

Revision of the Tribe Colpopterini Gnezdilov, 2003 (Homoptera, Fulgoroidea: Nogodinidae)

V. M. Gnezdilov

Zoological Institute, Russian Academy of Sciences, St. Petersburg, 199034 Russia

Received June 7, 2012

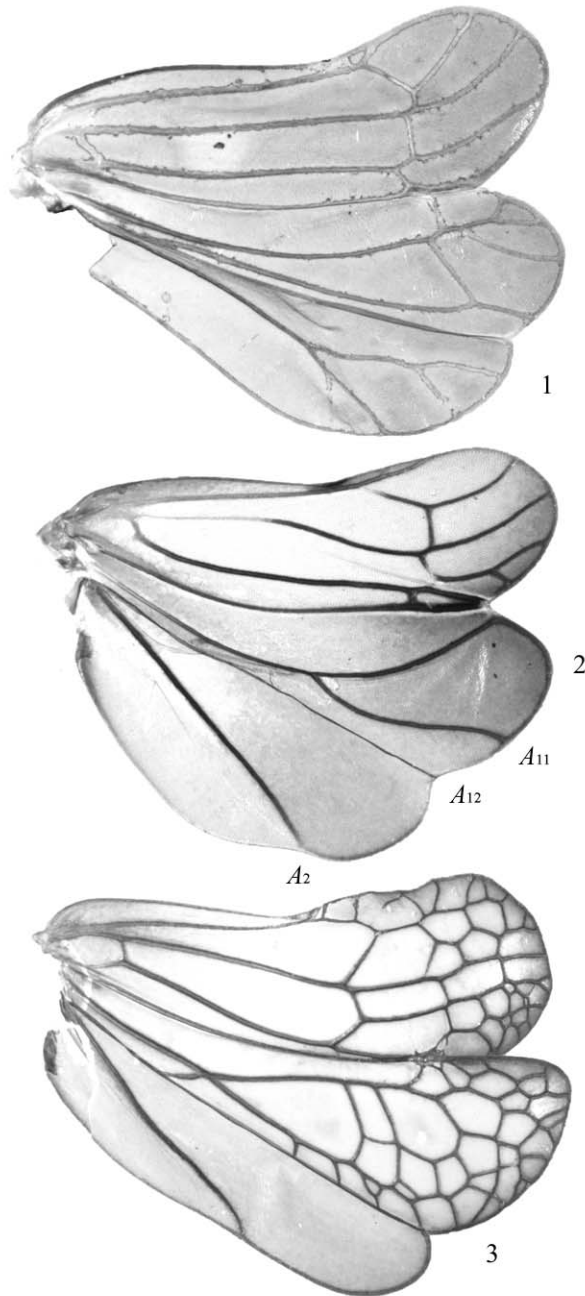
Abstract—The tribe Colpopterini Gnezdilov, 2003 is revised, upgraded to the subfamily Colpopterinae, stat. n., and transferred from the family Issidae Spinola to Nogodinidae Melichar. The tribe Colpopterini is recorded from the Afrotropical Region for the first time—*Bumerangum deckerti* gen. et sp. n. is described from Southern Africa. The tribe Colpopterini s. str. comprises 6 genera: *Bumerangum* gen. n., *Caudibeccus* Gnezdilov et O'Brien, 2008, *Colpoptera* Burmeister, 1835, *Jamaha* Gnezdilov et O'Brien, 2008, *Neocolpoptera* Dozier, 1931, and *Ugoa* Fennah, 1945. The genera *Cheiloceps* Uhler, 1895, *Tempsa* Stål, 1866, *Eupilis* Walker, 1857, and *Gabaloecca* Walker, 1870 are transferred to the tribe Issini Spinola of the family Issidae. *Issus longulus* Lethierry, 1890 is transferred to the genus *Colpoptera* Burmeister. A key to the genera and a list of the species of the tribe Colpopterini are given. Morphological data confirming independent evolution of similar ovipositor types in the families Issidae and Nogodinidae are provided. The term “styletization” is suggested for describing the transformation of the ovipositor from a rounded to an elongate type.

DOI: 10.1134/S0013873813030081

The tribe Colpopterini was established in 2003 within the family Issidae Spinola for two Neotropical genera, *Colpoptera* Burmeister, 1835 and *Neocolpoptera* Dozier, 1931, based on the characteristic shape and venation of its fore and hind wings (Gnezdilov, 2003). It was also noted that one of the species of the genus *Colpoptera* was characterized by a specialized beak-shaped ovipositor. One year later, the composition of the tribe was supplemented with several Oriental genera possessing a similar beak-shaped ovipositor (Fig. 6) (Gnezdilov et al., 2004). Although it seems quite reasonable to group genera with a similar structure of such a complex formation as the ovipositor, a comparative examination of the internal structure of the ovipositor and of the hind-wing venation in various representatives of the tribes Colpopterini, Issini *sensu* Gnezdilov, 2009, and Parahiraciini *sensu* Gnezdilov et Wilson, 2007 has shown that similar types of ovipositor could arise concurrently in two fulgoroid groups, the tribes Colpopterini *sensu stricto* in the Neotropical Region and Issini in the Oriental Region, rather than be formed only once in the tribe Colpopterini *sensu lato*.

In particular, the branching second anal vein (A_2 2–4) of the hind wing (Fig. 1) is characteristic of the American genera of the tribe Issini. This character was also found in an Oligocene genus from Mexican amber

(Grimaldi and Engel, 2005, figs. 2.25, 2.26), and in the recent genera *Amnisa* Stål, 1862, *Cheiloceps* Uhler, 1895, *Heremon* Kirkaldy, 1903, *Oronoqua* Fennah, 1947, and *Thionia* Stål, 1859. The genera *Picumna* Stål, 1864 and *Amphiscepa* Germar, 1830 are exceptions: their second anal veins is simple (A_2 1). The Oriental (*Darwallia* Gnezdilov, 2010, *Tempsa* Stål, 1866, *Sarima* Melichar, 1903, *Eupilis* Walker, 1857, *Gabaloecca* Walker, 1870, *Syrgis* Stål, 1870, *Eusarima* Yang, 1994, *Neokodaiana* Yang, 1994, *Paravindilis* Yang, 1994, *Parasarima* Yang, 1994, *Sinesarima* Yang, 1994, *Neosarima* Yang, 1994, *Scantinius* Stål, 1866, and *Thabena* Stål, 1866), Australian (*Orinda* Kirkaldy, 1907), and Afrotropical (*Chimetopon* Schmidt, 1910) genera of Issini and Parahiraciini are also characterized by a simple second anal vein (A_2 1) (Figs. 2, 3). Some American (for example, *Picumna*) and all the Oriental and Australian genera of the tribes Issini and Parahiraciini studied by me are characterized by the veins *Pcu* and A_1 fused in their middle section and subsequently diverging in the apical part (Figs. 2, 3). *Pcu* and A_1 are fused in the Oligocene representative of the tribe Issini (Grimaldi and Engel, figs 2.25, 2.26), which may imply plesiomorphy of this state. A partial fusion of *Pcu* and A_1 is also found in Cicadelloidea (*Bothrogonia* sp.) and Cercopoidea [Aphrophoridae, *Aphrophora salicina* (Goeze, 1778):



Figs. 1–3. Issidae, hind wing: (1) *Thionia producta* Van Duzee, (2) *Eusarima (Nepalius)* sp., (3) *Scantinius bruchoides* (Walker); A_{11} , anterior branch of first anal vein; A_{12} , posterior branch of first anal vein; A_2 , second anal vein.

see Anufriev and Emeljanov, 1988, fig. 5 (2), fig. 209 (2)]. The posterior branch of A_1 (A_{12} in Fig. 2) is weakened in comparison with the anterior branch (A_{11}), which may be caused by the position of the wing folding line running along it.

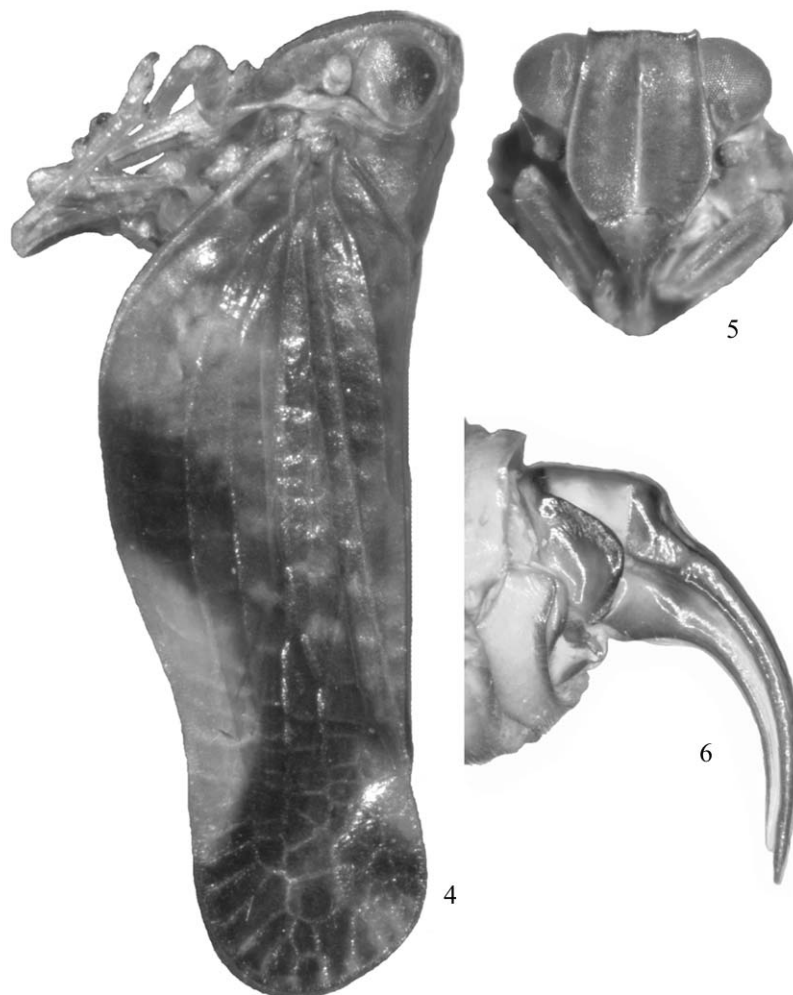
The independent origin of the specialized ovipositors in Colpopterini and in the Asian Issidae is proved

by a difference in the structure of the connective laminae of gonapophyses VIII and IX in these taxa. In Issini (*Eupilis* sp.), the posterior connective laminae of gonapophyses IX are flagelliform in the apical parts (Figs. 11, 12); the anterior connective laminae of gonapophyses VIII are heavily sclerotized, narrow, and bear a row of rather large teeth, and the endogonocoxal process is short (Fig. 13). Colpopterini [*Caudibeccus carlota* (Myers, 1928)], in contrast, are characterized by the posterior connective laminae short in the apical parts (Fig. 16) and by the anterior connective laminae as long as the endogonocoxal processes, weakly sclerotized, and bearing no teeth (Fig. 17). In both the species mentioned, the gonoplasts are elongate and fused dorsally to form a case (sheaths) for the stylet-shaped anterior connective laminae (Fig. 14).

