

Classification and Phylogenetic Relationships Between Genera of the Tribe Eucerini (Hymenoptera, Anthophoridae) with Two Submarginal Cells*

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Tribe Eucerini Latreille, 1802, belongs to the subfamily Anthophorinae and includes at least 550 species in 38 genera. A detailed diagnosis of it was given by Michener (Michener, 1944: 270-171, 281-282; Michener and Moure, 1957: 400-401). The tribe has almost universal distribution (except Australia), but has maximal representation in the New World, where 300 genera (29 endemic) have been found. In the Old World, only 9 genera are known so far. Among these, the poorly distributed and species rich genus *Tetralonia* Spinola is the only genus of the Old World tribe also represented in the Nearctic by a series of species which in some publications are separated a different genus *Synhalonia* Patton (for example, Hurd, 1979) without sufficient justification (Michener, 1944). LaBerge, 1957; Tkalcu, 1984b). The other 5 genera are relatively small, specialized, and have narrow distribution: *Eucera* Friese (Afrotropical, about 10 species), *Melissina* Cockerell (1 species from Pakistan and 1 species from Central Asia), *Notolonia* Popov (1 species from Turkmenia), *Thygatina* Cockerell (1 species from Sri Lanka), and *Teraloniella* Ashmead (a few species from Southern Europe, Central Asia, Sudan, and India; a possible synonym of the Nearctic *Xenoglossodes* Ashmead). The remaining 3 genera (*Eucera* Scopoli, *Cubitalia* Fresise, and *Pseudeucera* Tkalcu), which will be described below, are the only genera in the Eucerini with 2 submarginal cells on the forewing, all others (including all New World genera) have 3 submarginal cells.

Differences are also significant in the extent of study of Eucerini of the Old and New Worlds. Several important comparative-morphological studies and modern revisions at the generic and subgeneric levels have been made on the American fauna (Michener, LaBerge, and Moure, 1955; Moure and Michener, 1955; LaBerge, 1957, 1970), and monographs have appeared on the large genera (LaBerge, 1956a, 1956b, 1961; Hurd and Linsley, 1970) and many small genera. In the Old World, revisions and compilations (except a few regional ones—for example, Dusmet, 1926; Moczair, 1954; Iuga, 1958) on the tribe are virtually absent after the monograph of Friese (1896), wherein, all Eucerini were considered under *Eucera*, although many new species and several genera have been described since then (see above). Only very recently, studies have been started on the classification of Old World Eucerini at the present level through the efforts of the Czechoslovak amateur entomologist B. Tkalcu. Besides reinvestigation of the type specimens of many forms, listing of synonyms, and description of new species, he made the following important contributions: genus *Cubitalia* was revised (Tkalcu, 1984a), and classification of the large genus *Eucera* was started (Tkalcu, 1978, 1984b).

The phylogenetic relationships between Eucerini genera have not been examined. The direc-

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Relationships Between Hymenoptera, Antho- mal Cells*

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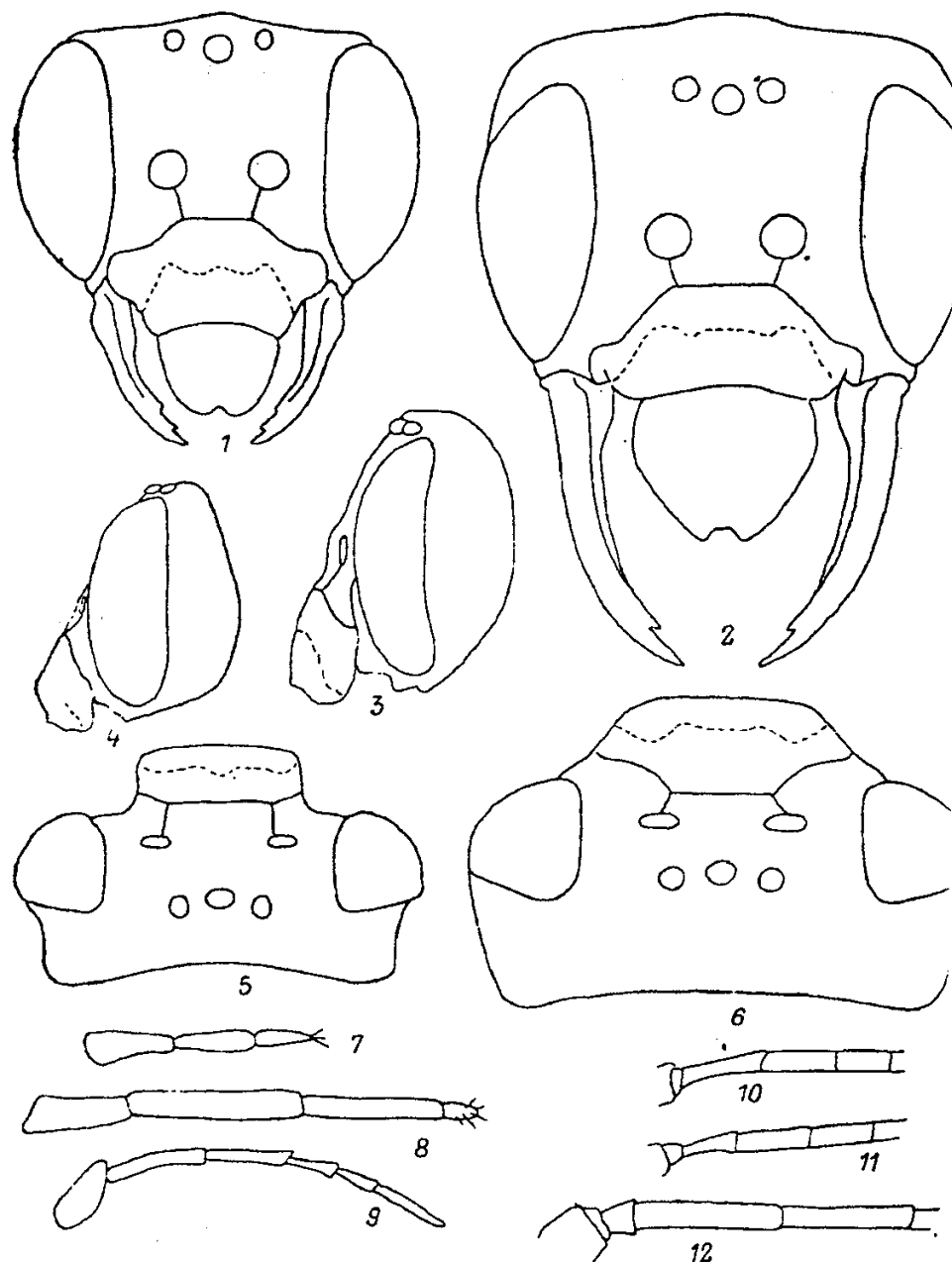


Fig. 1-12. Head of male and its appendages in *Opacula donatica* (1, 3, 5, 7, 10), *Pseudeucera parvicornis* (4, 11), *Cubitalia tristis* (2, 6), *C. morio* (8), *Eucera caspica* (9), and *E. grescens* (12). 1, 2) head in frontal view; 3, 4) head in lateral view; 5, 6) head in dors view; 7-9) maxillary palpus; and 10-12) basal antennal segments.

tion of evolution of some characters within genus *Melissodes* Latr. was discussed by LaBerge (1961). Only one fossil species of Eucerini is known (Zeuner and Manning, 1976), *Tetralonia berlandi* Theobald, 1937, described from the Oligocene. The other fossil species, described as *Eucera mortua* Meunier, 1920, actually belongs to *Anthidium* Latr. (Salt, 1931).

