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Generic definitions and species assignments in the Family Epipsocidae (Psocoptera)

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Abstract: The family Epipsocidae is defined, with the addition of one character not previously used. The genus *Didistriata* Li and Mockford is removed from Epipsocidae and tentatively placed in the family Dolabellopsocidae. The genus *Parepipsocus* Badonnel remains unplaceable to family. Eleven genera are recognized within Epipsocidae. *Bertkauia* Kolbe, which had been synonymized with *Epipsocus*, is recognized as a valid genus. Definitions of genera based on the type species and seemingly close relatives result in 38 new combinations. *Epipsocus* Hagen, which previously held most of the species, now serves a dual function, with 15 species in the strict sense and 15 species 'incertae sedis' retained in it, pending further investigation. *Goja* Navás, previously with 2 species, now contains 10, with 8 transferred from *Epipsocus*. *Mesepipsocus* Badonnel, previously with 5 species, receives 24 more from *Epipsocus* and 1 from *Dicropsocus*. Eight species are transferred from *Epipsocus* to *Epipsocopsis* Badonnel. Notable consistency in geographic distributions of genera results from these transfers. Some evolutionary trends within the family are discussed. *Epipsocus delicatus* (Hagen) and *E. completus* Banks, which had been assigned by recent authors to the genus *Pseudocaecilius* Enderlein (Family Pseudocaeciliidae), are returned to the Epipsocidae and assigned to *Epipsocopsis*. A lectotype is designated for *E. delicatus*.

Introduction

The Family Epipsocidae is a group of 133 described species, mostly tropical and subtropical in distribution. This is 1 of 5 families defined by Eertmoed (1973) for the family group Epipsocetae.

In this study, the definition of the Family Epipsocidae is reviewed and augmented. The genera of this family are defined, and the described species of each genus are listed. Prior to the present study, numerous species belonging in other genera had been placed in the genus *Epipsocus* Hagen (1866). In the present study 36 species are transferred out of *Epipsocus* to other genera. The need for these transfers has arisen in part from genera having been defined initially on too few characters and in part from authors not having adhered strictly to existing definitions. The ultimate goal of this study is the establishment of monophyletic taxa, but attainment of that goal must await further studies. Unfortunately, 15 species, about 11% of the named species, cannot be placed to genus on existing information. They are listed as *incertae sedis* but are retained for the present in *Epipsocus*. Thus, *Epipsocus* now has a dual function. In the strict sense, it is a group of closely-related species, and in the broad sense, it is a holding taxon for species of Epipsocidae *incertae sedis*. The genus *Parepipsocus* Badonnel (1986) must be placed 'incertae sedis' at the family level (as its author did) because of its extreme neoteny and lack of diagnostic characters. The genus *Di-*

midistriata Li and Mockford (1997) was assigned by its authors to the Epipsocidae. It probably belongs in the family Dolabellopsocidae because of its labral characters.

Published keys to species of *Epipsocus*, *s. lat.* in local faunas, such as that of New (1972) and Mockford (1996) remain useful, but the user must keep in mind that an author may have meant this genus to include the entire family Epipsocidae at the time, or an even broader set of species.

The earlier literature contains a few errors which have been perpetuated by subsequent authors and require correction. Enderlein (1919) placed *Psocus delicatus* Hagen in the genus *Pseudocaecilius*. In 1991 I looked at the type material of this species, which consisted of 2 specimens on points in the Museum of Comparative Zoology, Cambridge, Massachusetts. The species is clearly an epipsocid. Both specimens bear label data "Ceylon, type 10114". One, a female, is here designated lectotype and bears the additional label "Lectotype, *Epipsocus delicatus*, (Hagen), E. L. Mockford Nov. 1991 (unpub.)". The other specimen, a male, is here designated paralectotype. Smithers (1967) placed *Epipsocus completus* Banks in the synonymy of "*Pseudocaecilius*" *delicatus* (Hagen). I also examined the unique type of *E. completus*, and confirm it is a true epipsocid. I do not believe that the synonymy with *P. delicatus* is justified. The wing markings of both species indicate placement in the genus *Epipsocopsis*.

Materials and Methods

The characters for each genus were abstracted from the type species and seemingly close relatives. These characters were obtained from descriptions in the literature, verified where possible with specimens at hand. These same methods were used for assigning species to genera. A. N. Garcia Aldrete has kindly sent particulars about several species which I have not seen. No new genera are proposed here, although some may be found necessary in future studies of the group.