Both the tribes (Colpopterini and Issini) demonstrate distinct transitions from the ovipositor with the rounded gonoplasts to an elongate beak-shaped one. In the tribe Colpopterini (Neotropical Region), the gonoplasts are round in *Ugoa* Fennah, 1945 and *Jamaha* Gnezdilov et O'Brien, 2008, are insignificantly elongate in *Colpoptera* Burmeister, 1835 (Fig. 22), and are beak-shaped in *Caudibeccus* Gnezdilov et O'Brien, 2008; in the tribe Issini, the gonoplasts are round in the majority of the genera and beak-shaped in *Eupilis* Walker, 1857, *Gabaloecca* Walker, 1870, and *Tempsa* Stål, 1866 (Figs. 6, 14). The same tendency is also observed in styletization (narrowing) of the anterior connective laminae, for example, in the genera *Colpoptera* and *Caudibeccus* (Figs. 17, 19).

In the common ancestor of the higher Fulgoroidea, the ovipositor probably was unspecialized, of the raking-kneading type, and its transition to the piercing-sawing type occurred independently in different groups, in this case, in Colpopterini and Issini. A similar example of formation of the piercing-sawing ovipositor from the raking-kneading one is shown by the Neotropical tribe Cladodipterini Metcalf, family Dictyopharidae Spinola (Emeljanov, 1980). The monotypical subfamily Gastriniinae Fennah, family Nogodinidae Melichar, is also characterized by a long and narrow ovipositor (Fennah, 1987). In contrast to Colpopterini and Issini, in the genus *Gastrinia* Stål, 1859, the function of sheaths seems to pass to a large anal tube clasping the narrow gonoplasts dorsally and laterally.

Earlier (Gnezdilov, 2003) I supposed that the beak-shaped ovipositor of *Caudibeccus carlota* could be

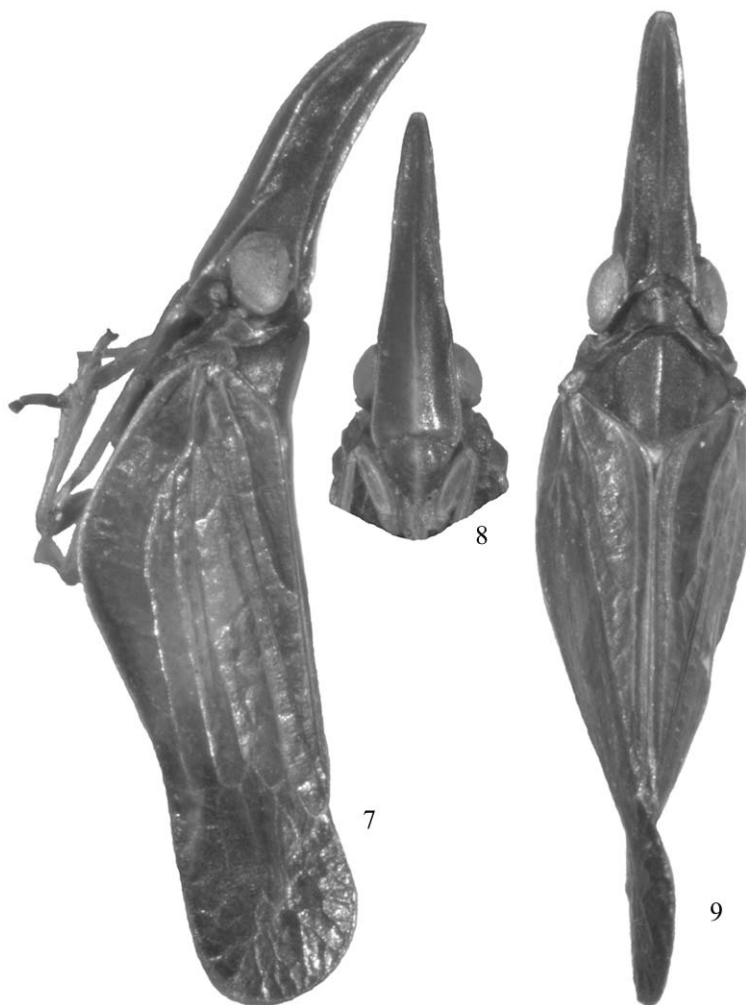


Figs. 4–6. Nogodinidae, *Colpoptera sinuata* Burmeister (4, 5) and Issidae *Eupilis* sp. (6) [(4) body, lateral view; (5) face; (6) ovipositor, lateral view].

used for piercing the plant tissues; however, another variant of oviposition is also possible, when the elongate ovipositor is used for laying eggs deeply in the axils of leaves, in flowers, in strobiles of gymnosperms, etc. The latter variant seems to be more probable, as the anterior connective laminae of gonapophyses VIII in *C. carlota* are weakly sclerotized and lack teeth (Fig. 17); however, in the Oriental genera *Eupilis* and *Tempsa*, these laminae appear stronger and are more heavily sclerotized (Fig. 13). Something similar is supposed for the most ancient Proboscidea—the Perm Archescytinidae Tillyard possessing a long slender ovipositor and laying eggs in the strobiles of Gymnospermae (Becker-Migdisova, 1972, cited after Popov, 1980). In the genus *Colpoptera*, the anal tube is long and narrow (Fig. 18), but the gonoplaes are not narrowed yet (Fig. 22), the posterior connective laminae of gonapophyses IX are slightly narrowed (Figs. 20, 21), and the structure of the anterior connec-

tive laminae of gonapophyses VIII is rather simple (Fig. 19).

The facts listed necessitate reconsidering the opinion that the tribe Colpopterini unites genera from the Neotropical and Oriental regions (Gnezdilov et al., 2004) and considering it polyphyletic. Moreover, material from Southern Africa, representing a new genus and a new species of the tribe Colpopterini s. str., changes radically our concept of the systematic position and distribution of the tribe. Characters of the male genitalia, found in the new genus, in particular, the stylus with a capitulum flattened laterally and lacking a lateral tooth (Fig. 39), testify to its attribution to the family Nogodinidae Melichar, and since the external structure of *Bumerangum* gen. n. and the Neotropical genera of the tribe Colpopterini s. str. [an elongate metope with a median carina (Figs. 5, 8), large mesonotum with median and lateral carinae (Figs. 9,



Figs. 7–9. Nogodinidae, *Bumerangum deckerti* Gnezdilov, gen. et sp. n., holotype: (7) lateral view; (8) face; (9) dorsal view.

27, 30, 31, 33), fore wings with a long clavus and with a rich cross-venation in the distal part (Figs. 4, 7, 35), a characteristic shape and simplified venation of the hind wing (Figs. 15, 36)] suggests their undoubted affinity, the whole tribe should be attributed to this family. Earlier, Colpopterini was placed in Issidae based namely on the characters of the male genitalia [the phallobase nearly lacking processes, except for the subapical one, the stylus with a pronounced capitulum bearing a lateral tooth (Figs. 23, 25, 26)]. However, already in *Caudibeccus carlota*, the stylus strongly differs from that typical of Issidae: the capitulum is not separated from the plate, and the lateral tooth is indistinct (Fig. 24).

Thus, I suggest that the tribe Colpopterini s. str. comprising the genera *Bumerangum* gen. n., *Caudibeccus* Gnezdilov et O'Brien, 2008, *Colpoptera* Bur-

meister, 1835, *Jamaha* Gnezdilov et O'Brien, 2008, *Neocolpoptera* Dozier, 1931, and *Ugoa* Fennah, 1945 should be transferred to the family Nogodinidae Melichar, whereas the genera *Cheiloceps* Uhler, 1895, *Tempsa* Stål, 1866, *Eupilis* Walker, 1857, and *Gabaloea* Walker, 1870 should be transferred from Colpopterini to the nominotypical tribe of the family Issidae.

The suprageneric classification and phylogeny of the family Nogodinidae are underdeveloped. Fennah first revised the family and divided it into two subfamilies: Nogodininae Melichar, 1898 with 7 tribes (Nogodinini Melichar, 1898, Bladinini Kirkaldy, 1907, Mithymnini Fennah, 1967, Pisachini Fennah, 1978, Varcini Fennah, 1978, Epacriini Fennah, 1978, Lipocalliini Fennah, 1984), and the monotypical Gastriniinae Fennah, 1987 (Fennah, 1978, 1984, 1987). Re-