Although more than 100 publications have appeared on nesting of Eucerini (cf. Linsley, MacSwain, and Smith, 1955; Michener and Lange, 1958; Miliczky, 1985), they do not cover more than 1-1.5% of the species of this tribe. A few larvae of different Eucerini genera studied were found to be very similar (Rozen, 1965). There are species with extremely multifarious types of trophic relationships among eucerines, but most species of the tribe with known food habits, including most representatives of the large genera (*Tetralonia*, *Eucera*, *Melissodes*), are polyphages. Some fairly abundant eucerine species play a significant role in the pollination of entomophilous crops. For example, the oligotroph of leguminous crops, *Eucera clypeata* Erichson, has been noted as one of the most important pollinators of lucerne in Eurasia.

The present article deals with the classification and understanding the phylogenetic relationships of Eucerini genera with 2 submarginal cells, which are considered by us as a monophyletic group (see discussion below). This study is related to the taxonomic revision of *Eucera* and close genera in the fauna of the USSR and adjoining countries by one of the present authors (A. A. Sitdikov). The discovery of a male not placeable in any of the Eucerini genera served as the direct impetus for the comparative-morphological study presented here. Analysis of the voluminous collection at the Zoological Institute, Academy of Sciences of the USSR (more than 10,000 specimens of *Eucera* and 20 of *Cubitalia* and *Pseudeucera*) formed the basis of this study. Type and comparative material from the Zoological Museum, Moscow State University (Moscow), and from six museums abroad were also studied. In all, type specimens of 32 nominal species were studied. The article comprises the following sections: 1) key to 4 genera (including *Opacula* gen. n) on the basis of males involving the main characters common to both sexes (a key for females of *Eucera*, *Cubitalia*, and *Pseudeucera* was published by Tkalcu (1978), and genus *Opacula* is so far known only on the basis of a male); 2) list of genera; 3) identification of the direction of evolution of the diagnostic characters of genera; 4) reconstruction of phylogenetic relationships between genera; and 5) description of *Opacula donatica* sp. n. The morphological terminology follows the "Fauna of the USSR" for tribe Nomiodini (Pesenko, 1983).

KEY TO GENERA ON BASIS OF MALES

- 1 (2). Maxillary palpi 6-segmented (very rarely 5-segmented) (Fig. 9). 1st submarginal cell of forewing smaller than 2nd, and accordingly, 2nd section of medial vein longer than 4th (Fig. 14). Segment I of antennal flagellum short, ratio of its length to maximum width 0.9-2.5, and ratio of length of segments I and II 1.7-5 (Fig. 12). Gradulus of sternum VI arcuate (Fig. 30). Middle region of sternum VII of metasoma more or less flat (Fig. 35, 36).... 1. *Eucera* Scopoli.
- 2 (1). Maxillary palpi 3-4 segmented (Fig. 7, 8). 1st submarginal cell of forewing equal to 2nd, 2nd section of medial vein equal to 4th (Fig. 15). Segment I of antennal pedicellus long, its length to that of maximum width 3.3-4, and ratio of lengths of segments II and I 0.7-1.2 (Fig. 10, 11). Gradulus of sternum VI on lateral branches twisted backward with formation of distinct angle, sometimes smoothened in *Cubitalia* (Fig. 29). Middle region of sternum VII of metasoma arcuately convex downward posteriorly (Fig. 31-34).
- 3 (4). Postgradular field of sternum V with 2 tufts of stiff setose hairs directed laterally. Probasis-tarsus bent, of normal length: ratio of its length to total length of 3 following segments 1.8

(Fig. 16, 17). Gonostyle with pointed lamellate ventral process, sharply bent medially at apex. Clypeus (in lateral view) directed downward in lower part (Fig. 3). Midtibiae bent (Fig. 20).....4. *Opacula* Pesenko and Sitdikov, gen. n.

4 (3). Postgradular field of sternum V more or less uniformly pubescent. Probasitarsus straight, reduced; ratio of its length to total length of 3 following tarsal segments 1.2-1.5 (Fig. 18). Gono-style without such process, broadened at apex (Fig. 40, 41). Clypeus bent backward in lower part (Fig. 4). Midtibiae not bent (Fig. 21).

5 (6). Larger: 16-18 mm. Mandibles very long, strongly curved, inner anterior carina not forming subapical projection (Fig. 2). Inner orbits divergent ventrally (Fig. 2). Antennae reduced, reaching only propodeum. Anterior margin of mesobasitarsus and metabasitarsus with notch (Fig. 21, 23). Sternum VII with large transverse vesicular swellings along sides of middle carina (Fig. 33, 34).....3. *Cubitalia* Friese.

6 (5). Smaller: 11-14 mm. Mandibles moderately long, weakly curved, inner anterior carina forming subapical projection (Fig. 1). Inner orbits parallel. Antennae long, extending onto metasoma. Anterior margin of mesobasitarsus and metabasitarsus straight (Fig. 21). Sternum VII without swellings.....2. *Pseudeucera* Tkalcu.

1. Genus *Eucera* Scopoli, 1770.

Scopoli, 1770: 8; Lepeletier, 1841: 114; Friese, 1896: 102, 185 (*Eucera* subg.); Dusmet, 1926: 83; Schmiedeknecht, 1930: 792; Alfken, 1936: 1; Osychnyuk et al., 1978: 488; Tkalcu, 1978: 156; 1984b: 1.

Type species *Apis longicornis* Linne, 1758, by subsequent designation (Latreille, 1810: 439; cf. Sandhouse, 1943: 549).

At present the genus includes 130 species, of which only 35 have been distributed into 6 distinct subgenera (*Eucera* s. str., *Hetereucera*, *Pareucera*, *Stilbeucera*—Tkalcu, 1978; *Atopeucera*, *Pteneucera*—Tkalcu, 1984b), and 8 species are included under the group of species of *E. atricornis* F. (Tkalcu, 1978). The area of distribution of the genus covers the entire Palearctic (except its extreme north), but does not spread beyond its limits. On the whole, the genus may be characterized as inhabitants of arid and semiarid regions. Only 7 species (5.4%) have been found in the forest areas of Eurasia. The genus is most abundantly represented in the Mediterranean Subregion (121 species, of which 108 are found in that area).