The characters which appear to be important in distinguishing genera in this family are the following:

1) lacinial tip: whether or not denticles are present in the outer cusp, and the nature of denticles when present;

2) presence or absence of a row of cuticular cones arising on setal bases on the fore and hind femur;

3) presence or absence of a preapical denticle on the pretarsal claw;

4) extent of development of wings in females; states are apterous, micropterous, brachypterous (rare), and fully winged;

5) extent of development of multiple veins in Rs and M, primarily in the forewing (this character should not be used alone for recognition of genera);

6) nature of the Rs-M junction in the hindwing; states are long fusion, short fusion, at a point, or by a crossvein;

7) nature of the female subgenital plate: whether or not the hind margin is rounded or extended as a process, and nature of the process if present;

8) presence or absence of v1 (= ventral valvula) of the ovipositor and, if present, nature of its basal attachment;

9) nature of the composite v2+3 (= dorsal + lateral valvulae): whether or not v3 forms a lobe on the side of v2 and nature of the distal process;

10) extent of development of external parameres of the phallosome; states are absent, rudimentary, and well developed;

11) presence or absence of endophallic sclerotizations and their nature when present;

12) nature of the anterior margin of the phallosome; states are membranous (open phallosome) and well sclerotized (closed phallosome).

Results and Discussion

1. Definition and included genera of the family Epipsocidae. This family is here regarded as including all genera of the group Epipsocetae in which tarsi are 2-segmented; the antennal scape is membranous over much of its anterior (ventral) surface, being well sclerotized only at the base (Fig. 1); the pair of sclerotic rods of the labrum (labral sclerites) run the entire length of the labrum and curve outward at the base to reach the sides of the labrum (Fig. 2); anteriorly the labral sclerites are joined by only a weak sclerotic connection, if any; macropterous individuals have only one anal vein in the forewing; the pterostigma lacks crossveins; the first ovipositor valvula (v1) is present or absent, and the third (v3) is represented as a swelling or field of setae on the side of the second (v2) (Fig. 3).

Type genus: *Epipsocus* Hagen (1866). Other included genera: *Bertkauia* Kolbe (1882), *Cubitiglabra* Li (1995a), *Dichoepipsocus* Li and Mockford (1997), *Dicropsocus* Smithers and Thornton (1977), *Epipsocopsis* Badonnel (1955), *Goja* Navás (1927), *Heteroepipsocus* Li (1995a), *Hinduipsocus* Badonnel (1981), *Meseipsocus* Badonnel (1969), *Odontopsocus* Badonnel (1987).

Although all of these genera are probably not equivalent cladistically, they all appear to be useful in designating sets of related species.

2. Definitions of genera and lists of included species:

Epipsocus Hagen, 1866

Type species: *Psocus avus* Roesler, 1943 (replacement name for *Psocus ciliatus* Pictet-Baraban and Hagen, 1856, preoccupied), (only original species).

Definition: Outer cusp of lacinial tip denticulate (as in Fig. 4). No row of cones on fore or hind femur. Preapical denticle present on pretarsal claw. Adults of both sexes fully winged. Venation as in Figs. 5 and 6. Multiple veins extremely rare. Rs and M in hindwing fused for a distance. Female subgenital plate rounded posteriorly. In ovipositor (Fig. 3) v1 present, usually joined by a sclerotic strip to clunium; v3 developed as a field of setae on side of v2. Phallosome (Fig. 7) with external parameres absent or vestigial, aedeagal arch generally terminating in a slender process; endophallus without sclerotizations or these forming a

central mass; anterior margin of phallosome membranous.

Included species: (note: a question mark precedes the name here and subsequently where some doubt remains about the placement. In each such case the name is annotated with my reason for the placement):

?*acanthus* New, 1980, Brazil (Amazonas). Retained here because it appears to be close to *E. foliatus* Mockford, which is known to belong here.

?*argutus* New, 1980, Brazil (Amazonas). Retained here for same reason as noted for *E. acanthus* New (above).

avus (Roesler), 1943, Baltic amber.

badonneli Mockford, 1991, Brazil (Roraima).

foliatus Mockford, 1991, Brazil (Roraima).

latistigma Roesler, 1940, Brazil (Santa Catharina).

meruleus New, 1980, Brazil (Amazonas).

?*pereirai* Badonnel, 1974, Brazil (Mato Grosso). Retained here on basis of relatively few denticles in lacinial tip.

petenensis Mockford, 1957, Guatemala.

quercus Roesler, 1940, Brazil (Santa Catharina).

?*roraimensis* Mockford, 1991, Brazil (Roraima).

Retained here for same reason as for *E. acanthus* New (above).

serenus Roesler, 1940, Brazil (Santa Catharina).

uniformis New, 1972, Brazil (Mato Grosso).

?*verrucosus* New, 1980, Brazil (Amazonas). Retained here for same reason as for *E. acanthus* New (above).

willineri New, 1972, Brazil (Mato Grosso).