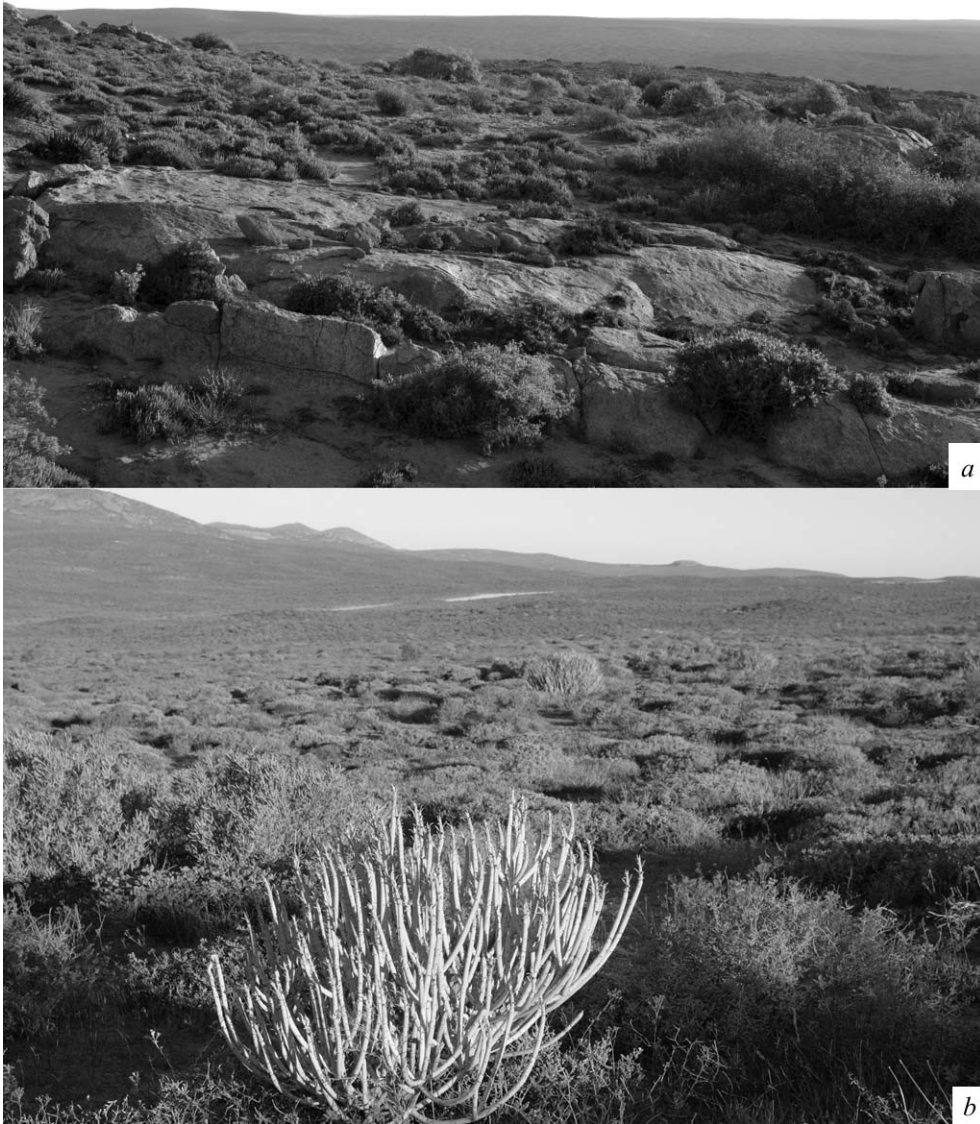


Fig. 10. Type locality (Namaqualand Soebastfontein) of *Bumerangum deckerti* gen. et sp. n. (photograph by J. Deckert).

cently Nogodininae was supplemented with the tribe Tongini Kirkaldy, 1907 transferred from the family Issidae, but the subtribe Gaetuliina Fennah, 1978 was, in contrast, excluded from the tribe Bladinini Kirkaldy, transferred to the family Tropicuchidae, and upgraded to a tribe (Gnezdilov, 2007). Despite the underdeveloped classification and phylogeny of Nogodinidae, I propose to transfer there the tribe Colpopterini, based on the above characters of the structure of the stylus, and also to regard it as a subfamily Colpopterinae stat. n., based on a very peculiar shape and venation of the fore and hind wings.

The nomenclature of parts of the head follows that of Emeljanov (1995), of the male genitalia, that of

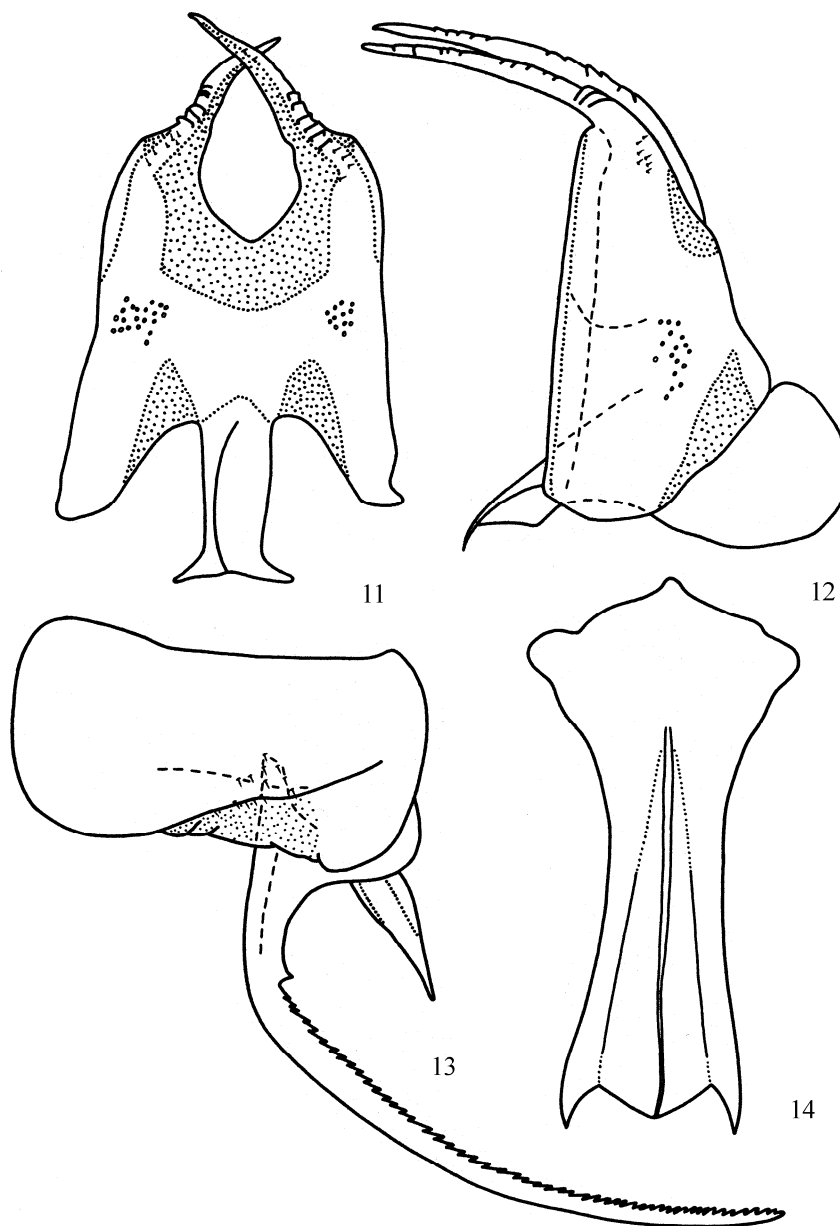
Gnezdilov (2002a), and of the female genitalia, those of Bourgoïn (1993) and Gnezdilov (2002b).

The material examined is deposited in the following collections: SAMC, Iziko South African Museum, Cape Town, Republic of South Africa; MNB, Museum für Naturkunde, Berlin, Germany; MNHN, Muséum national d'Histoire naturelle, Paris, France; and ZIN, the Zoological Institute, the Russian Academy of Sciences, St. Petersburg, Russia.

Family **NOGODINIDAE** Melichar

Subfamily **Colpopterinae** Gnezdilov, **stat. n.**

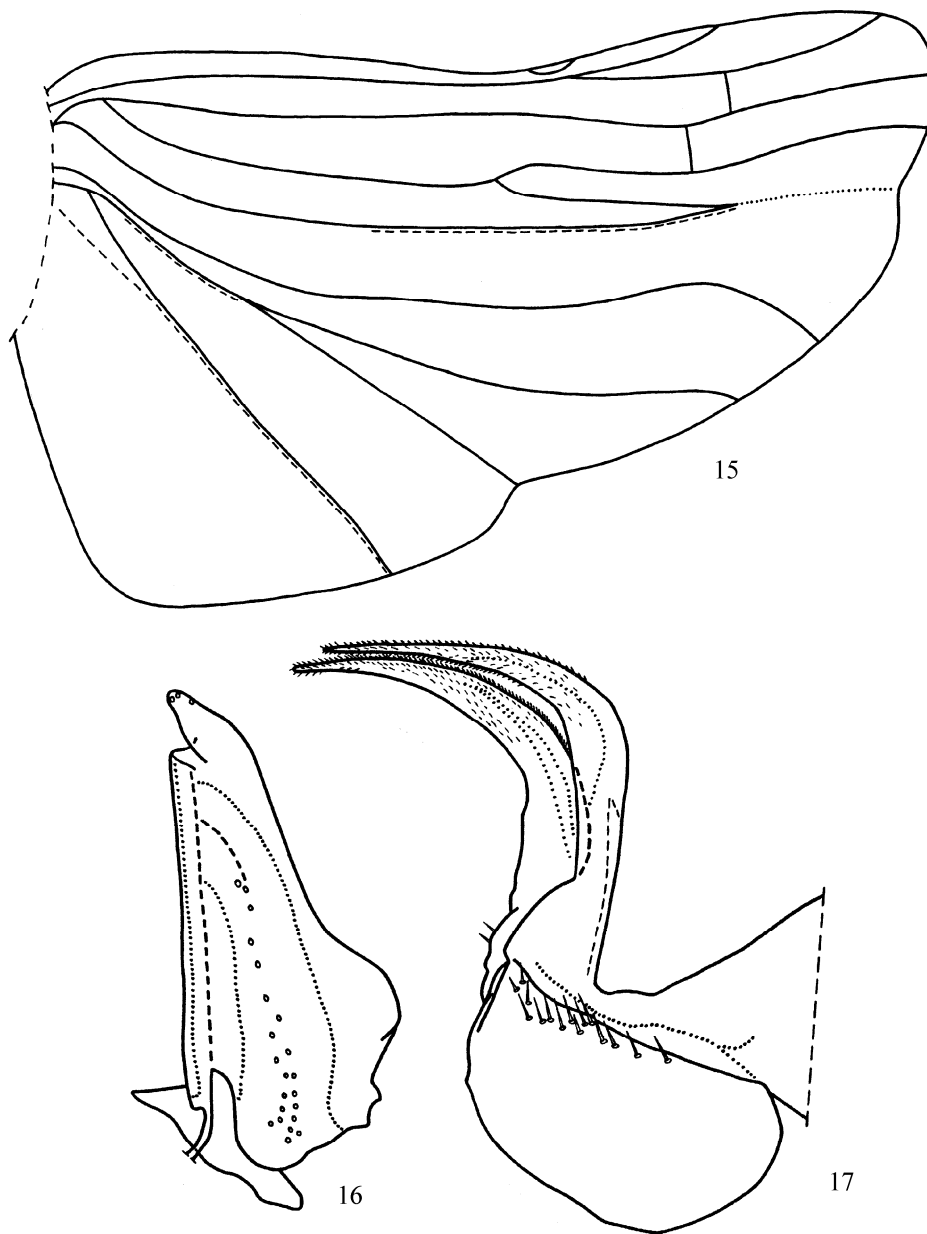
Colpopterini Gnezdilov, 2003 : 307. Type genus *Colpoptera* Burmeister, 1835.



Figs. 11–14. Issidae, *Eupilis* sp., ovipositor: (11) posterior connective laminae of gonapophyses IX, dorsal view; (12) posterior connective laminae of gonapophyses IX, lateral view; (13) anterior connective lamina of gonapophysis VIII and gonocoxa VIII, lateral view; (14) gonoplags, dorsal view.

