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BLACK FLIES OF THE GENERA *GYMNOPAIS* STONE, 1949 AND *TWINNIA* STONE ET JAMNBACK, 1955 (DIPTERA: SIMULIIDAE) FROM THE FUND COLLECTION OF THE ZOOLOGICAL INSTITUTE OF THE RUSSIAN ACADEMY OF SCIENCES

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ABSTRACT

As a result of examination of the fund collection of black flies (Diptera: Simuliidae) of the Zoological Institute of the Russian Academy of Sciences, detailed redescriptions and original drawings of 9 species (of 12 known in the World fauna) of the genus *Gymnopais* Stone, 1949 and 4 species (of 10 known in the World fauna) of the genus *Twinnia* Stone et Jamnback, 1955 are given. Keys to all known12 species of *Gymnopais* and 9 species of *Twinnia* of the World fauna are provided. The information on *Twinia changbaiensis* Sun, 1994 (China, Liaoning) is insufficient, and this species is not included in the key.

Key words: black flies, distribution, *Gymnopais,* Simuliidae, systematics, *Twinnia*

МОШКИ РОДОВ *GYMNOPAIS* STONE, 1949 И *TWINNIA* STONE ET JAMNBACK, 1955 (DIPTERA: SIMULIIDAE) ИЗ ФОНДОВОЙ КОЛЛЕКЦИИ ЗООЛОГИЧЕСКОГО ИНСТИТУТА РОССИЙСКОЙ АКАДЕМИИ НАУК

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РЕЗЮМЕ

В результате ревизии фондовой коллекции мошек (Diptera: Simuliidae) Зоологического института Российской академии наук сделаны подробные переописания и оригинальные рисунки деталей строения 9 (из 12 известных в мировой фауне) видов рода *Gymnopais* Stone, 1949 и 4 (из 10 известных в мировой фауне) видов рода *Twinnia* Stone et Jamnback, 1955. Приведены определительные ключи для всех известных 12 видов рода *Gymnopais* и 9 видов рода *Twinnia* мировой фауны. Данные, приведенные в описании *Twinia changbaiensis* Sun, 1994 (Китай, Ляонинг) не дают достаточной информации для использования их в определительных таблицах.

Ключевые слова: мошки, распространение, *Gymnopais,* Simuliidae, систематика, *Twinnia*

INTRODUCTION

The absence of cephalic fans in larvae of all instars and the modification of the frontoclypeal apotome, connected with this absence, wide and flat hypostomal teeth and apical mandibular teeth in the genus *Gymnopais* Stone, 1949, were the main characters, used by Rubzov (1955) for distinguishing the subfamily Gymnopaidinae. Later into this subfamily the genera *Twinnia* Stone et Jamnback, 1955 and *Levitinia* Chubareva et Petrova, 1981 also were included (Rubzov 1956; Chubareva and Petrova 1981). On the other hand Wood (1978), taking into account the comparative insignificant differences between adults of these

two genera and of *Prosimulium* s.l., considered them as evolutionary derivates of the genus *Prosimulium* Roubaud, 1906. Wood treated pupation of last instar larvae without cephalic fans in *Twinnia* and *Gymnopais* as a result of inhibition of development of fans (first instar larvae of *Prosimulium* also have no cephalic fans), but proceeding from important morphological peculiarity of larvae and, partially, pupae, he supported the consideration of *Twinnia* and *Gymnopais* as separate genera in the tribe Prosimuliini of the subfamily Simuliinae. This point of view now is accepted by the majority of authors (Crosskey 1987, 1990; Crosskey and Howard 1997; Adler et al. 2004 and others).

Rubzov (1974) and some of the earlier authors assumed the lack of cephalic fans as a primitive character, and treated *Gymnopais* and, in lesser degree, *Twinnia* as ancestors of *Prosimulium* and all other more advanced groups (i.e. as ancestor morphological type of all the family Simuliidae). In that time Rubzov did not possess the later data on fossil black flies. The morphology of larvae and pupae of Mesozoan black flies (Jurassic and Cretaceous periods) is closely related to the morphology of modern Simuliidae of the genus *Prosimulium* (Zhang 1986; Kalugina 1991; Currie and Grimaldi 2000). The larvae of Mesozoan black flies had completely developed cephalic fans and not narrowed frontoclypeal apotome, pupal gills being very similar to the gills of *Prosimulium*.