Discussion: Details about the type species of *Epipsocus* are provided by Enderlein's (1911) and Hagen's (1882, 1884) descriptions and figures of this amber fossil. Character states not known for the type (presence or absence of a row of cones on the front and hind femur, nature of the attachment of v1, extent of development of v3, and the characters of the phallosome) are provided by the extant South- and Central American species assigned to this genus. These are species which agree with the type in its known generic characters. The genus appears to be restricted now to the American Tropics but seems probably to have had a much wider distribution in the past.

***Bertkauia* Kolbe, 1882**

(= *Lapithes* Bertkau, 1883)

Type species: *B. prisca* Kolbe, 1882=*Psocus lucifugus* Rambur, 1842, (only original species).

Definition: Outer cusp of lacinial tip den-

ticulate (Fig. 4). No row of cones on fore or hind femur. Preapical denticle present on pretarsal claws. Males fully winged, females completely apterous. No development of multiple veins except an occasional extra Rs or M branch in forewing sometimes expressed as an unilateral anomaly. In hindwing Rs and M fused for a distance. Ovipositor with v1 present, generally based in membrane; v3 a large bulge on side of v2; v2 terminating in a very long, acuminate process. Phallosome (Fig. 8) membranous anteriorly, with broad, basally articulated external parameres, no endophallic sclerotization.

Included species:

crobyana Chapman, 1930, U.S.A.

lepicidinaria Chapman, 1930, U.S.A.

loebli Badonnel, 1981, India

lucifuga (Rambur), 1842, Europe.

remyi (Badonnel), 1966, Réunion Isl., new combination from *Epipsocus*.

reticularis Li and Mockford, 1997, China.

Discussion: The genus *Bertkauia* was synonymized with *Epipsocus* by Pearman (1935) when he ascertained that the wing venation of the male of *B. lucifuga* is like that of the type of *Epipsocus*. Several authors have accepted this synonymy, while others have not. The above definitions differ sufficiently that it seems reasonable to accept *Bertkauia* as a valid genus. This small genus is primarily Holarctic in distribution, with one species extending south in the mountains of eastern Mexico and one on the island of La Réunion in the Indian Ocean. Males of most species are exceedingly rare.

***Cubitiglabra* Li, 1995a**

Type species: *C. quadripunctata* Li, 1995a.

Definition: Lacinial tip broad but not denticulate. Pretarsal claws lacking preapical denticle or with a minute one. Males fully winged (females unknown). In forewing Rs 4-branched, M 6-branched. In hindwing Rs and M joined by a cross-vein or fused a short distance. Phallosome sclerotized ('closed') basally, with well developed external parameres, lacking endophallic sclerotizations.

Included species:

quadripunctata Li, 1995a, China.

polyphebia Li, 1995b, China.

Discussion: The genus *Cubitiglabra* appears to be very close to the genus *Heteroepipsocus*. It differs primarily by having extra veins in Rs and M of the forewing. In the family Epipsocidae such a difference, alone, seems unreliable as a generic

character, and it may be necessary to combine this genus with *Heteroepipsocus* when more material is known. The 2 genera appear to be restricted to southeastern Asia and nearby island groups.

***Dichoepipsocus* Li and Mockford, 1997**

Type species: *D. micropterus* Li and Mockford, 1997 (original designation).

Definition: Lacinial tip with short outer cusp bearing few, short denticles. Pretarsal claws lacking preapical denticle. Females micropterous (males unknown). Subgenital plate extended posteriorly in a short, median tongue with truncate or shallowly bifid apex. Ovipositor with v1 present, joined at base to base of v2 or to clunium; v3 forming a decided swelling on side of v2.

Included species:

micropterus Li and Mockford, 1997, China.

thimphuensis (New), 1978, Bhutan, new combination from *Epipsocus*.

Discussion: Although this genus resembles *Hinduipsocus* in shape of the subgenital plate, differences in head shape, structure of the lacinial tip, and structure of the pretarsal claw seem to rule out the possibility of a close relationship.

***Dicropsocus* Smithers and Thornton, 1977**

Type species: *D. montanus* Smithers and Thornton, 1977 (original designation).

Definition: Outer cusp of lacinial tip un-toothed, with acuminate tip. Pretarsal claws with preapical denticle. No row of cones on front or hind femur. Both sexes fully winged. In forewing Rs and M multi-branched with at least one Rs branch and at least one M branch re-branching. In hindwing Rs and M fused for a distance. Ovipositor lacking v1, with v3 forming only a field of setae on v2. Phallosome membranous anteriorly, with broad external parameres; aedeagal arch broad-tipped; endophallus with only slight median denticulation.

Included species:

complexus Smithers and Thornton, 1977, New Guinea.

montanus Smithers and Thornton, 1977, New Guinea.

rugosus Smithers and Thornton, 1977, New Britain.

Discussion: *Dicropsocus* appears to be an offshoot of *Epipsocopsis*, in which the cones of the front and hind femur have been suppressed (or were absent in the parental form), and a multi-

vein complex has arisen in Rs and M of the forewing.