Diagnosis. Metope with distinct median carina, occasionally also with weak sublateral carinae (Figs. 5, 8). Pair of ocelli present. Mesonotum large, with median (in most genera) and lateral carinae (Figs. 9, 27, 30, 31, 33). Fore wing elongate, with large oblong-oval basal cell, with relatively wide subcostal area (Figs. 28, 29, 35), with hypocostal plate. Clavus long (3/4 of wing length). *Sc + R* 2, *M* 2 *CuA* 1–2. *CuA* (or its posterior branch) running into apex

of clavus. Longitudinal veins densely branching behind apex of clavus. Cross-venation rich, usually on both wings. Hind wing well developed, with wide anal lobe; apical margin of wing with 2 weak clefts between remigium and vannus and between anterior part of vannus and anal lobe; venation simple: longitudinal veins weakly branching, only 2 cross-veins present. *Sc + R* 2 *rm* 1 *M* 1–2 *mcu* 1 *CuA* 2 *CuP* 1 *Pcu* 1 (distal part curved toward *CuP*) *A*₁ 2–3



Figs. 15–17. Nogodinidae, *Caudibeccus carlota* (Myers) (after: Gnezdilov, 2003, modified): (15) hind wing; (16) posterior connective laminae of gonapophyses IX, lateral view; (17) anterior connective lamina of gonapophysis VIII and gonocoxa VIII, lateral view.

(anterior branch diverging toward *Pcu*), A_2 1. Hind tibia with or without 1 or 2 lateral teeth. 1st metatarsomere with intermediate spines, 2nd metatarsomere only with 2 lateroapical spines. Structure of male and female genitalia varying.

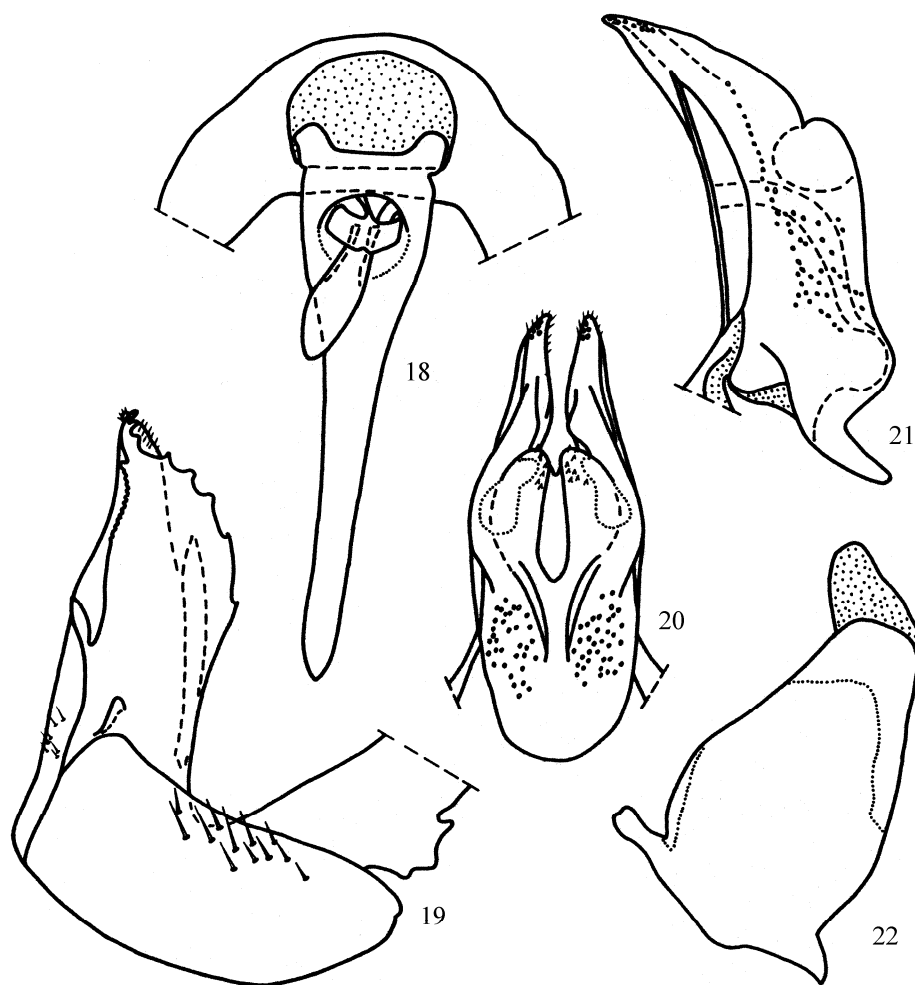
Notes. The genera *Colpoptera* Burmeister, 1835, *Neocolpoptera* Dozier, 1931, and *Jamaha* Gnezdilov et O’Brien, 2008 are characterized by the subcosta and radius of the fore wing originating from one point of the basal cell (Fig. 28), while in the genera *Caudibec-*

cus Gnezdilov et O’Brien, 2008, *Ugoa* Fennah, 1945, and *Bumerangum* gen. n., the subcosta and radius originate from the basal cell as a common stem (Figs. 29, 35).

A List of the Genera and Species of the Subfamily Colpopterinae

Genus **CAUDIBECCUS** Gnezdilov et O’Brien

Caudibeccus Gnezdilov et O’Brien, 2008 : 22. Type species *Colpoptera carlota* Myers, 1928.



Figs. 18–22. Nogodinidae, *Colpoptera sinuata* Burmeister, ovipositor (after: Gnezdilov and O'Brien, 2008): (18) anal tube, dorsal view; (19) anterior connective lamina of gonapophysis VIII and gonocoxa VIII, lateral view; (20) posterior connective laminae of gonapophyses IX, dorsal view; (21) posterior connective laminae of gonapophyses IX, lateral view; (22) gonoplacs, lateral view.

Five species known from Cuba, the Lesser Antilles, and the Bahamas (Myers, 1928; Metcalf, 1954; Fennah, 1955; Gnezdilov and O'Brien, 2008): *Caudibecus carlota* (Myers, 1928), *C. emeljanovi* Gnezdilov et O'Brien, 2008, *C. lucaris* (Fennah, 1955), *C. meleagris* (Fennah, 1955), *C. punctata* (Metcalf, 1954).

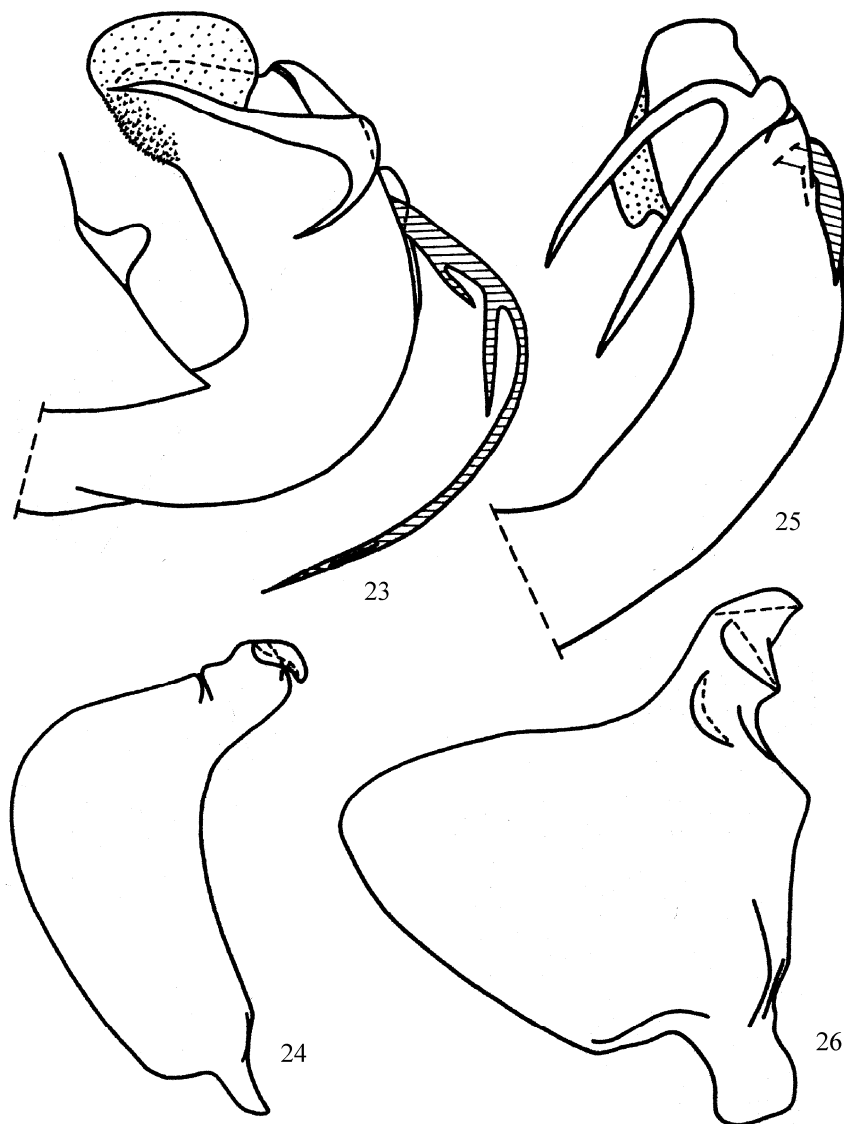
Genus **COLPOPTERA** Burmeister

Colpoptera Burmeister, 1835 : 155. Type species *Colpoptera sinuata* Burmeister, 1835.

= *Hesperophara* Kirkaldy, 1904 : 279 (type species *Flata rustica* Fabricius, 1803), synonymy after: Gnezdilov and O'Brien, 2008 : 21.

Twenty-nine species and subspecies were described in the genus (Metcalf, 1958); however, attribution to this genus should be verified for the majority of them,

as the concept of the genus *Colpoptera* changed, and new genera were established (Gnezdilov and O'Brien, 2008). Most of the species (18) are known from the Greater and Lesser Antilles, 10 species, from Mexico, and only 1 species, from South America (Fabricius, 1803; Burmeister, 1835; Lethierry, 1890; Van Duzee, 1907; Muir, 1924; Dozier, 1931; Osborn, 1935; Dozier, 1936 (in Wolcott, 1936); Caldwell, 1945; Caldwell and Martorell, 1951; Fennah, 1955, 1965; Metcalf, 1958; Bartlett, 2000): *Colpoptera acutata* Caldwell, 1945, *C. albavenosa* Caldwell, 1945, *C. bifurcata* Caldwell, 1945, *C. brunneus* Muir, 1924, *C. caldwelli* Metcalf, 1958, *C. clerodendri* Dozier, 1931, *C. cyathae* Fennah, 1955, *C. elongata* Caldwell, 1945, *C. fusca* Caldwell et Martorell, 1951, *C. galatea* Fennah, 1965, *C. insularis* Dozier, 1931, *C. maculifrons maculifrons* Muir, 1924, *C. m. carinata* Dozier, 1936



Figs. 23–26. Nogodinidae, male genitalia, penis (23, 25) and stylus (24, 26), lateral view [(23, 24) *Caudibeccus emeljanovi* Gnezdilov et O'Brien; (25, 26) *Colpoptera sinuata* Burmeister].