The data available in no way confirm that *Gymnopais*-like type of larval morphology was the prototypic model of the family Simuliidae. On the contrary, it seems to be assumed, that during several glacial periods some groups of *Prosimulium*-like black flies became adapted to biotopes formed as the result of thawing of the giant circumpolar and mountain glaciers – the numerous springs and rivers near the borders of glaciers. Streams of this type probably were almost devoid of flora and fauna in water flow. Filtration was not adequate to provide black fly larvae with the amount of food enough for the complete development of fat body. The sufficient food extraction was possible only by scraping. As a result, complex filtering apparatus (cephalic fans) and muscular and sclerotized structures of the larval head, connected with this apparatus, were reduced. Because of the widening and the flattening of hypostomal teeth and apical mandibular teeth the mouthparts became adapted to scraping of periphyton.

Assuming that morphology of *Prosimulium* includes the majority of archaic features of Simuliidae, it seems to be accepted, that the evolutionary process has followed from *Prosimulium*-like ancestors to *Levitinia* Chubareva et Petrova, 1981 (imaginal antennae with 11 articles, posterolateral branches of larval anal sclerite remain), then to *Twinnia* Stone et Jamnback, 1955, and as a result to *Gymnopais* Stone, 1949 (as the most specialized and morphologically modified variant). In this case the disjunctive distribution of *Levitinia* (2 species in Middle Asia and 1 species in Palestine) and *Twinnia* (mountains of Central Europe, Northern Russian Far East, Japan, Western Nearctic, Eastern Nearctic) could be supposedly explained by the elder origin of these genera compared with the distribution of *Gymnopais* without large disjunction (Eastern Siberia, Russian Far East, Northern Nearctic). By our point of view, on the ground of quite enough advanced specialization and distinct difference in preimaginal structures, we can treat these three genera as the tribe Gymnopaidini Rubzov, 1955 (separate from the tribe Prosimuliini Enderlein, 1921) in the subfamily Prosimuliinae Enderlein, 1921 (about equal in content to the tribe Prosimuliini *sensu* Crosskey 1987). The generic and suprageneric system of the family Simuliidae now is in quaestionable position, and either the "British and USA" point of view (Crosskey and Howard 1997; Adler et al. 2004) or the point of view of Rubzov (1974) and Yankovsky (2002) must be taken into account. These phylogenetic considerations are out of the aims of this paper and probably will be discussed in further publications.

MATERIAL AND METHODS

The material examined (96 specimens) includes nine species of the genus *Gymnopais* Stone 1949: males, females, larvae and pupae of *G. bifistulatus* Rubzov, 1955, *G. frontatus* Yankovsky, 1982, *G. trifistulatus* Rubzov, 1955 and *G. lindneri* Rubzov, 1963, males and females of *G. andrei* Worobez,1984, females, larvae and pupae of *G. dichopticus* Stone, 1949, larvae and pupae of *G. rubzovi* Bobrova, 1967, *G. sexcornutus* Bodrova, 1975 and *G. holopticus* Stone, 1949; and of 4 species of the genus *Twinnia* Stone et Jamnback, 1955: males, females, larvae and pupae of *T. hydroides* (Novák, 1956), and *T. sedecimfistulata* (Rubzov, 1955), females of *T. magadensis* Rubzov, 1973 and *T. nova* (Dyar et Shannon, 1927).

Institutional abbreviation. ZIN, Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia.

SYSTEMATICS

Family Simuliidae Newman, 1834
Subfamily Prosimuliinae Enderlein, 1921
Tribe Gymnopaidini Rubzov, 1955

Gymnopaidini; Rubzov 1955: 329 Yankovsky 1993: 208; 2002: 116.

Type-genus. *Gymnopais* Stone, 1949, by original designation.

Genera included. *Gymnopais* Stone, 1949, *Levitinia* Chubareva et Petrova, 1981, *Twinnia* Stone et Jamnback, 1955.