2. Genus *Pseudeucera* Tkalcu, 1978

Tkalcu, 1978: 157, 158.

Type species *Eucera parvicornis* Mocsáry, 1878, by original designation and monotypy.

The genus includes one species, known from Hungary (Mocsáry, 1878; Moczár, 1954), Greece (Friese, 1896), Romania (Iuga, 1958), and SE Ukraine (Odessa and Kherson Provinces; Osychnyuk, 1957). A polytrophic species found on flowers of plants belonging to 5 families. Nesting not known.

3. Genus *Cubitalia* Friese, 1911

Friese, 1911: 136 (*Eucera* subg.); Tkalcu, 1978: 157, 158; 1984a: 1.

Type species *Eucera (Cubitalia) breviceps* Friese, 1911, by monotypy.

The genus includes 4 species, found in the NE Mediterranean: *C. breviceps* Friese (Turkey), *C. boyadjani* Vachal (Turkey), *C. tristis* (Morawitz) (Turkey, Caucasus: Borzhomi), and *C. morio* Friese (Yugoslavia, Bulgaria, Greece, Turkey). *C. morio* is reported for the first time for the USSR: Crimea: Kerch' (Pesenko), 1 male; Simferopol', 16.IV.1924, 1 female; Krasnodar Terr.: Anapa, 11.V.1918 (Skorikov), 1 male. New records of *C. tristis*: Krasnodar terr.: Anapa, 1 male and 4 female; Novorossiysk, 1 female. Trophic relationships and nesting of the species of this genus are unknown.

4. Genus *Opacula* Pesenko et Sitdikov, gen. n.

Type species *Opacula donatica* Sitdikov, sp. n.

A monotypic genus. The only species is described at the end of this article on the basis of 1 male from W Kirgizia. The generic name is derived from the Latin word *Opacus* dull, dark; grammatically the genus is feminine. The genus is included in the key, and complete description on the basis of 26 characters may be found in Table 1.

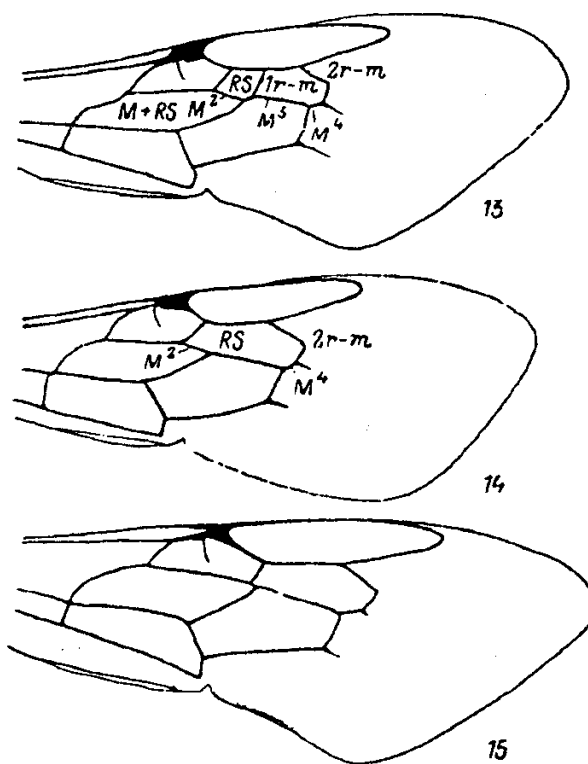


Fig. 13-15. Forewings of *Tetralonia velutina* (13), *Eucera caspica* (14), and *Opacula donatica* (15).

DIRECTION OF EVOLUTION OF CHARACTERS

The complete list of characters (total 27) on the basis of which the 4 genera of Eucerini are distinguished, is given in Table 1. Of these, 10 characters (Nos. 1, 4, 8, 14, 16, 18, 20, 21, 22, and 25 in Table 1) vary within the large genus *Eucera* but are included in the analysis for reconstruction of phylogenetic relationships between the 3 remaining genera. Besides the diagnostic characters at the generic level (and partly at subgeneric level for *Eucera*) included in Table 1, the main characters being illustrated in Fig. 1-41, the following 3 have also been considered, the change in which was associated with the early stages of evolution of the group analyzed (Fig. 42): a) presence or absence of crossvein 1 *r-m* on forewings, b) structure of hairs (branched or unbranched) of the collecting apparatus (baskets) on the hind-tibia of the female and c) the nature (nonspecialized or specialized) of the pubescence on the inner surface of the hindtibia of the female. All characters analyzed pertain to adult morphology, inasmuch as the biology and preimaginal stages of 3 of the 4 genera (except *Eucera* partly) have not been studied at all.

The baskets were analyzed simultaneously (and parallel) with proposal and confirmation of various phylogenetic hypotheses (concerning sister groups, closest hypothetical ancestors, etc.); therefore, discussion on the direction of character evolution (i.e., their polarity) in a particular section is to some extent artificial and is dictated only by logical construction. Paleontological data on the tribe, as indicated above, are practically nonexistent. Therefore, the main criterion for determining polarity of characters was functional-structural (comparative-morphological), based on identification of specialization, oligomerization, irreversible reduction, and other known trends in the evolution of morphological structures. This was supported by the logical criterion based on the principle of economy (minimum evolution) and out-group comparison. Genus *Tetralonia* in the first place, and all genera of tribe Eucerini (including *Tetralonia*) with 3 submarginal cells, were included subsequently as such "external" groups (in relation to the genera analyzed). The use of these criteria leads to a definite conclusion concerning the apomorphic nature of changes in the following characters, determining the major difficulties (being synapomorphic) in the phylogenetic scheme of the genera under consideration.

"Disappearance" of one submarginal cell as a reduction of vein 1 *r-m* (Fig. 13-15, and character a in Fig. 42). It serves as the main diagnostic feature of the entire group of 4 genera under discussion. It originates independently in many families and subfamilies of Apoidea (Michener, 1944) and often characterizes subfamilies, tribes or groups of genera, although sometimes reduction of this vein is observed in individual specimens of species with 3 submarginal cells.

Shift of vein *RS* to the distal margin of the forewing (character 5). This is directed toward enlargement of the submarginal region of the wing, which is weakened after the reduction of vein 1 *r-m* (Fig. 13 and 14, in which venation of wings of *Tetralonia* and *Eucera* differs only by the presence or absence of vein 1 *r-m*), and leads to equalization of size of the remaining two submarginal cells and relative elongation of the 4th section of vein *M* (at the cost of 2nd section; Fig. 14 and 15) in the genera *Pseudeucera*, *Cubitalia*, and *Opacula*.