(in Wolcott, 1936), *C. m. angustior* Fennah, 1955, *C. m. dominicana* Fennah, 1955, *C. m. grenadana* Fennah, 1955, *C. m. flavifrons* Osborn, 1935, *C. m. maculata* Dozier, 1931, *C. marginalis* Burmeister, 1835, *C. minuta* Caldwell et Martorell, 1951, *C. nana* Dozier, 1931, *C. nigradorsa* Caldwell, 1945, *C. rotunda* Caldwell, 1945, *C. rugosa* Van Duzee, 1907, *C. rustica* (Fabricius, 1803), *C. sinuata* Burmeister, 1835, *C. stigmata* Caldwell, 1945, and *C. thyone* Fennah, 1955.

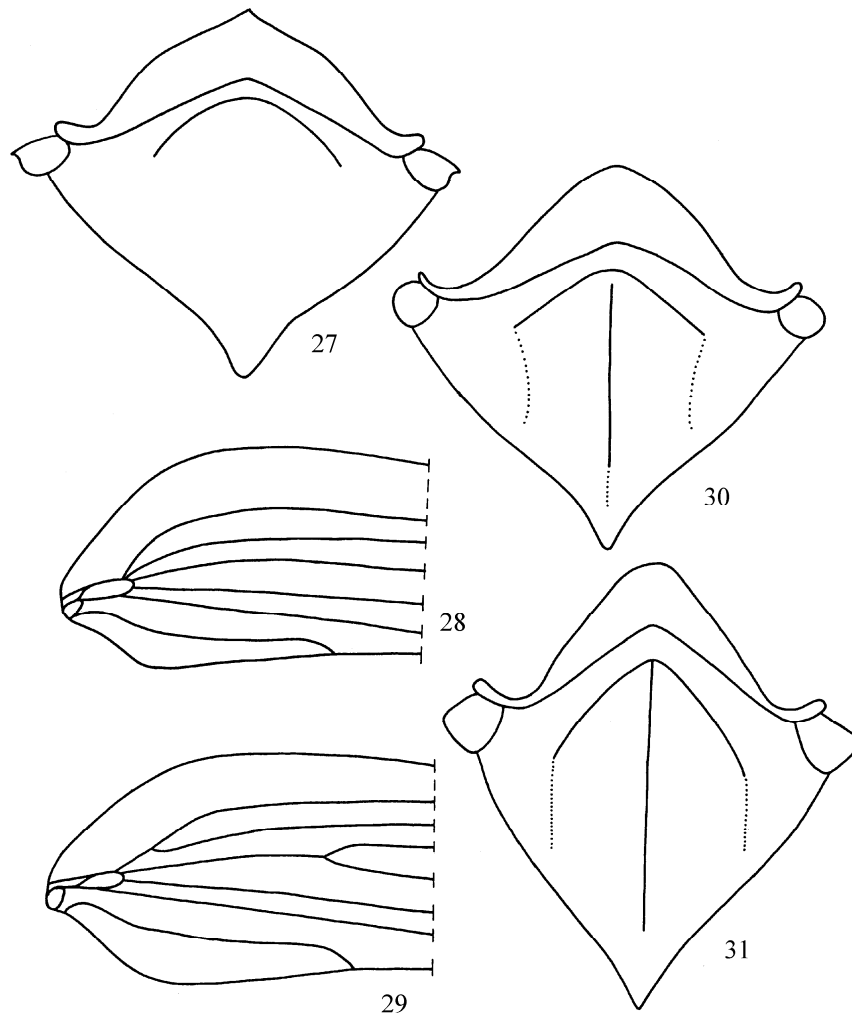
***Colpoptera longula* (Lethierry, 1890), comb. n.**

Issus longulus Lethierry, 1890 : 149.

Thionia longula: Melichar, 1906 : 286.

Material. Holotype: ♀, with the hand-written label “*Issus longulus* Leth., Venezuela” and the printed label “San Esteban, E. Simon, III.88” (MNHN (EH) 7487).

Notes. The species was described from a male collected in Venezuela (Lethierry, 1890). Sex of the specimen described apparently was erroneously determined by Lethierry. The female with a hand-written label deposited in the collection of Muséum national d’Histoire naturelle, Paris, France, corresponds to the original description and is considered here as holotype. *Issus longulus* was erroneously transferred to the genus *Thionia* Stål, 1859 by Melichar (1906). Actually the species belongs to the genus *Colpoptera* Burmeis-



Figs. 27–31. Nogodinidae, *Colpoptera sinuata* Burmeister (27, 28), *Caudibeccus emeljanovi* Gnezdilov et O'Brien (29, 30), and *Neocolpoptera portoricensis* Dozier (31) [(27, 30, 31) pro- and mesonotum, dorsal view; (28, 29) proximal part of fore wing].

ter, 1835, which is evident from the structure of its elongate, subtriangular gonoplasts.

Genus **JAMAHA** Gnezdilov et O'Brien

Jamaha Gnezdilov et O'Brien, 2008 : 24. Type species *Poeciloptera elevans* Walker, 1858.

The genus includes 2 species from Jamaica (Walker, 1858; Fennah, 1955; Gnezdilov and O'Brien, 2008): *Jamaha elevans* (Walker, 1858) and *J. chrysops* (Fennah, 1955). Record of *J. elevans* from Haiti Island (Melichar, 1902) requires verification.

Genus **NEOCOLPOPTERA** Dozier

Neocolpoptera Dozier, 1931 : 22. Type species *Neocolpoptera portoricensis* Dozier, 1931.

The genus includes 5 species distributed on the Lesser Antilles (Dozier, 1931; Caldwell et Martorell, 1951; Fennah, 1955): *Neocolpoptera memnonia* (Fennah, 1955), *N. monticolens* Dozier, 1931, *N. nemonticolens* Caldwell et Martorell, 1951, *N. portoricensis* Dozier, 1931, and *N. rara* Caldwell et Martorell, 1951.

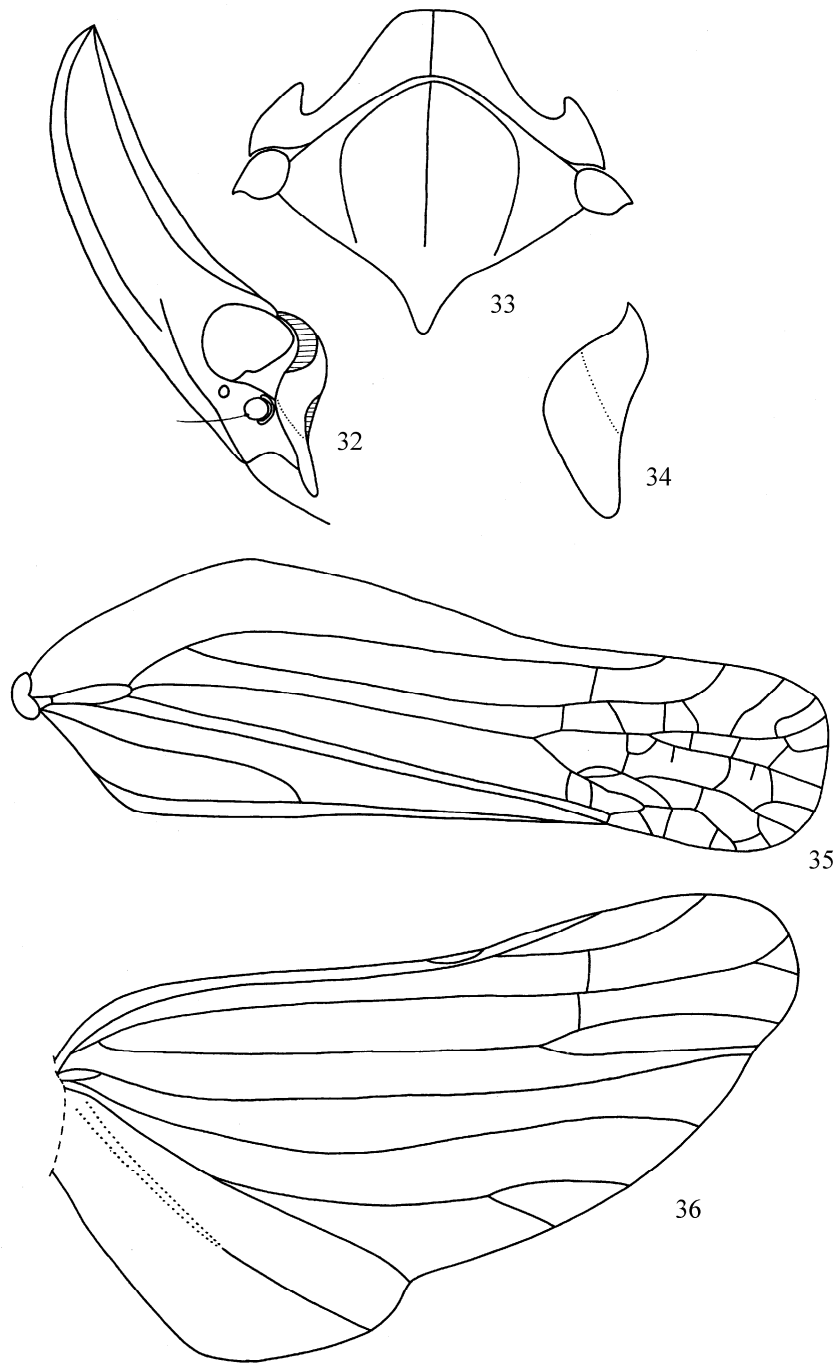
Genus **UGOA** Fennah

Ugoa Fennah, 1945 : 505. Type species *Ugoa glauca* Fennah, 1945.

This monotypical genus is known from Trinidad Island (Fennah, 1945).

Genus **BUMERANGUM** Gnezdilov, gen. n.