Key to genera of the tribe Gymnopaidini

1. *Imago:* antennae of 11 articles. *Larva:* anal sclerite with 5 branches. *Pupa:* gills of 8–10 thin filaments . . . . . *Levitinia* Chubareva et Petrova, 1981
– *Imago:* antennae of 9 articles. *Larva:* anal sclerite with 3 branches, Y-shaped. *Pupa:* gills of 2–6 swollen or of 14–16 thin filaments 2
2. *Male:* head dichoptic or holoptic, markedly narrower than thorax; gonostyli with 2–5 (very rarely 1) apical spines; gonopleurites with 2–15 setae (or rarely without setae). *Female:* mouthparts of not bloodsucking type; boundary between anal lobes and cerci incomplete and hardly distinguished. *Larva:* on outer surface of distal part of mandibles 7–15 rows of comb-like scales. *Pupa:* gills of 2–6 swollen filaments . . . . . *Gymnopais* Stone, 1949
– *Male:* head always holoptic, about equal in width to thorax; gonostyli with 1 apical spine; gonopleurites without setae. *Female:* mouthparts of bloodsucking (very rarely of not bloodsucking) type; anal lobes and cerci distinctly separated by membranous zone. *Larva:* on outer surface of distal part of mandibles 3–6 large spine-like setae. *Pupa:* gills of 14–16 thin filaments . . . . . *Twinnia* Stone et Jamnback, 1955

Genus *Gymnopais* Stone, 1949

Gymnopais Stone 1949: 260; Rubzov 1956: 187; 1960: 129; Wood 1978: 1308; Rubzov and Yankovsky 1984: 26; 1988: 115; Crosskey and Howard 1997: 15; Yankovsky 2002: 117; Adler et al. 2004: 238.

Type-species. *Gymnopais dichopticus* Stone,1949, by original designation.

Diagnosis. *Imago*. Antennae of 9 articles. Proboscis distinctly shorter than clypeus. Body black or dark-gray, with short, erect hairs; scutum with dark hairs, without silvery reflecting spots. Thorax slightly arched. Wings slightly wrinkled, vein Rs bifurcated, veins R1 and C with hairs only, basal radial cell ⅓ of wing length. Legs black, brown or yellowish. Calcipala and pedisulcus absent. Fore basitarsi thin, cylindrical.

Male. Head markedly narrower than thorax. Head holoptic or dichoptic (if dichoptic, frons with long sublateral hairs). Hind basitarsi usually moderately widened (4.5–5.0 times as long as wide), rarely very widened (2.7–3.0 times as long as wide). Gonocoxites equal in length or slightly longer than gonostyli, from about equal in length to 1.6 times as long as maximal wide (ventral view). Gonostyli narrowed and sometimes slightly curved inwards in distal part, width in basal part 1.5–4.0 times width in distal part, from about equal in length to 1.7 times as long as maximal wide (ventral view), armed with 1–5 apical spines. Body of ventral plate lamellate, weakly curved, from about equal to 3 times as wide as long, with distinct medial keel. Gonopleurites narrow, pointed basally, without setae or with 2–15 setae.

Female. Mouthparts not of bloodsucking type, laciniae and mandibles without teeth; palpomere V 1.3–2.0 times as short as palpomeres III+IV. Claws toothless or (rarely) with small basal tooth. Hypogynal valves simple, about triangular, from 1.5 times as short to 1.5 times as long as middle part of abdominal sternite VIII, anteromedial angles of valves rostriform. Stem of genital fork not widened distally, from about equal in length to 2 times as long as branches, branches with well developed posteromedial apodeme, anterolateral apodeme absent. Boundary between anal lobes and cerci incomplete and hardly distinguished. Anal lobes 1.3–2.3 times as high and 1.2–1.8 times as long as cerci. Anal lobes 2–4 times, cerci 1.2–2.5 times as high as long; lower blade of anal lobes with 5–13 spiniform setae. Spermatheca rounded (length about equal to width) rarely slightly shortened or slightly elongated, with or without trunk at base; surface smooth, pigmented.

Larva. Cephalic apotome narrow, tapered posteriorly. Labral fans absent. Boundary between articles I and II of antennae hardly distinguishable, their common length 1.3–2.0 times length of article III. Hypostoma with broad flat teeth; each side of hypostoma with 3–10 sublateral setae. Postgenal cleft absent. On outer surface of distal part of mandibles 7–15 rows of comb-like scales; apical mandibular teeth flat; inner

mandibular teeth 12–17; mandibular serration of 1–2 small notches. Anal sclerite Y-shaped. Abdominal posterior circlet of 84–120 rows with 10–18 hooklets in each row. Rectal organ of 3 simple lobes.