***Epipsocopsis* Badonnel, 1955**

Type species: *E. machadoi* Badonnel, 1955 (original designation).

Definition: Outer cusp of lacinial tip with few or no denticles, frequently with acuminate tip (Fig. 9). Pretarsal claws with preapical denticle. Front and hind femora with a row of cones at bases of setae (Fig. 10) (row sometimes much reduced). Both sexes fully winged or females occasionally brachypterous. Generally no tendency for multiple veins. In hindwing Rs and M usually fused for a distance (rarely, a short Rs-M crossvein). Ovipositor lacking v1; v3 represented only by a field of setae on v2. Phallosome with well developed external parameres; anterior margin membranous; endophallus unsclerotized.

Included species:

angolensis (Badonnel), 1955, Angola. Transferred from *Epipsocus* by Badonnel, 1969.

apicalis New and Thornton, 1975, Malaysia.

basalis New and Thornton, 1975, Malaysia.

cameronensis New and Lee, 1991, Malaysia.

cincta Badonnel, 1969, Gabon.

completa (Banks), 1916, Philippines, new combination from *Epipsocus*.

costalis (Banks), 1914, India (Assam), Indonesia. Transferred from *Epipsocus* by Thornton, 1984.

delicata (Hagen), 1859, (Sri Lanka), new combination from *Psocus*.

dubia (Karny), 1925, Sarawak. Transferred from *Epipsocus* by Thornton, 1984.

fasciata Smithers and Thornton, 1977, New Guinea.

formosa Li, 1992, China, new combination from *Epipsocus*.

fumipennis (Banks), 1920, Philippines, transferred from *Epipsocus* by New and Thornton, 1975.

greeni New, 1977, Sri Lanka.

hakgalensis (New), 1977, Sri Lanka, new combination from *Epipsocus*.

hyalina (Banks), 1920, Singapore, transferred from *Epipsocus* by New and Thornton, 1975.

longiceps (Enderlein), 1926, Java, new combination from *Epipsocus*.

machadoi Badonnel, 1955, Angola.

maclurei New and Thornton, 1975, Malaysia.

macrostigma Smithers and Thornton, 1977, New Guinea.

maculata New and Thornton, 1975, Malaysia.

magna (New and Thornton), 1975, Malaysia, new combination from *Epipsocus*.
mouldsi Smithers, 1976, Australia.
?murcus (Enderlein), 1903, Malaysia, new combination from *Epipsocus*. The figure of the female genitalia accompanying the original description seems to place the species here.
murphyi New and Thornton, 1975, Malaysia.
nebulifera Smithers and Thornton, 1977, Solomon Islands.
nubilipennis Karny, 1925, Sarawak.
obuduensis New, 1973, Nigeria.
paraselena Vaughan *et al.*, 1989, Indonesia (Krakatau, Java).
peradenayense New, 1977, Sri Lanka.
prominens (Banks) 1937, Philippines, new combination from *Epipsocus*.
punctata Smithers and Thornton, 1977, New Guinea.
sclerota New and Thornton, 1975, Malaysia.
selena New and Thornton, 1975, Malaysia.
singaporensis New and Thornton, 1975, Singapore.
spatulata Smithers, 1964, Madagascar.
stuckenbergi Smithers, 1957, Madagascar.
taprobanensis (New), 1977, Sri Lanka, new combination from *Epipsocus*.
thailandensis New, 1973, Thailand.
truncatula Badonnel, 1967, Madagascar.
vilhenai Badonnel, 1955, Angola.

Discussion: *Epipsocopsis* is restricted to the Old World Tropics but is widely distributed there. Species occur from West Africa east to the Philippines, with species on Madagascar and northern Australia. As noted above, it apparently gave rise to the genus *Dicrosocus* in the New Guinea region.

Goja Navás, 1927

Type species: *G. ditata* Navás, 1927 (only original species).

Definition. Lacinial tip with a few large denticles in outer cusp. Pretarsal claws with preapical denticle. Fore and hind femora lacking rows of cones. Males fully winged, females micropterous. In male fore- and hindwing venation either normal or with multiple veins in Rs and M. In hindwing Rs and M joined either by a crossvein, at a point, or by a very short fusion. Ovipositor with v1 present, either based in membrane or joined to clunium by a sclerotic strip; v3 forming a bulge on side of v2. Phallosome (Fig. 11) with anterior margin membranous, paired lateral endophallic sclerotizations, no external parameres, or these very small and partially sunk into endophallus.