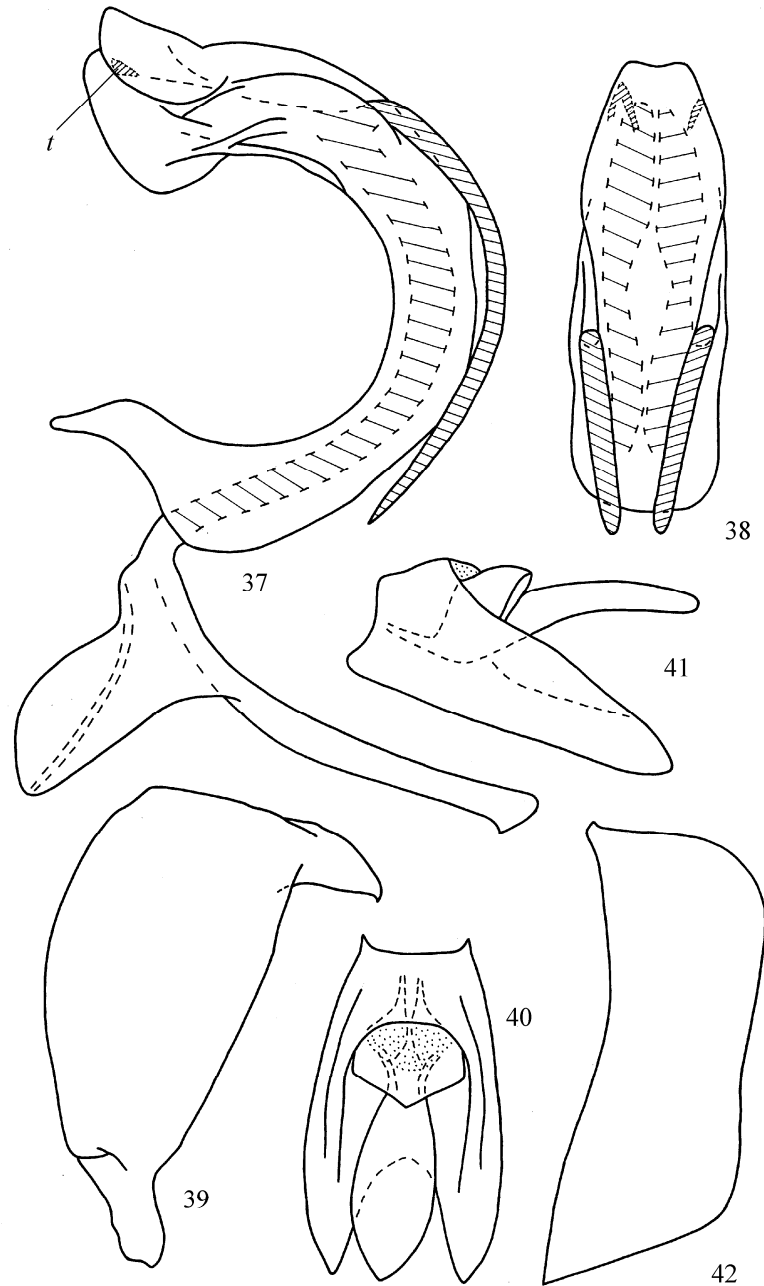
Type species *Bumerangum deckerti* sp. n.



Figs. 32–36. Nogodinidae, *Bumerangum deckerti* gen. et sp. n.: (32) head, lateral view; (33) pro- and mesonotum, dorsal view; (34) paranotal lobe, lateral view; (35) fore wing; (36) hind wing.

Description. Metope narrow, long, pointed toward apex, with distinct median carina running from its upper margin and continuing onto post- and anteclypeus (Fig. 8). Median carina interrupted by metopoclypeal suture, latter slightly arcuately protruding into metope. Lateral carinae of metope bend onto

lateral parts of cephalic process (Fig. 32). Ocelli present. Sublateral carinae of metope distinct in its dorsal part, broken above level of eyes. Median and sublateral carinae of metope converging at apex of cephalic process. Coryphe long, narrow, with lateral margins gradually converging toward pointed apex, with dis-



Figs. 37–42. Nogodinidae, *Bumerangum deckerti* gen. et sp. n., holotype, male genitalia: (37) penis and connective, lateral view; (38) penis, ventral view; (39) stylus, lateral view; (40) anal tube, dorsal view; (41) anal tube, lateral view; (42) pygophore, lateral view; *t*, tooth on inner side of dorsolateral lobe of phallobase.

tinct median carina running from its posterior margin toward apex (Fig. 9). Posterior margin of coryphe arcuately emarginate. Cephalic process slightly bent apically (in lateral view: Fig. 32). Pronotum with approximately semicircular basal part bearing median carina (Figs. 9, 33). Anterior margin of pronotum steeply raised, posterior margin steeply deflexed. Paradiscal areas rather wide, with triangular projection below eyes. Paranotal lobes wide, without carinae,

acute-angularly projecting downwards (Fig. 34). Mesonotum large, with median and lateral carinae connected in form of characteristic trident (Fig. 33). Dorsal part of mesonotum depressed. Tegulae large, without carinae. Fore wing long, rather narrow, weakly narrowed toward rounded apex, with narrow hypocostal plate and wide subcostal area (Figs. 7, 35). Basal cell narrowly oval. *Sc* and *R* originating from basal cell as common stem. *Sc* + *R* 2 (branching in

proximal part of wing), *M* 2 (branching before apex of clavus), *CuA* 1 (bent toward apex of clavus). Clavus closed: *Pcu* + *A*₁ running into *A*₂ before apex of clavus. Hind wing well developed, with 2 weak clefts: one between *CuA* and *CuP*, other between 1st and 2nd anal veins (Fig. 36). *CuA*₂ and *CuP* running into cleft, not merging apically. Anterior margin of hind wing weakly emarginate in area of coupling lobes. *Sc* + *R* 2 (branching behind coupling lobe), *rm* 1, *M* 2 (short bifurcation in distal part), *mcu* 1, *CuA* 2, *CuP* 1, *Pcu* 1 (distal part curved toward *CuP*), *A*₁ 3 (branch *A*₁₁–*A*₁₂ diverging toward *Pcu*), *A*₂ 1 (flattened proximally). Hind tibia with 2 lateral spines in distal half and with 8 apical spines. 1st metatarsomere wider than 2nd and 3rd ones, all of subequal length. 1st metatarsomere with 8 apical spines forming continuous row. 2nd metatarsomere only with 2 lateroapical spines. Pretarsus not projecting beyond claws.

Male genitalia (Figs. 37–42). Pygophore wide, with rounded dorsal angles and with posterior margin very weakly (shallowly) emarginate in lower part (Fig. 42). Anal tube rather wide and long, with deep emargination at apex (in dorsal view: Figs. 40, 41). Anal column large, long (2/3 of length of anal tube). Phallobase narrow (in lateral view), narrowly horseshoe-curved (Fig. 37). Dorsolateral lobes of phallobase fused dorsally in form of weakly sclerotized sack. Each dorsolateral lobe with large tooth at apex (on inner side) (Fig. 37). Ventral lobe of phallobase long, wide, widened and collar-shaped deflexed apically (Figs. 37, 38). Aedeagus with pair of long narrow ventral hooks (not shorter than 2/3 of length of phallobase) narrowed toward apices and directed toward base of phallobase. Connective ladle-shaped proximally (Fig. 37). Stylus large, with straight posterior margin and with obtuse caudodorsal angle (Fig. 39). Capitulum of stylus without neck and lateral tooth (in lateral view), compressed laterally.

Female genitalia (Figs. 43–46). Anal tube short, relatively wide, widely emarginate at apex (Fig. 46). Anal column large, long, approximately 1.5 times as long as anal tube. Gonoplares flat, rounded, convex at base of lobes dorsally, with membranous caudal part and long setae (Fig. 43). Sclerotized part of gonoplares with teeth at base of membranous part. Gonoplares connected only at base of separated 3rd lobes. Gonocoxa VIII with straight posterior margin bearing no setae (Fig. 44). Anterior connective laminae of gonapophyses VIII with wide ridge, with 3 large rounded teeth in apical group, and with 3 carinate teeth in lat-

eral group. Endogonocoxal process bifurcate at apex. Posterior connective laminae of gonapophyses IX rather narrow (in dorsal view) (Fig. 45), flat (in lateral view). Distal parts of posterior connective laminae very weakly inclined toward midline. Median area flat, with single lobe. Lateral areas flat. Gonospiculum bridge narrow (in dorsal view).

Etymology. The name of the genus refers to the boomerang-shaped (in lateral view) insect body (Fig. 7).

Bumerangum deckerti Gnezdilov, sp. n.
(Figs. 7–9)

Description. Head, except for genae and carinae on metope, and pro- and mesonotum dark brown, nearly black. Pedicel brown. Ocelli reddish. Carinae on metope and clypeus, genae above antennae, thorax, and legs yellowish pale brown. Median carina of pronotum pale brown. Tegulae and abdominal sternites dark brown. Fore wing brown or dark brown, nearly black in apical part. Hind wing matte, with brown or dark brown veins pale in places. Spines of legs black.

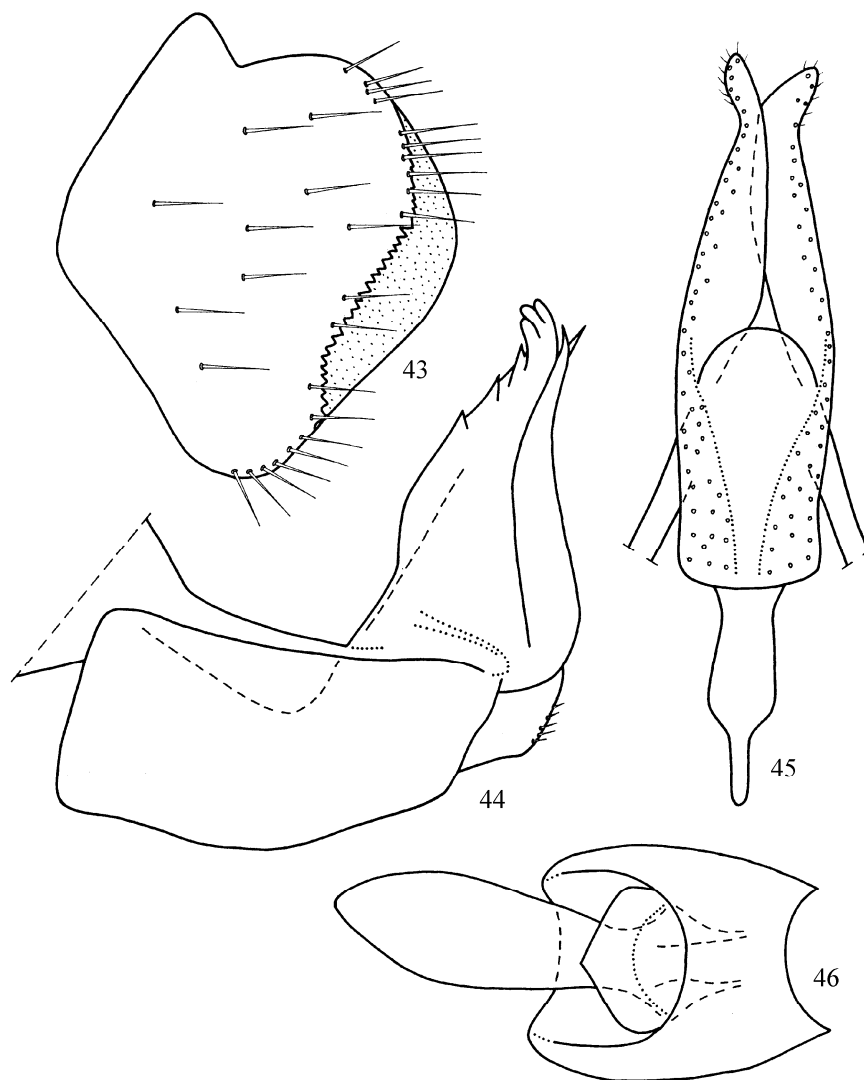
Body length: males 6.5–7.2 mm, female 7.5 mm.