Pupa. Respiratory organ (gills) 1.5–2.5 times as short as body length, of 2–6 filaments, usually swollen; angle between basal parts of upper and lower filaments 20–45°, rarely about 90°. Spine combs on abdominal tergites absent, hooks on dorsum of abdomen reduced. Cocoon reduced.

Distribution. Holarctic.

Species included. *G. andrei* Worobez, 1984 (PA), *G. bifistulatus* Rubzov, 1955 (PA), *G. dichopticoides* Wood, 1978 (NA), *G. dichopticus* Stone, 1949 (NA), *G. fimbriatus* Wood, 1978 (NA), *G. frontatus* Yankovsky, 1982 (PA), *G. holopticoides* Wood, 1978 (NA), *G. holopticus* Stone, 1949 (NA), *G. lindneri* Rubzov, 1963 (PA), *G. rubzovi* Bobrova, 1967 (PA), *G. sexcornutus* Bodrova, 1975 (PA), *G. trifistulatus* Rubzov, 1955 (PA) [PA – Palaearctic, NA – Nearctic].

In the descriptions of species in square brackets the additional characters of species from the literature data are given, the features of larvae of last instar (with well developed dark pupal gill histoblasts) are used.

1. *Gymnopais andrei* Worobez, 1984
(Fig. 1)

Gymnopais andrei Worobez 1984: 74, figs. 1, 2.

Description. *Male*. Head holoptic. Body black. Legs yellowish brown, tibiae dark on ⅓ from the base and on ¼ in distal part (Worobez, 1984: 74). Hind basitarsus moderately widened, 5 times as long as wide, hind tarsomere II 3 times as short and 2 times as narrow as basitarsus, 3.5 times as long as wide. Length of gonostyli slightly more than length of gonocoxites. Gonocoxites about equal in length to gonostyli, 1.5–1.6 times as long as maximal wide (ventral view). Gonostyli moderately tapered distally (width in basal part 2.7–3.0 times width in distal part), in ventral view 1.4–1.6 times as long as wide at base, apical spines 2. Body of ventral plate 2 times as wide as long (ventral view), posterior edge about straight, medial keel moderately developed. Gonopleurites with 2 long setae.

Female. The single preparation in the collection of Zoological Institute is in bad condition: legs, genital fork and hypogynal valves hardly can be seen. [Body black. Frons very wide (height ⅔ of least width). Legs dark, with large hairs. Anal lobes 2 times as high as long, 1.5 times as high as cerci; cerci 2 times as high as long. Spermatheca without trunk at base, its size about width of posterior cleft of genital fork (Worobez 1984: 74, fig. 1)]. Palpomere V 2 times as short as palpomeres III+IV, palpomere III about cylindrical; sensory vesicle ⅓ of length of palpomere III. Claws toothless. Hypogynal valves slightly shorter than middle part of sternite VIII, with rare short hairs only on basal parts. Stem of genital fork 1.5–1.6 times as long as branches, posteromedial apodeme of branches large, serrated; posterior cleft of genital fork oval, 1.5 times as wide as long.