Included species:

aviceps (Badonnel), 1986, Colombia, new combinations from *Epipsocus*.
bogotana (Roesler), 1940, Colombia, new combination from *Epipsocus*.
cubitalis (Mockford), 1996, Venezuela, new combination from *Epipsocus*.
ditata Navás, 1927, Costa Rica.
molinae (Williner), 1949, Bolivia, new combination from *Epipsocus*.
nebulosa (Roesler), 1940, Brazil (Santa Catharina), new combination from *Epipsocus*.
pechi (Williner), 1949, Bolivia, new combination from *Epipsocus*.
?picta (Banks), 1920, Brazil, new combination from *Epipsocus*. Placed here because it appears to be close to *G. plaumanni* (Roesler), which is known to belong here.
plaumanni (Roesler), 1940, Brazil (Santa Catharina), new combination from *Epipsocus*.
semiaptera Mockford, 1996, Venezuela.

Discussion: The genus *Goja* was based on a species with multiple veins in Rs and M of both the forewing and the hindwing. The genus is held together by an array of characters, and within it are species with normal venation, *i.e.*, no extra veins in either fore- or hindwing. This genus appears to be restricted to the American Tropics and south to about 40° in Chile.

Heteroepipsocus Li, 1995a

Type species: *H. longicellus* Li, 1995a (original designation).

Definition: Lacinial tip slender, non-denticulate. Pretarsal claws lacking preapical denticle. Both sexes fully winged (? see note under *H. inornatus* [Banks], below). Venation normal, with no extra veins in Rs or M. In hindwing Rs and M joined by a short crossvein or at a point. Ovipositor with v1 present, slender, attached at base to clunium; v3 represented only by field of setae on v2; v2 terminating in extremely slender process. Phallosome with anterior margin sclerotized (closed), external parameres well developed; endophallus without sclerotizations.

Included species:

brevicellus Li, 1995a, China
?inornatus (Banks), 1916, Philippines, Indonesia, new combination from *Epipsocus*. If the figures by Vaughan *et al.* (1989) truly represent this species, the wing-venational details suggest placement here.
longicellus Li, 1995a, China.

Discussion: As noted in the discussion of *Cubitiglabra*, a close relationship seems to exist between these 2 genera. The Rs-M crossvein in the hindwing, seen also in *Goja*, probably does not indicate a close relationship to that genus. Several other characters separate them. Regardless of the accuracy of determination of the species determined as *Epipsocus inornatus* Banks from Krakatau by Vaughan, *et al.* (1989), it seems to belong here and thus to provide female characters for the genus.

***Hinduipsocus* Badonnel, 1981**

Type species: *H. annulipes* Badonnel, 1981 (original designation).

Definition: Outer cusp of lacinial tip with numerous denticles. Pretarsal claw with preapical denticle. No row of cones on fore or hind femur. Females micropterous (males unknown). Subgenital plate extended posteriorly as a median tongue bearing 2 slender processes at tip. Ovipositor with v1 present, based in membrane; v3 represented by a field of setae on side of v2.

Included species:

annulipes Badonnel, 1981, India.

atratus Badonnel, 1981, India.

coleoptratus New, 1987, Nepal.

hongkongensis Li and Mockford, 1997, Hong Kong.

Discussion: As noted above, *Hinduipsocus* resembles *Dichoeipsocus* in subgenital plate, but differs in several other characters. It shows much similarity to *Bertkauia*, differing in the known characters only in the presence of minute winglets and in the posterior extension of the subgenital plate.

***Mesepipsocus* Badonnel, 1969**

Type species: *M. grassei* Badonnel, 1969 (= *Psocus mobilis* Hagen, 1861).

Definition: Outer cusp of lacinial tip with numerous small denticles. Pretarsal claws with preapical denticle. No row of cones on front or hind femur. Both sexes fully winged. Venation normal, rarely with extra veins, except 4 M veins dichotomously branched in forewing of several South American and Antillean species, 2 South American species with 5-branched M, and 1 of these with extra veins in Rs and Cula. In hindwing Rs and M fused for a distance. Ovipositor lacking v1(a very short, slender v1 present in some undescribed species noted by A. N. Garcia Aldrete, *in litt.*); v3 usually a lobe on side of v2, but the lobe sometimes not conspicuous. Phallosome membranous on an-

terior margin, with rudimentary or no external parameres; endophallus without sclerotizations.

Included species:

andrewsi Turner, 1975, Jamaica, new combination from *Epipsocus*.

antillanus Banks, 1924, Jamaica, new combination from *Epipsocus*.

arborescens New and Thornton, 1988, Peru, new combination from *Epipsocus*.

bordoni (Badonnel), 1987, Venezuela, new combination from *Epipsocus*.

brazilianus (New), 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

braziliensis (New), 1980, Brazil (Amazonas), new combination from *Dicropsocus*

brevistigma (New), 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

broadheadi Turner, 1975, Jamaica, new combination from *Epipsocus*

brunellus (New), 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

campanulatus (Thornton and Woo), 1973, Galápagos, new combination from *Epipsocus*.

capitulatus (New) 1980, Brazil (Amazonas), new combination from *Epipsocus*.