Material. Republic of South Africa. Holotype, ♂: Northern Cape Province, Quaggafontein b. Soebatsfontein, 30°11'17"S, 17°33'02"E, 30.IX.2002, J. Deckert leg. (SAMC). Paratypes: Northern Cape Province: 1 ♂, 1 ♀, Quaggafontein, 29.IX–5.X.2002, "BIOTA, Malaise trap 2202420020704377," "BIOTA," K. Ebert leg. (SAMC, ZIN); 1 ♂, Quaggafontein b. Soebatsfontein, 30°11'11"S, 17°33'59"E [BIOTA], "BIOTA," 3.X.2002, J. Deckert leg. (MNB).

Etymology. The species is named after J. Deckert who collected it.

A Key to the Genera of the Subfamily Colpopterinae

- 1 (2). Cephalic process long (Figs. 7, 9). Clavus closed: *Pcu* + *A*₁ running into *A*₂ before apex of clavus (Fig. 35) *Bumerangum* gen. n.
- 2 (1). Cephalic process absent (Fig. 4). Clavus open: *Pcu* + *A*₁ running into *A*₂ at apex of clavus 3.
- 3 (8). Subcosta and radius of fore wing originating from one point of basal cell (Fig. 28) 4.
- 4 (5). Hind tibia without lateral spines *Neocolpoptera* Dozier.



Figs. 43–46. Nogodinidae, *Bumerangum deckerti* gen. et sp. n., paratype, female genitalia: (43) gonopods, lateral view; (44) anterior connective lamina of gonapophysis VIII and gonocoxa VIII, lateral view; (45) posterior connective laminae of gonapophyses IX and gonospiculum bridge, dorsal view; (46) anal tube, dorsal view.

- 5 (4). Hind tibia with one lateral spine 6.
- 6 (7). Median area of posterior connective laminae of gonapophyses IX with spines. Aedeagus without ventral hooks. Posterior margin of pygophore of males with long median process
..... *Jamaha* Gnezdilov et O'Brien.
- 7 (6). Median area of posterior connective laminae of gonapophyses IX smooth. Aedeagus with pair of ventral hooks. Posterior margin of pygophore of males without processes
..... *Colpoptera* Burmeister.
- 8 (3). Subcosta and radius of fore wing originating from basal cell as common stem (Fig. 29) 9.
- 9 (10). Ovipositor rounded. Hind tibia without lateral spines *Ugoa* Fennah.
- 10 (9). Ovipositor beak-shaped. Hind tibia with one lateral spine
..... *Caudibeccus* Gnezdilov et O'Brien.

The subfamily Colpopterinae is a compact group of fulgoroids, comprising 6 genera with 43 species and subspecies in the Neotropical and Afrotropical regions. It is beyond doubt that further investigation of the faunas of these regions and revision of the genus *Colpoptera* will increase the number of the known genera and species of this subfamily. Colpopterinae clearly differs from the other subfamilies of Nogodini-

dae in a shape and venation of the fore and hind wings (Figs. 4, 7, 15, 35, 36). It is noteworthy that the simple venation of the hind wing (longitudinal veins weakly branch, cross-veins are scanty) of Colpopterinae is also characteristic of other families of the Fulgoroidea: Delphacidae, Cixiidae, Derbidae, Tropiduchidae (see figs.: Fennah, 1956; Anufriev and Emeljanov, 1988; Rahman et al., 2012).

The position of *Bumerangum deckerti* gen. et sp. n. among Colpopterinae is not quite clear. On the one hand, the new genus is characterized by the closed clavus of the fore wing (Fig. 35), which is generally typical of the primitive Fulgoroidea (Anufriev and Emeljanov, 1988) and can be considered an ancestral state in comparison with the open clavus characteristic of the American genera of the subfamily Colpopterinae. *Bumerangum deckerti* also differs in a more complex venation of the hind wing, in particular, in the bifurcate median and in the trifurcate first anal vein (Fig. 36)—in the other genera of the subfamily, the median is simple, and the first anal vein is bifurcate (Fig. 15); in addition, the apices of the posterior branch of *CuA* (*CuA*₂) and of *CuP* are not fused, similarly to those in species of the American genera. The non-fused apices of the veins *CuA*₂ and *CuP* can also be considered a plesiomorphic state. On the other hand, *B. deckerti* is similar to the genera *Caudibeccus* Gnezdilov et O'Brien and *Ugoa* Fennah (Fig. 29) in the fore-wing veins *Sc* and *R* originating from the basal cell as a common stem (Fig. 35). However, according to Emeljanov (1987), the separation of the basal areas of *Sc* and *R*, in particular, in the cercopocicadoids, is apparently secondary. On the whole, *Bumerangum* clearly differs from the other genera of the subfamily Colpopterinae in the peculiar shape of its cephalic process (Figs. 7–9, 32); in the other genera, the coryphe is transverse (Figs. 4, 5). The boomerang-shaped body (in lateral view) of *B. deckerti* is similar to that of the Southern African *Bowesdorpia tricornis* Synave, 1956 also belonging to the family Nogodinidae (subfamily Nogodininae, tribe Mithymnini Fennah) (Gnezdilov, 2007).

The ecological features of representatives of the subfamily Colpopterinae remain unknown. The Neotropical species may dwell in forest or ecotone communities. In particular, *Colpoptera sinuata* Burmeister, 1835 was found in Mexico in a sparse flood-plain forest (D.R. Kasparyan, pers. comm.), and *Caudibeccus emeljanovi* Gnezdilov et O'Brien, 2008 was collected in Cuba from roadside grasses (A.F. Emeljanov,

pers. comm.). *Bumerangum deckerti* especially stands out; it inhabits arid landscapes with Succulent Karoo biome on the eastern coast of the Republic of South Africa (*Biodiversity in Southern Africa*, 2010) (Fig. 10). There are few reports on the trophic associations of several species of the genus *Colpoptera* and *Jamaha elevans* (Walker), which were found on representatives of the families Arecaceae, Cyathaceae, Polygonaceae, and Verbenaceae; records of *Colpoptera* from Verbenaceae are most frequent (Wilson et al., 1994).

Most genera and species of the subfamily are known from the Greater and Lesser Antilles. The Greater Antilles are considered to be formed not earlier than in the middle Eocene, and the formation of the existing Quarternary fauna of the islands is dated respectively to the period following the middle Eocene. For example, fossil records demonstrate that the majority of the land vertebrates appeared on the Greater Antilles during the Eocene–Oligocene (Iturralde-Vinent and MacPhee, 1999). Colpopterinae are reliably known from the early/middle Miocene. The insect shown in a photograph in the book of Grimaldi and Engela (2005, fig. 1.1) seems to be an undescribed representative of this subfamily from Dominican amber (Shcherbakov, 2006) and most likely belongs to one of the recent genera. Origination of the genus *Bumerangum* gen. n. should be associated with the transformation of the Miocene (25 million years ago) subtropical forests in the recent fynbos owing to the aridization of the Cape Province 8–7 million years ago (Richardson et al., 2001), which was caused by the separation of Antarctica from South America and resulted in formation of the cold circum-Antarctic currents about 14–11 million years ago.

In my opinion, the disjunctive distribution of the subfamily Colpopterinae in Central and South America and Southern Africa gives no grounds to suppose the ancient age of this taxon (for example, over 100 million years, which corresponds to the age of the Atlantic Ocean). According to Szwedo (2002), the families of the issidoid group, to which nogodinids also belong, might emerge at the boundary of the Cretaceous and the Neogene and underwent a rapid diversification in the Eocene–Miocene. I am inclined to agree with Eskov (1984) who asserts that “the formation of the southern disjunctive ranges by means of extinction of “connecting” forms on the northern continents is not an exception but a fundamental general rule.” In particular, Nogodinidae are known from the

late Eocene (55–53 million years ago) Oise amber in France (Szwedo, 2011). Thus, we probably deal with a reduction of the initially wide range of the subfamily Colpopterinae, also extending into the Northern hemisphere.

ACKNOWLEDGMENTS

I am grateful to Dr J. Deckert (MNB, Berlin, Germany), Prof. Dr T. Bourgoin (MNHN, Paris, France), and Mr J. J. Mutyorauta (The Northern Cape Nature Conservation Service, Republic of South Africa) for the material supplied for examination, to Prof. Dr H. Hoch (MNB) for his hospitality during my work in the Museum für Naturkunde, Berlin, Germany, and also to Alexander von Humboldt Stiftung (Bonn, Germany), to the Muséum national d'Histoire naturelle (Paris, France), and to the Ministry of Education and Science of the Russian Federation (contract no. 16.518.11.7070) for the financial support.

