: 126–130.
- SWOFFORD, D. L., 1989. PAUP, phylogenetic analysis using parsimony, version 3.0b.
- YASUMATSU, K., 1955. Taxonomic notes of three wireworm parasites of the genus *Pristocera* from the Far East (Hymenoptera: Bethyloidea). *J. Fac. Agr. Kyushu Univ.*, **10**: 233–249.

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