Reduction of the number of segments of maxillary palpus from 6 to 3-4 (character 3 in Table 1). In some *Eucera*, which are generally characterized by the initial type (Fig. 9), corresponding to 6-segmented telopodite of the maxilla I of crustaceans, the maxillary palpus becomes 5-segmented (relatively more frequently in *E. clypeata* Erichson; Tkalcu, 1978) as a result of fusion of segments III and IV. Segment IV (when present) has a rudimentary appearance (Fig. 8) in the genera with 3-4 segmented palpus (from the group with 2 submarginal cells). Contrary to the indication of Tkalcu (1978), specimens with 3-segmented palpus are sometimes found among *Cubitalia*, and with 4-segmented palpus among *Pseudeucera*. Most probably, evolution of the entire

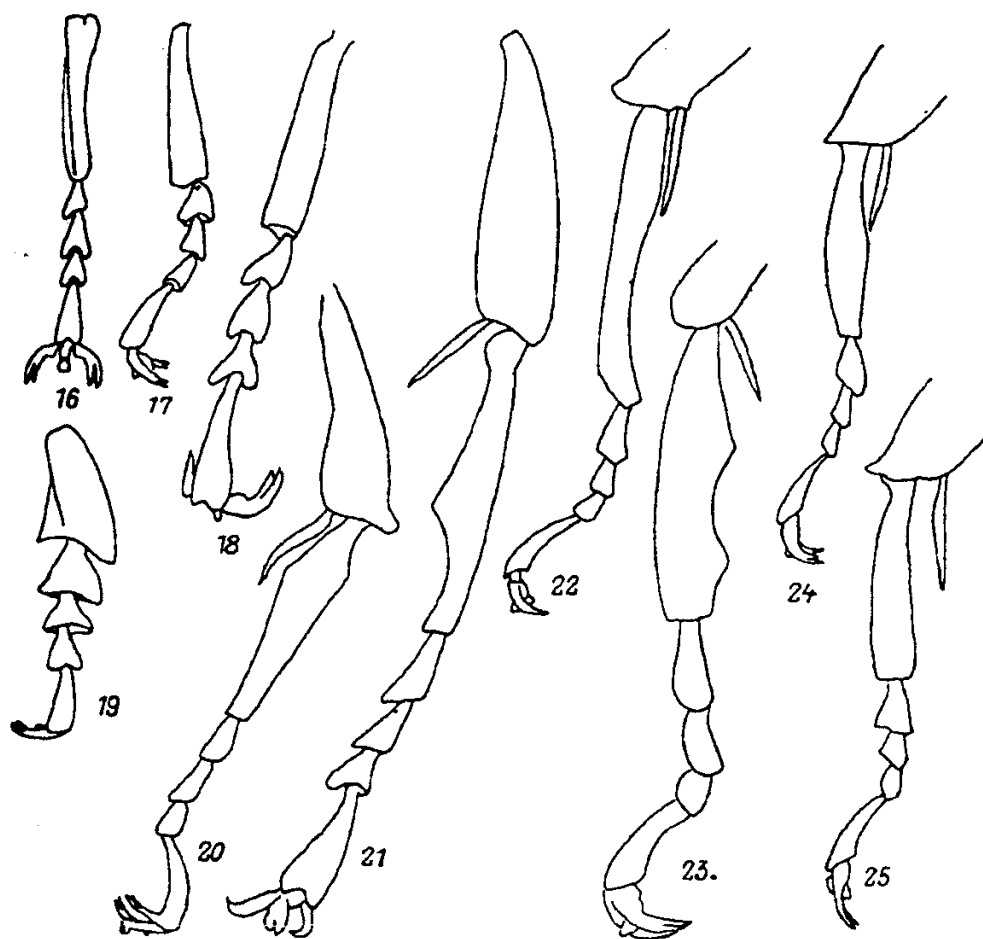


Fig. 16-25. Legs of males of *Opacula donatica* (16, 17, 20, 22), *Cubitalia morio* (18, 21, 23), *Pseudeucera parviconis* (24), *Eucera longicornis* (25), and females of *Pseudeucera parviconis* (19). 16-19) Foretarsus (16: anterior view, 17-19: lateral view); 20, 21) mid-tibia and tarsus; and 22-25) end of hindtibia and tarsus.

tribe *Eucerini* was accompanied by reduction of maxillary palpi. In reality, besides *Eucera*, only *Tetralonia* (+*Synhalonia*) and some species of the 3 New World genera have 6-segmented palpi. Palpi in most genera of this tribe are 5-segmented, and in some 4- or 3-segmented. This trend is best expressed in the genus *Melissopilia*, some of whose species have 2-segmented palpi.

Elongation of segment I of antennal flagellum of male (character 13). Almost all genera of the tribe, including the generalized genera *Tetralonia* and *Eucera* (Fig. 12), have strongly reduced segment I of flagellum ($1/8$ - $1/4$ as long as segment II, besides very small and specialized genera, such as *Syntrichalonia*, *Xenoglossa*, and *Martinaois*, and some species of other genera (for example, *Peponapis*). Therefore, its elongation, typical of *Pseudeucera* (Fig. 11), *Cubitalia*, and *Opacula* (Fig. 10), should be considered as secondary homonomization of antennae. LaBerge (1961) expressed a similar opinion concerning the much weaker tendency of relative increase in segment I (up to 0.4 length of segment II) in some subgenera of *Melissodes*, but there it is associated with relative reduction of antennae.