clarus (Mockford), 1969, Mexico (amber), new combination from *Epipsocus*.

fuscatus (New), 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

fuscivenatus (New and Thornton), 1988, Peru, new combination from *Epipsocus*.

icarus (Banks), 1941, Dominican Republic, new combination from *Epipsocus*.

latiphallus (New and Thornton), 1988, Peru, new combination from *Epipsocus*.

mobilis (Hagen), 1861, Cuba and Gabon

newi Badonnel, 1974, Brazil (Sao Paulo)

niger (New), 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

obscurus New, 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

ornatus (Mockford), 1974, Cuba, new combination from *Epipsocus*.

peruanus New and Thornton, 1988, Peru, new combination from *Epipsocus*.

proctus New and Thornton, 1988, Peru, new combination from *Epipsocus*.

roesleri New, 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

roncadorensis New, 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

semiclarus (Mockford), 1991, Brazil (Roraima), new combination from *Epipsocus*.

sinuatus New, 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

taitubai New, 1972, Brazil (Mato Grosso), transferred by Badonnel, 1974

tambopatensis New and Thornton, 1988, Peru, new combinations from *Epipsocus*.

umbratus New and Thornton, 1988, Peru, new combination from *Epipsocus*.

Discussion: This large assemblage of species is primarily restricted to tropical America, except for one species found in Cuba and West Africa. Several species and species complexes within this genus are very distinctive, and it may be useful to break this genus into several genera at some future time.

***Odontopsocus* Badonnel, 1987**

Type species: *O. orghidani* Badonnel, 1987 (original designation).

Definition. Outer cusp of lacinial tip elongate, slender, with several denticles. Pretarsal claws lacking preapical denticle. Front and hind femora lacking row of cones. Females apterous (males unknown). Subgenital plate not extended on posterior margin in middle. Ovipositor with v1 present, based in membrane; v3 a conspicuous lobe on side of v2.

Included species:

badonneli Mockford, 1996, Venezuela.

orghidani Badonnel, 1987, Venezuela.

Discussion: *Odontopsocus* shows a number of similarities to *Dichoepipsocus*. In both genera the head is rounded, the outer cusp of the lacinial tip is elongate and denticulate, the pretarsal claw lacks a preapical denticle, the winglets are developed to the same extent, and v1 is present. They differ in the somewhat shorter, rounder head and shorter outer cusp of the lacinial tip in *Dichoepipsocus*, also in the posterior extension of the subgenital plate and in the nature of the basal attachment of v1 in that genus. Males of neither genus are known. A macropterous nymph of *Odontopsocus* is at hand, but its sex cannot be determined.

Species incertae sedis

Epipsocus argentinus Badonnel, 1962, Argentina (described from a nymph).

Epipsocus atratus New, 1980, Brazil (Amazonas).

Epipsocus beguiristaini Williner, 1949, Bolivia.

Epipsocus blandus New and Thornton, 1988, Peru.

Epipsocus borgmeieri R. Karny, 1926, Brazil.

Epipsocus conspersus Banks, 1914, India (Assam).

Epipsocus fuscareolatus New, 1980, Brazil (Amazonas).

Epipsocus hageni Banks, 1937a, Taiwan.

Epipsocus maculithorax New, 1980, Brazil (Amazonas).

Epipsocus marginatus Enderlein, 1903, New Guinea.

Epipsocus nepos Enderlein, 1900, Peru.

Epipsocus opticus New and Thornton, 1988, Peru.

Epipsocus pennyi New, 1980, Brazil (Amazonas).

Epipsocus phaeus New, 1980, Brazil (Amazonas).

Epipsocus stigmaticus Mockford, 1991, Brazil (Roraima).

3. General discussion

The Family Epipsocidae differs from the Family Neurostigmatidae (Eertmoed, 1973) by only a few known characters. These are the presence in the latter Family of crossveins in the pterostigma, Cu1a arising from the wing margin, and a series of tubercles on the preclunial abdominal terga. These few characters confer such a striking difference in overall appearance between members of the 2 Groups that it seems reasonable at present to regard them as different families. At present, however, we cannot assume a Sister-group relationship of these 2 Families. There is no information to rule out the possibility that Neurostigmatidae has arisen from within Epipsocidae.

The reassignment of species from *Epipsocus* to other Genera has resulted in greater consistency of geographic distribution shown by the Genera. Thus, all of the extant species of *Epipsocus* are tropical American (although *E. avus* from the Baltic amber suggests a wider distribution in Eocene-Oligocene times). All of the species of *Bertkauia* are Holarctic except for *E. remyi* on La Réunion Island; all of those of *Epipsocopsis* are Old World tropical, etc.

There is not yet enough information to allow one to determine polarity of character states. Therefore, we cannot yet propose a cladistic classification for the Family. Nevertheless, by comparison with other Families of Group Epipsocetae and Suborder Psocomorpha, it is possible to point out a few evolutionary trends within the family. These include the following.