REFERENCES

- Anufriev, G.A. and Emeljanov, A.F., "Suborder Cicadinea (Auchenorrhyncha)," in *A Key to the Insects of the Far East of the USSR. Vol. 2. Homoptera and Hemiptera*, Ed. by Lehr, P.A. (Nauka, Leningrad, 1988), pp. 12–495 [in Russian].
- Bartlett, C., "An Annotated List of Planthoppers (Homoptera: Fulgoroidea) of Guana Island (British West Indies)," *Entomol. News* **111** (2), 120–132 (2000).
- Becker-Migdisova, E.E., "Relationship of the Phylogeny of Psyllomorpha to Its Trophic Adaptation on Host-plants," in *The Session Dedicated to the 100th Anniversary of the Date of Birth of Academician A.A. Borisyak* (Moscow, 1972), pp. 3, 4 [in Russian].
- Biodiversity in Southern Africa. Vol. 1. Patterns at Local Scale—the BIOTA Observatories*, Ed. by Jürgens, N., Haarmeyer, D.H., Luther-Mosebach, J., Dengler, J., Finckh, M., and Schmiedel, U. (Klaus Hess Publishers, Göttingen and Windhoek, 2010).
- Bourgoin, T., "Female Genitalia in Hemiptera Fulgoroidea, Morphological and Phylogenetic Data," *Ann. Soc. Entomol. Fr. (N. S.)* **29** (3), 225–244 (1993).
- Burmeister, H.C.C., "Schnabelkerfe. Rhynchota," *Handbuch der Entomologie* **2** (1), 1–396 (1835).
- Caldwell, J.S., "Notes on Issidae from Mexico (Homoptera, Fulgoroidea)," *Ann. Entomol. Soc. Amer.* **38** (1), 89–120 (1945).
- Caldwell, J.S. and Martorell, L.F., "Review of the Auchenorrhynchos Homoptera of Puerto Rico. II. The Fulgoroidea Except Kinnaridae," *J. Agr. Univ. Puerto Rico* **34** (2), 133–269 (1951).
- Dozier, H.L., "New and Interesting West Indian Homoptera," *Amer. Mus. Nov.* **510**, 1–24 (1931).
- Emeljanov, A.F., "Phylogeny and Evolution of the Subfamilies Orgeriinae (Homoptera, Dictyopharidae)," in *Readings in Memory of N.A. Kholodkovsky* (Nauka, Leningrad, 1980), vol. 32, pp. 1–95.
- Emeljanov, A.F., "Phylogeny of Cicadina (Homoptera) According to the Comparative Morphological Data," *Trudy Vses. Entomol. O-va* **69**, 19–109 (1987).
- Emeljanov, A.F., "On the Problem of the Classification and Phylogeny of the Family Delphacidae (Homoptera, Cicadina), with Larval Characters Taken into Account," *Entomol. Obozr.* **74** (4), 780–794 (1995).
- Eskov, K.Yu., "The Continent Drift and the Problems of Historical Biogeography," in *Faunogenesis and Phylogenogenesis*, Ed. by Chernov, Yu.I. (Nauka, Moscow, 1984), pp. 24–92 [in Russian].
- Fabricius, J.C., *Systema Rhyngotorum secundum ordines, genera, Species, adiectis synonymis, locis, observationibus, descriptionibus* (Apud Carolum Reichard, Brunsvigae, 1803).
- Fennah, R.G., "The Fulgoroidea or Lantern Flies, of Trinidad and Adjacent Parts of South America," *Proc. U. S. Natn. Mus.* **95** (3184), 411–520 (1945).
- Fennah, R.G., "Lanternflies of the Family Issidae of the Lesser Antilles (Homoptera: Fulgoroidea)," *Proc. U. S. Natn. Mus.* **105** (3350), 23–47 (1955).
- Fennah, R.G., "Fulgoroidea from Southern China," *Proc. Calif. Acad. Sci.* **4** (28), 441–527 (1956).
- Fennah, R.G., "New Species of Fulgoroidea from the West Indies," *Trans. R. Entomol. Soc. London* **117**, 95–125 (1965).
- Fennah, R.G., "The Higher Classification of the Nogodinidae (Homoptera, Fulgoroidea) with Description of a New Genus and Species," *Entomologist's Month. Mag.* **113**, 113–119 (1978).
- Fennah, R.G., "Revisionary Notes on the Classification of the Nogodinidae (Homoptera, Fulgoroidea), with Description of a New Genus and a New Species," *Entomologist's Month. Mag.* **120**, 81–86 (1984).
- Fennah, R.G., "A New Subfamily of Nogodinidae (Homoptera: Fulgoroidea) with the Description of a New Species of Gastrinia," *Proc. Entomol. Soc. Wash.* **89** (2), 363–366 (1987).
- Gnezdilov, V.M., "New Species of the Genus *Tshurtshurnella* Kusnezov, 1927 (Homoptera, Cicadina, Issidae) from Turkey and Lebanon," *Russ. Entomol. J.* **11** (3), 233–240 (2002a).
- Gnezdilov, V.M., "Morphology of the Ovipositor in the Subfamily Issinae (Homoptera, Cicadina, Issidae)," *Entomol. Obozr.* **81** (3), 605–626 (2002b) [*Entomol. Rev.* **82** (8), 957–974 (2002)].
- Gnezdilov, V.M., "A New Tribe of the Family Issidae (Homoptera, Cicadina) with Comments on the Family as a Whole," *Zoosyst. Ross.* **11** (2), 305–309 (2003).
- Gnezdilov, V.M., "On the Systematic Positions of the Bladinini Kirkaldy, Tonginae Kirkaldy, and Trienopinae

- Fennah (Homoptera, Fulgoroidea),” *Zoosyst. Ross.* **15** (2), 293–297 (2007).
26. Gnezdilov, V.M., “Revisionary Notes on Some Tropical Issidae and Nogodinidae (Hemiptera: Fulgoroidea),” *Acta Entomol. Mus. Natn. Pragae* **49** (1), 75–92 (2009).
 27. Gnezdilov, V.M., Drosopoulos, S., and Wilson, M.R., “New Data on the Taxonomy and Distribution of Some Fulgoroidea (Homoptera, Cicadina),” *Zoosyst. Ross.* **12** (2), 217–223 (2004).
 28. Gnezdilov, V.M. and O’Brien, L.B., “New Taxa and New Combinations in Neotropical Issidae (Hemiptera: Fulgoroidea),” *Insecta Mundi* **31**, 1–26 (2008).
 29. Gnezdilov, V.M. and Wilson, M.R., “Review of the Genus *Scantinius* Stål with Notes on the Tribe Parahira-cini Cheng & Yang (Hemiptera: Auchenorrhyncha: Fulgoroidea: Issidae),” *Arthr. Syst. Phyl.* **65** (1), 101–108 (2007).
 30. Grimaldi, D. and Engel, M.S., *Evolution of the Insects* (Cambridge University Press, 2005).
 31. Iturralde-Vinent, M.A. and MacPhee, R.D.E., “Palaeogeography of the Caribbean Region: Implications for Cenozoic Biogeography,” *Bull. Amer. Mus. Nat. Hist.* **238**, 1–95 (1999).
 32. Lethierry, L., “Voyage de M. E. Simon au Venezuela (Décembre 1887–Avril 1888). 9^e Mémoire (1). Hémiptères Homoptères,” *Ann. Soc. Entomol. Fr., Ser. 6* **10**, 147–160 (1890).
 33. Melichar, L., “Monographie der Acanaloniiden und Flatiden (Homoptera) (Fortsetzung),” *Ann. Nat. Hofmus. Wien* **17**, 1–253 (1902).
 34. Melichar, L., “Monographie der Issiden (Homoptera),” *Abhandlungen der K. K. Zoologisch-botanischen Gesellschaft in Wien, Ser. 4* **3**, 1–327 (1906).
 35. Metcalf, Z., “Homoptera from the Bahama Islands,” *Amer. Mus. Novit.* **1698**, 1–46 (1954).
 36. Metcalf, Z., *General Catalogue of the Homoptera. Fulgoroidea. Issidae* (Waverly Press, INC, Baltimore, 1958), vol. 4, issue 15.
 37. Muir, F.A.G., “New and Little Known Fulgorids from the West Indies (Homoptera),” *Proc. Haw. Entomol. Soc.* **5**, 461–472 (1924).
 38. Myers, J.G., “Notes on Cuban Fulgoroid Homoptera,” *Studies on Cuban Insects*, 13–28 (1928).
 39. Osborn, H., “Insects of Porto Rico and the Virgin Islands. Homoptera (Excepting the Sternorrhynchi),” *Sci. Surv. Porto Rico and Virgin Islands* **14**, 111–260 (1935).
 40. Popov, Yu.A., “Superorder Cimicidea. The Cimicida Group. Hemiptera or Proboscidea,” in *Historical Development of the Class of Insects*, Ed. by Rodendorf, B.B. and Rasnitsyn, A.P. (Nauka, Moscow, 1980), pp. 58–69 [in Russian] (*Trudy Paleontol. Inst. Akad. Nauk SSSR* **175**).
 41. Rahman, M.A., Kwon, Y.J., and Suh, S.J., “Two Newly Recorded Genera and Three New Species of the Tribe Cedusini (Hemiptera: Fulgoromorpha: Derbidae) from Korea,” *Zootaxa* **3261**, 59–68 (2012).
 42. Richardson, J.E., Weitz, F.M., Fay, M.F., Cronk, Q.C.B., Linder, H., Reeves, G., and Chase, M.W., “Rapid and Recent Origin of Species Richness in the Cape Flora of South Africa,” *Nature* **412**, 181–183 (2001).
 43. Shcherbakov, D.E., “The Earliest Find of Tropiduchidae (Homoptera: Auchenorrhyncha), Representing a New Tribe, from the Eocene of the Green River, USA, with Notes on the Fossil Record of Higher Fulgoroidea,” *Russ. Entomol. J.* **15** (3), 315–322 (2006).
 44. Szwedo, J., “Amber and Amber Inclusions of Planthoppers, Leafhoppers and Their Relatives (Hemiptera, Archaeorrhyncha et Clypeorrhyncha),” *Denisia* **04**, zugleich Kataloge des OÖ. Landesmuseums, N. F. **176**, 37–56 (2002).
 45. Szwedo, J., “*Ordralfabetix sirophatanis* gen. et sp. n.—the First Lophopidae from the Lowermost Eocene Oise Amber, Paris Basin, France (Hemiptera: Fulgoromorpha),” *Zootaxa* **2822**, 52–60 (2011).
 46. Van Duzee, E., “Notes on Jamaican Hemiptera: A Report on a Collection of Hemiptera Made on the Island of Jamaica in the Spring of 1906,” *Bull. Buffalo Soc. Nat. Sci., Ser. 5* **8**, 3–79 (1907).
 47. Walker, F., *List of the Specimens of Homopterous Insects in the Collection of the British Museum. Suppl.* (1858).
 48. Wilson, S.W., Mitter, C., Denno, R.F., and Wilson, M.R., “Evolutionary Patterns of Host Plant Use by Delphacid Planthoppers and Their Relatives,” in *Planthoppers. Their Ecology and Management*, Ed. by Denno, R.F. and Perfect, T.J. (Chapman and Hall, New York, London, 1994), pp. 7–113.
 49. Wolcott, G.N., “Insectae Borinquenses. A Revised Annotated Check-list of the Insects of Puerto Rico,” *J. Agr. Univ. Puerto Rico* **20**, 1–600 (1936).