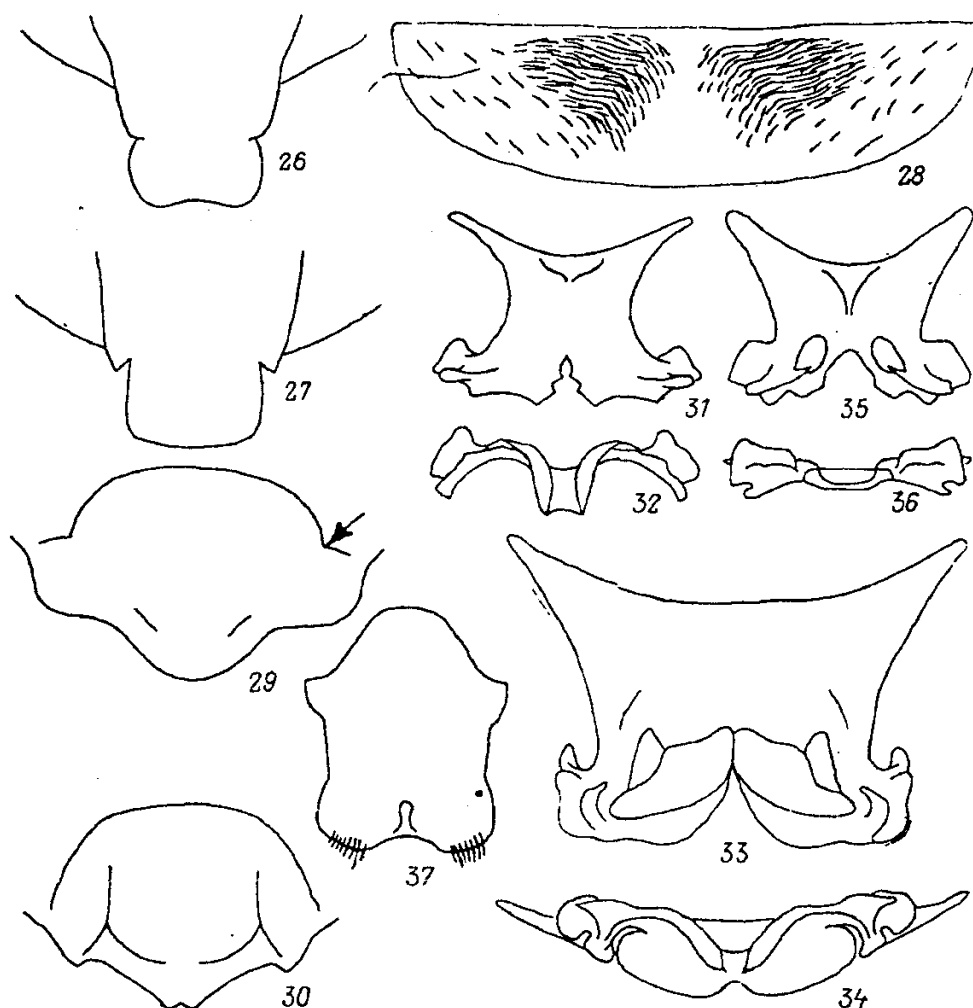


Fig. 26-37. Posterior targa and sterna of *Opacula donatica* males (26, 28, 29, 31, 32, 37), *Eucera longicornis* (27, 30, 35, 36), and *Cubitalia morio* (33, 34) males. 26, 27) Posterior part of tergum VII with pygidium; 28) sternum V; 29, 30) postgradular field of sternum VI; 31-36) sternum VII (31, 33, 35—ventral view; 32, 34, 36—posterior view); and 37) sternum VIII (ventral view).

Backward twisting of lateral branches of gradulus of sternum VI of male with the formation of a distinct angle (character 23). This is a unique character in the Eucerini, typical only to *Pseudeucera*, *Cubitalia*, and *Opacula* (Fig. 29). Apparently, it is a modification of the original (II-shaped or arcuate, Fig. 30) shape of the gradulus in these.

Modification of sternum VII in posteroa medial region (character 24). The sternum VII of *Tetralonia* and *Eucera* (Fig. 35, 36) in this part is more or less flat, usually with well developed paired posteromedial processes, directed posteriorly or posteroventrally. It becomes carinately convex downward in *Pseudeucera*, *Opacula* (Fig. 31, 32), and *Cubitalia*, and besides forms large vesicular transverse swellings along the sides of the carina in the last genus (Fig. 33, 34). In general, the posterior structure of sternum VII of *Eucerini* is extremely complex (inner and outer pro-

cesses of various shape, depressions, elevations, etc. present) and is subject to strong modification within the tribe, the major trends of which still await special study.

Increase in elevation of clypeus (character 9). The clypeus of *Cubitalia* and *Pseudeucera* (Fig. 4) turns backward in the lower part, which distinguishes them from *Eucera* and *Opacula* (Fig. 3) as well as from *Tetralonia* (appearing as "out-group"), and are characterized by relatively poorly convex clypeus, directed downward or slightly forward in the lower part. Character 15 also has similar distribution of conditions and is therefore interpreted as reduction of probasitarsus (compare Fig. 17 and 18).

Reduction of ventral process of gonostyle (character 25; Fig. 38-41). The presence of a ventral process or a rudiment of it in most members of Eucerini with generalized gonostyle (geniculately bent) and its complete absence in the groups with straight gonostyle points particularly toward such direction of evolution of the characters.

The characters of the scopa in females need special mention. The change is within the genus *Eucera* (see characters b and c in Fig. 42). Although the *Opacula* female is unknown, it can be concluded with sufficient assurance that for these characters it is similar to that of females of the closely related genera *Pseudeucera* and *Cubitalia*, wherein differentiation from *Opacula* was pre-

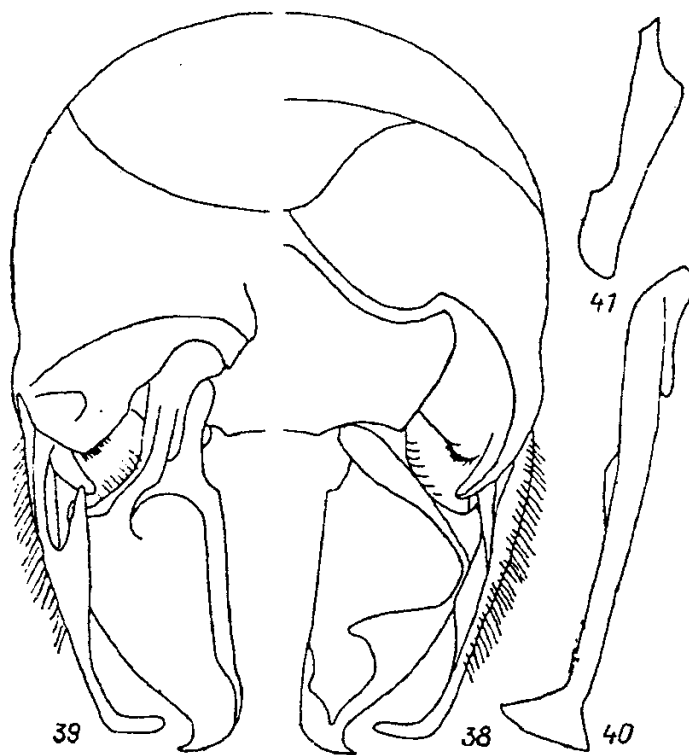


Fig. 38-41. Male genitalia of *Opacula donatica* (38, 39), *Cubitalia morio* (40), and *Pseudeucera parvicornis* (41). 38, 39 genital capsule (38—dorsal view, 39—ventral view); 40, 41) gonostyle (dorsal view).