1) A lacinial tip with broad outer cusp bearing numerous small denticles is seen in the Genera *Epipsocus*, *Mesepipsocus*, *Goja*, *Hinduipisocus*, and *Bertkauia*. It also is seen in the Families Cladiopsocidae, Ptiloneuridae, and Neurostigmatidae, as

well as in some members of the Families Asiopsocidae and Caeciliusidae of the Group Caecilietae. It is probably the plesiomorphous state in the Epipsocidae, and probably from it have been derived the narrower but still denticulate outer cusp of *Odontopsocus* and *Dichoepipsocus*, the condition in *Epipsocopsis*, wherein some species have a few large denticles and others none, and the condition in the generic pair *Cubitiglabra* and *Heteroepipsocus*, in which there is no trace of denticles and an outer cusp cannot be clearly separated from an inner cusp.

2) A trend toward multiple Rs and M branches in the forewing is identifiable. Without much doubt, the plesiomorphous condition for the Family is a 2-branched Rs and a 3-branched M. This condition is called "normal venation" in the generic definitions and discussions above. A dichotomously 4-branched M has arisen at least once in the genus *Mesepipsocus*. More complex venation is present in *M. taitubai*, where Rs may be dichotomously 4-branched, a pterostigma-Rs crossvein is present, and M may be up to 5-branched. A still more complex venation is seen in *M. brasiliensis*, in which there are, in addition to the complexities of *M. taitubai*, a crossvein within the pterostigma, two small closed cells below the pterostigma, a M-Cula crossvein, and a 2-branched Cula. In the genus *Goja* some species have normal venation, whereas others have up to a 4-branched Rs and 7-branched M in the forewing. The hindwing may also be affected in this genus, with up to 4 branches of Rs and 5 of M. A complex system of multiple Rs and M veins is also seen in the forewing of *Dicropsocus*, which has probably arisen out of normal venation in *Epipsocopsis*.

3) The Rs-M junction in the hindwing appears to be normally via a rather long fusion. This is seen in all species of *Epipsocus*, *Epipsocopsis* (with a few exceptions), *Mesepipsocus*, and males of *Bertkauia*. It is also seen in all of the other families of Group Epipsocetae. At least 3 times in the Epipsocidae an Rs-M crossvein has arisen in the hindwing, namely in the genus *Goja*, in the generic pair *Cubitiglabra* and *Heteroepipsocus*, and in *Epipsocopsis costalis* and a few close relatives.

4) Wing reduction is seen in several lines. In *Epipsocopsis* a single species, *E. angolensis*, has brachypterous females in which venation persists in the short wings. In *Goja*, males are fully winged while females are micropterous. The winglet is articulated basally but shows no venation. The

same is true for females of *Dichoepipsocus* and *Odontopsocus*, 2 Genera which show enough other similarities to suggest a common origin. In *Hinduipsocus*, the winglets of females are mere sac-like extensions of the thoracic terga with little or no basal articulation. Unfortunately, males remain unknown for these last 3 genera. In *Bertkauia*, with fully winged males, females are completely wingless.

5) Absence of v1 is seen in the 2 genera *Mesepipsocus* and *Epipsocopsis*. It has arisen, then, either once or twice (or more if *Mesepipsocus* represents more than 1 genus). It would be tautological to suggest that these 2 genera are closely related based on a single shared character. Their relationship will have to be resolved on other still unknown characters.

6) Reduction of the external parameres is seen in several genera. Well developed external parameres exist in the Genera *Bertkauia*, *Cubitiglabra*, *Dicropsocus*, *Epipsocopsis* (most species), and *Heteroepipsocus*. They are also found in members of the other Families of Epipsocetae (see figures of Eertmoed, 1973). They are either greatly reduced, sunk into the endophallus, or lost entirely in *Epipsocus*, *Mesepipsocus*, *Goja*, and at least one species of *Epipsocopsis* (note Fig. 54 in New and Thornton, 1975). Such reduction has probably occurred in more than one evolutionary line in the family.

7) Changes in endophallic sclerotization have occurred, but it is not possible at present to state which direction they have gone. Well developed endophallic sclerotization is relatively rare in the Epipsocidae. It is restricted to the genus *Goja* and a few species of *Epipsocus*. Elsewhere in the Epipsocetae it is seen in the Dolabellopsocidae, Ptiloneuridae, and Neurostigmatidae, but not in the Cladiopsocidae (Eertmoed, 1973, 1986). It is not at all obvious that these structures are homologous from one family to another within the Epipsocetae or between *Epipsocus* and *Goja* in the Epipsocidae. In *Goja* it seems likely that some of them have arisen from the bases of the external parameres, which seems not to be the case in *Epipsocus*.