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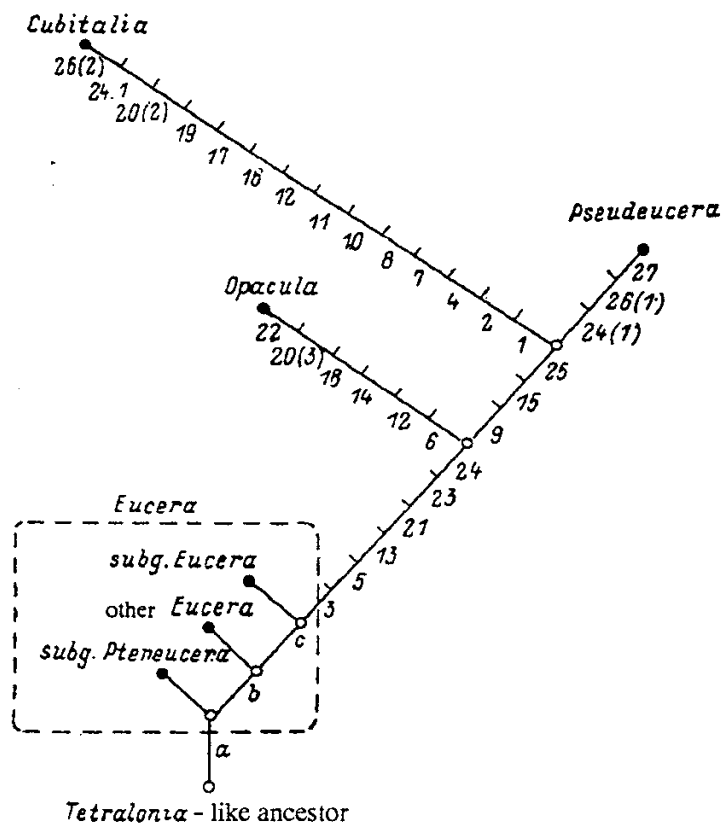


Fig. 42. Diagram of phylogenetic relationships between the genera of tribe Eucerini with 2 submarginal cells. The numerals are those of characters listed in Table 1, which changed in a given internode.

ceded by a long path of evolution from their common ancestor. Each of these characters is represented in the group of genera under consideration by two conditions: in particular, character b—outer hairs of hindtibia branched (only in subgenus *Ptneucera* of *Eucera*) or unbranched (simple; sometimes with the exception of a few branched hairs along the margin of the scopa); and character c—pubescence of the inner hindsurface of the hindtibia made of simple elongate hairs (with the exception of a small narrow triangular area) (in all *Eucera*, except the nominate subgenus) or almost completely of specialized hairs (very short, with flat and sharp widening at the apex). These conditions of both characters are widely distributed in different genera and subgenera of Eucerini. However, defining their evolution as loss of hair branching on the scopa (character b) and specialization of pubescence on the inner surface of hindtibia in female (c) appears quite convincing. In particular, LaBerge (1961) also pointed toward similar direction of evolution of hairs of the scopa (based on character b) within the limits of *Melissodes*.

The polarity of the remaining 18 characters from Table 1, whose advanced conditions determine autapomorphy of *Pseudeucera*, *Opacula*, and especially a large number in *Cubitalia*, is based on the fact that their condition in one of these genera or uniquely among all Eucerini is either more or less distinctly specialized (at least within the limits of the tribe), or is associated with reductions.

Table 1

Comparison of genera of tribe Eucerini with 2 submarginal cells based on 27 characters

Character	<i>Eucera</i>	<i>Pseudocera</i>	<i>Cubitalia</i>	<i>Opacula</i>
I. Both sexes				
1. Body size (length in mm)	10-14 (rarely 7 or 15-17)	11-14	*16-18	13
2. Mandibles (relative length and general shape); ratio of length to distance between bases (externally)	Medium length, little curved, not crossed, 0.6-0.75	Medium length, weakly curved, not crossed, 0.65	Very long, curved, 0.9 (Fig. 2)	Medium long, little curved, 0.9 (Fig. 1)
3. Number of segments of maxillary palpus	6 (rarely 5) (Fig. 9)	*3 (sometimes 4)	*4 (sometimes 3) (Fig. 8)	*3 (Fig. 7)
4. Maxillary palpus seg. I (relative length); ratio of length of segments II and I.	Long; 1 (sometimes 2)	Long; 0.9	*Short; 1.7-2.2 (Fig. 8)	*Long; 1.1 (Fig. 7)
II. Male				
5. Relative size of 1st submarginal cell; ratio of sections II and IV of vein M of forewing	Less than 2nd; $M^2 > M^4$ (Fig. 14)	*Equal to 2nd; $M^2 < M^4$	*Equal to 2nd; $M^2 < M^4$ (Fig. 15)	*Equal to 2nd; $M^2 < M^4$
6. Genal area (dorsal view of head)	Weakly convex (sometimes concave)	Weakly convex	Weakly convex	*Concave (Fig. 5)
7. Position of ocelli; distance from upper margin of middle ocellus to posterior margin of head (in number of ocellar diameters) (dorsal view of head)	Weak; 1.5-2	Weak; 1.5	*Strong; 3-4 (Fig. 6)	Weak; 1.5 (Fig. 5)
8. Inner orbits: distance apart	Close on lower side or parallel (rarely divergent below)	Parallel	*Divergent below (Fig. 2)	Parallel (Fig. 1)
9. Nature of elevation of clypeus (lateral view of head, vertical line along hindmargin of eye)	Evenly convex, lower part directed downward or a little forward	*Lower half turning backward (Fig. 1)	*Lower 1/3 sharply turned backward	Evenly convex, lower part directed downward (Fig. 3)
10. Position of lower margin of clypeus relative to lower margin of eye	Usually well below eye (rarely almost at same level)	Below eye	*Almost even with eye (Fig. 2)	Below eye (Fig. 1)
11. Subapical projection of mandible formed by anterior carine	Present	Present	Lacking (Fig. 2)	Present (Fig. 1)
12. Antenna (relative length)	Long, reaching metasoma, usually beyond some middle; may be reduced	Long; reaching metasoma	*Shorter; only reaching propodeum	*Shorter; only reaching propodeum

13. Segment I of antennal flagellum; ratio of length to max. width; ratio of lengths of segments II and I

*Long; 3.2; 0.8 (Fig. 10)

*Long; 3-4; 0.7-0.8

*Long; 3-4; 1.2 (Fig. 11)

*Long; 0.9-2.5; 1.7-5; (Fig. 12)

Short; 0.9-2.5; 1.7-5; (Fig. 12)

Short; 0.9-2.5; 1.7-5; (Fig. 12)

Short; 0.9-2.5; 1.7-5; (Fig. 12)

14. Proboscis (shape)

*Curved (Figs. 16, 17)

Normal (Fig. 18)

Normal

Normal

Normal

Normal

Normal

15. Proboscis (ratio of length to that of 3 following segments together)

*Shortened; 1.2-1.3

*Shortened; 1.2-1.3

*Shortened; 1.5

*Shortened; 1.5

*Shortened; 1.5

*Shortened; 1.5

*Shortened; 1.5

9. Nature of elevation of clypeus (lateral view of head, vertical line along hindmargin of eye)	Evenly convex, lower part directed downward or a little forward	*Lower half turning backward (Fig. 1)	*Lower 1/3 sharply turned backward (Fig. 3)	*Evenly convex, lower part directed downward (Fig. 3)
10. Position of lower margin of clypeus relative to lower margin of eye	Usually well below eye (rarely almost at same level)	Below eye	*Almost even with eye (Fig. 2)	Below eye (Fig. 1)
11. Subapical projection of mandible formed by anterior carinae	Present	Present	Lacking (Fig. 2)	Present (Fig. 1)
12. Antenna (relative length)	Long, reaching meta- some, usually beyond some middle; may be reduced	Long; reaching meta- some, usually beyond some middle; may be reduced	*Shorter; only reaching propodeum	*Shorter; only reaching propodeum
13. Segment I of antennal flagellum; ratio of length to max. width; ratio of lengths of segments II and I	Short; 0.9-2.5; 1.7-5; (Fig. 12)	*Long; 3-4; 1.2 (Fig. 11)	*Long; 3-4; 0.7-0.8 (Fig. 10)	*Long; 3.2; 0.8 (Fig. 10)
14. Probasitarsus (shape)	Normal	Normal	Normal (Fig. 18)	*Curved (Figs. 16, 17)
15. Probasitarsus (ratio of length to that of 3 following segments together)	Long; c. 2	*Shortened; 1.5	*Shortened; 1.2-1.3 (Fig. 18)	Long; 1.8 (Figs. 16, 17)
16. Anterior margin of mesobasitarsus (shape)	Straight	Straight	*Emarginate in distal half (Fig. 21)	Straight (Fig. 20)
17. Midtibial spur (ratio of lengths of mesobasitarsus and spur)	Long; 2-2.2	Long; 2	*Shortened (Fig. 21)	Long; 2.2 (Fig. 20)
18. Midtibial spur (shape)	Straight	Straight	Straight (Fig. 21)	*Curved (Fig. 20)
19. Hindtibial spur (ratio of length of metatarsus to that of spur)	Long; 2-2.1 (Fig. 25)	Long; 2 (Fig. 24)	Shortened; 3.2 (Fig. 23)	Long; 2 (Fig. 22)
20. Anterior margin of metatarsus (shape)	Straight (Fig. 25)	*1 Convex (Fig. 24)	*2 Medially emarginate (Fig. 23)	*3 Weakly emarginate distally (Fig. 22)
21. Posterior margin of pygidial plate (tergum VII)	Usually straight or weakly emarginate (Fig. 27)	*Medially emarginate	*Medially emarginate (sometimes weakly)	*Medially emarginate (Fig. 26)
22. Vestiture of postgradular area of sternum V	Usually more or less even	More or less even	More or less even	*Pair of tufts of setae directed sidewise (Fig. 28)
23. Lateral angle of gradulus of sternum VI	Lacking (Fig. 30)	*Present	*Present (sometimes weak)	*Present (Fig. 29; v. arrow)
24. Sternum VII, shape of posteromedial part	More or less flat (Figs. 35, 36)	*Carinate ventral projection	*Carinate projection with lateral swellings (Figs. 33, 34)	*Carinate projection below (Figs. 31, 32)
25. Ventral process of gonostyles	*Lacking (except in <i>Peneucera</i>)	*Lacking (Fig. 41)	*Lacking (Fig. 40)	Present (Fig. 38, 39)
26. Tip of gonostyles (shape)	*Club-shaped (gonostyle at the end, sharply bent medially) or modified (in advanced subgenera)	*1 Elongate mesal widening (Fig. 41)	*2 Triangular widening (Fig. 40)	Clavate (at end sharply bent medially) (Figs. 38, 39)
27. Foretarsal segments I-III (shape)	Normal	*Strongly widened (Fig. 19)	Normal	(Female unknown)

III. Females

Note. Single asterisk (*) indicates apomorphic condition of character.

PHYLOGENETIC RELATIONSHIPS BETWEEN GENERA

One of the key problems in reconstruction of phylogeny of Eucerini genera with 2 submarginal cells is related to the establishment of monophyly of this group. Reduction of vein 1 *r-m* of the forewing, distinguishing them from other genera of the tribe, could in principle have originated independently and repeatedly (at least within the limits of the large and generalized genus *Tetralonia*). So far, other potential synapomorphies of *Eucera* with advanced and undoubtedly related genera *Pseudeucera*, *Cubitalia*, and *Opacula* have not been found. However, there are more direct or indirect data in support of their polyphyletic origin. The accepted hypothesis concerning monophyly of *Eucera* and consequently the entire group of 4 genera is not only "economical" (single reduction instead of repeated), but also permits us to maintain *Eucera* intact as accepted by all taxonomists (as a subgenus in the studies of the last century).

More convincing evidence in favor of monophyly (or, which is less probable, polyphyly) of *Eucera* would be possible only after reconstruction of the phylogenetic relationships between the genera and subgenera of the entire tribe Eucerini, or at least in the most generalized genus *Tetralonia* (+*Synhalonia*). It may also be mentioned that while considering *Eucera* as a polyphyletic group, the main relationships between the other three genera and their relationship with subgenus *Eucera* s. str. as a sister group do not change (Fig. 42).

The analysis of distribution of 27 diagnostic (generic) characters (Table 1) for the genera taking into account their probable evolution (see the previous section), as well as 29 characters distinguishing subgenera and groups of *Eucera* species, did not reveal a single synapomorphy characterizing all members of the latter. Thus, the genus *Eucera* turned out to be a paraphyletic group (Fig. 42). The phylogenetic relationships between subgenera of *Eucera* will be analyzed in detail in a separate publication, where a new subgeneric classification based on taxonomic revision of the genus will also be given. It may only be mentioned here that the subgenus *Pteneucera* is characterized by a few distinct synapomorphies, whereas the other two branches within *Eucera*, originating from the main trunk (with change in characters b and c; their discussion given in the previous section), are very poor in them: mainly, reduction of the ventral process of the gonostyle, which also occurs in the line leading to *Cubitalia* + *Pseudeucera* (character 25).

Monophyly of the group consisting of *Opacula*, *Cubitalia*, and *Pseudeucera* is based on 6 synapomorphies, including the very reliable ones for characters 5, 13, 23, and 24. Therefore, vari-

Table 2

Number of characters for which genera differ in Fig. 42

Genus	<i>Eucera</i>	<i>Opacula</i>	<i>Pseudeucera</i>	<i>Cubitalia</i>	Total	Average per association
<i>Eucera</i>	—	13	13	24	50	16.7
<i>Opacula</i>	13	—	12	23	48	16.0
<i>Pseudeucera</i>	13	12	—	17	42	14.0
<i>Cubitalia</i>	24	23	17	—	64	21.3
Total					204	17.0

Note. Distance from *Opacula*, *Pseudeucera*, and *Cubitalia* to *Eucera* calculated to closest subgenus *Eucera* s. str.

ation in different characters (1, 4, 8, 14, 16, 17). Monophyly of the group is supported by several morphologies (for character 1, the hypothesis of monophyly of *Opacula* and *Cubitalia* for parallelism, since the example, *E. interrupta* Baes, *E. glossa*, and *Pachysva* nae).