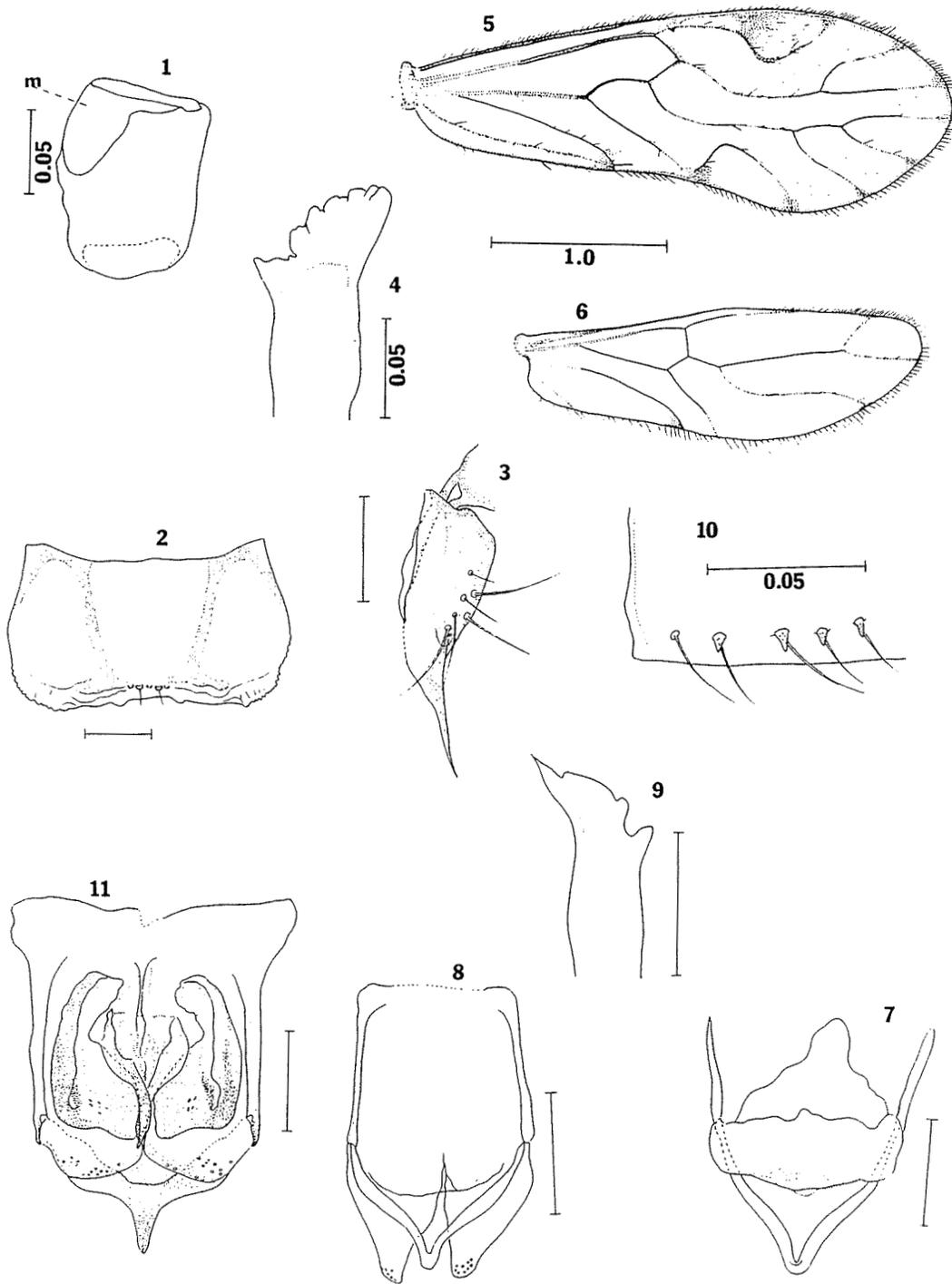
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Figs. 1-11. Fig. 1. *Epipsocus* sp., antennal scape; m = membranous area of anterior face. Fig. 2. *Epipsocus* sp., labrum. Fig. 3. *Epipsocus* sp. ♀, ovipositor valvulae. Fig. 4. *Bertkauia crosbyana* Chapman ♀, lacinial tip. Fig. 5. *Epipsocus* sp. ♀, forewing. Fig. 6. *Epipsocus* sp. ♀, hindwing. Fig. 7. *Epipsocus* sp. ♂, phallosome. Fig. 8. *Bertkauia crosbyana* Chapman ♂, phallosome. Fig. 9. *Epipsocopsis* sp. ♀, lacinial tip. Fig. 10. *Epipsocopsis* sp. ♀, base of front femur with cone-based setae. Fig. 11. *Goja* sp. ♂, phallosome.

Scale lines = 0.1 mm unless otherwise indicated.