Cubitalia with 1 the closest common ancestor and *Pseudeucera* only of these genera also (equal) distances between genera in 21.3 characters, and *Pseudeucera* *Opacula* indirectly but ver-

Opacula donatic

Male. (Holotype) level of eye by 1/2 of width at base of mandible (Fig. 7). Ratio of post-tal body length. Ratio 1:0.9:0.71:0.67:0.9. Mandible of terga I-III occupying gum VI with well developed represented by short teeth (Fig. 31, 32, 37). Gonostylus the total length of gonostylus

Clypeus more or less in lower part; fairly broadly reduced toward middle; superficial punctations on face of tergum I shagreened margin, 30-40 micrometers diameter punctate with punctations on tergum II shagreened, shining with shagreened, shining with punctate with scattered

Black. Eyes light (Fig. 1). Labrum light dark yellow spots.

genera with 2 submarginal reduction of vein 1 *r-m* of principle have originated generalized genus *Tetralo-* and undoubtedly related over, there are more direct thesis concerning mono- "economical" (single re- as accepted by all tax-

probable, polyphyly) of relationships between the generalized genus *Tetralo-* *ucera* as a polyphyletic relationship with subgenus

Table 1) for the genera well as 29 characters dis- synapomorphy charac- be a paraphyletic group will be analyzed in detail in taxonomic revision of genus *Ptенеucera* is char- es within *Eucera*, origi- sion given in the previ- cess of the gonostyle, 25).

deucera is based on 6 and 24. Therefore, vari-

Total	Average per association
50	16.7
48	16.0
42	14.0
64	21.3
204	17.0

ed to closest subgenus

ation in different combinations within the large genus *Eucera* of character 25 and 9 other characters (1, 4, 8, 14, 16, 18, 20, 21, and 22) may be considered without any doubt as parallel variation. Monophyly of the group *Cubitalia* + *Pseudeucera* is somewhat poorly established: only 3 synapomorphies (for characters 9, 15, and 25), of which only the first 2 are sufficiently reliable. However, the hypothesis of their monophyletic origin is contradicted only by the similarity between *Opacula* and *Cubitalia* for character 12 (reduction of antenna), which can be easily considered as parallelism, since the reduction of antennae takes place independently in some *Eucera* (for example, *E. interrupta* Baer) and in other branches of Eucerini (for example, males of *Peponapis*, *Xenoglossa*, and *Pachysvastra*, and some species of *Melissoptila* and *Melissodes* have reduced antennae).

Cubitalia with 14 autapomorphies is most specialized. The other two genera diverged from the closest common ancestor to the same extent (based on 6 characters), although *Opacula* has 6 and *Pseudeucera* only 3 autapomorphies (Fig. 42). Differences in the number of autapomorphies of these genera also affected the length of conditional (characters for calculations are taken as equal) distances between them (Table 2). *Cubitalia* (on an average, differing from the remaining 3 genera in 21.3 characters) is most isolated in the group of 4 Eucerini genera with 2 submarginal cells, and *Pseudeucera* (14 characters) is least isolated. The importance of this parameter for *Opacula* indirectly but very definitely confirms its independent generic status.

Opacula donatica Sitdikov, sp. n.

Male. (Holotype). Body length 13 mm. Head 0.8 as high as wide (Fig. 1). Clypeus below level of eye by 1/2 of its height, with roundishly emarginate lower margin. Malar distance 0.22 width at base of mandible. Ratio between lengths of segments of maxillary palpus as 1:0.9:0.7 (Fig. 7). Ratio of postpalpar part of galea to height of clypeus 4.49. Antennae equal to half of total body length. Ratio of lengths of segments I, II, VI, X, and XI of antennal flagellum as 1:0.9:0.71:0.67:0.9. Mesobasitarsus strongly broadened subbasally (Fig. 20). Hindmarginal fields of terga I-III occupying slightly more than 1/3 length of postgradular part, weakly depressed. Tergum VI with well developed lateral gradular teeth. Carinae of postgradular field of sternum VI represented by short transverse section of medial branch (Fig. 29). Sterna VII and VII shown in Fig. 31, 32, 37. Gonostyle fairly thin, apex sharply bent medially, bent part approximately 1/7 of the total length of gonostyle (Fig. 38, 39).

Clypeus more or less uniformly punctate with roundish punctations, becoming irregular pits in lower part; fairly broad nonpunctate stripe extending through middle part of upper half cuneately reduced toward midpoint. Scutum fairly roughly shagreened, matt, densely punctate with very superficial punctations of 30-40 μ m diameter, intervals between them 0.5-1 diameter. Dorsal surface of tergum I shagreened, shining, densely punctate with shallow punctations with smooth hindmargin, 30-40 μ m diameter; marginal field superficially shagreened, shining. Legs densely punctate with punctations decreasing toward hindmargin (from 40 to 20 μ m). Postgradular field of tergum II shagreened, shining, with fairly distinct superficially punctations with maximum diameter (40 μ m) in middle and minimum (15 μ m) in region adjoining tergal gradulus; marginal field shagreened, shining with narrow nonpunctated stripe along hindmargin, remaining part uniformly punctate with scattered punctations of 25-30 μ m diameter, intervals between them 2-4 diameters.

Black. Eyes light brown. Clypeus with large bright yellow spot in middle of lower half (Fig. 1). Labrum light yellow, except narrow lateral dark stripes. Mandibles subapically with dark yellow spots.

Pubescence of head, mesosoma, and first 2 terga of metasoma predominantly consisting of long gray hairs. Terga III-VII pubescent with dark brown-black, moderately long hairs. Postgradular field of sternum V with triangular bare area in middle, along sides with 2 tufts of stiff, setose hairs apically sharply bent and directed laterally.

Holotype: male, "Soryun-Tyube, Kugarta Valley, Fergana Valley" (W Kirgizia), 9.V.1925 (Dobrzanskiy). Preserved in the Zoological Institute, Academy of Sciences of the USSR, Leningrad.

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On the Beefly

Zoologic

The beefly fauna (1975) listed 212 species for the fauna of India and species are known from the Palearctic. The data on the species of the 1920s-1930s (probably the beefly fauna and study of the fauna 2.5-3 times. The present small beefly collections (specimens) and collected material from Sri Lanka, *Petrorossia*, *Anthrax*, *Sys* 30 species, of which 8 number of species known.

Eight new species (sev, 1987, 1988). New known only from a few types.

The type specimens (ZMC) and Zoological Institute.

1. *Phthiria gracili*

Material. 6 male 4.VII.1978 (ZMC Exp.); (Mary), 17.VIII-7.IX.1978

Distribution. India

2. *Systoechus srila*

Only 4 species of the closest to *S. flavospinosus* ment II yellow, setae on dark brown.

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