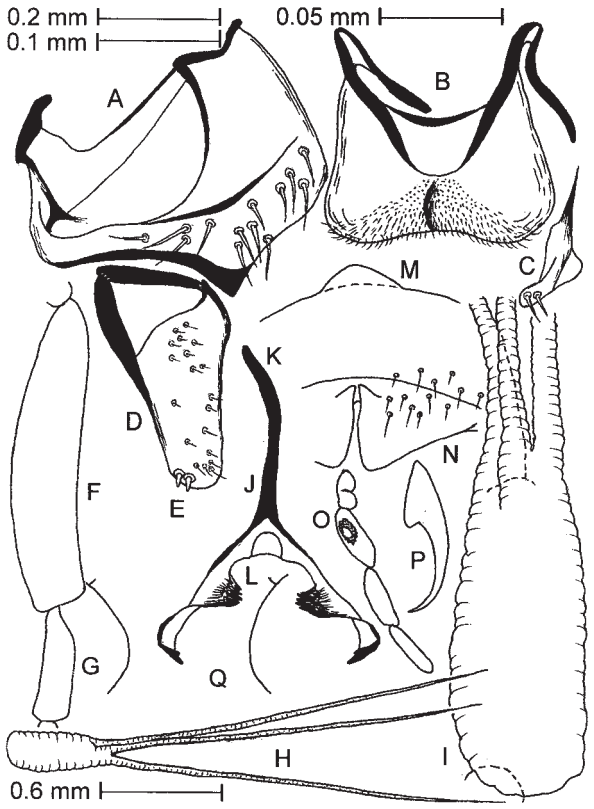

Fig. 1. *Gymnopais andrei* Worobez, 1984. Holotype pupa (male) (A–I): A – gonocoxite; B – ventral plate; C – gonopleurite; D – gonostylus; E – apical spines on gonostylus; F – hind basitarsus; G – hind tarsomere II; H – pupal gill; I – basal part of pupal gill. Paratype pupa (female) (J–Q): J – genital fork; K – stem of genital fork; L – posterior cleft of genital fork; M – abdominal sternite VIII; N – hypogynal valves; O – maxillary palp; P – claw; Q – frons. Scale bar: 0.6 mm = H; 0.2 mm = F, G, I, O, Q; 0.1 mm = A, B, C, D, E, J, K, L, M, N; 0.05 mm = P.

Larva. In the collection of ZIN larvae of this species are absent (characters see: Worobez 1984: 74–76, fig. 2).

Pupa. In the collection of ZIN only pupal gills in slides of 1 male and 1 female reared from pupae. Gills of 3 thin filaments, approximately equal in length, very slightly widened in basal part, all filaments diverge immediately from swollen basal trunk (3 times as long as wide); angle between basal parts of upper and lower filaments about 20°.

Holotype. Male with pupal exuviae (ZIN, slide 21404), Southern Yakutia, spring near Neryungri, 20 August 1977, coll. E.I. Worobez.

Paratype. 1 female with pupal exuviae (ZIN, slide 21403), same data.

Distribution. NE Siberia (Yakutia) (Crosskey and Howard 1997; Yankovsky 2002).

2. *Gymnopais bifistulatus* Rubzov, 1955
(Figs. 2 and 3)

Gymnopais bifistulatus Rubzov 1955: 336, figs. 2, 6, 7; 1956: 195, figs. 13, 42–44; 1960: 133, figs. 40–42.

Description. *Male*. Length about 3 mm. Head holoptic. Scutum mat black, with rare black rough hairs, scutellum with long dark hairs. Abdomen black, with rare short dark hairs. Legs wholly dark; hind basitarsus very widened, 2.7–3.0 times as long as wide, hind tarsomere II unusual large, 2 times as short and 1.2 times as narrow as basitarsus, 2 times as long as wide.

Conocoxites 1.3 times as long as gonostyli; in ventral view length about equal to maximal width. Gonostyli moderately tapered distally (width in basal part 2.5–3.0 times width in distal part), in ventral view 1.3–1.4 times as long as wide at base, apical spine 1. Body of ventral plate very widened, 3 times as wide as long (ventral view), posterior edge straight, medial keel moderately developed. Gonopleurites with 6–7 short setae.

Female. Length 3.2–3.5 mm. Frons wide (height equal to least width), dull black, with rare hairs. Maxillary palpi relatively short and thick, palpomere V 1.5–1.6 times as short as palpomeres III+IV, palpomere III wide; sensory vesicle less than ¼ of length of palpomere III. Scutum black, shiny in medial part, in frontal view with 3 weakly distinguishable slightly more bright (not silvery) stripes, with very rare short hairs; abdomen and legs brown black. Claws with very small but distinctly distinguishable pointed basal tooth. Abdominal sternite VIII moderately sclerotized, strongly protruding forwards. Hypogynal valves 1.5 times as short as middle part of sternite VIII, with long hairs; anteromedial angles of valves weakly sclerotized. Stem of genital fork 1.5 times as long as branches, branches broadly widened distally, posteromedial apodeme wide, about triangular, tapered, serrated on medial edge, their terminations curving toward each other; posterior cleft of genital fork wide, width slightly more than length. Anal lobes 2 times as high and 1.2 times as long as cerci. Anal lobes 3.5 times, cerci 2.5 times as high as long; lower blade of anal lobes with 5–6 spiniform setae. Spermatheca with moderate trunk at base, its size about width of posterior cleft of genital fork.

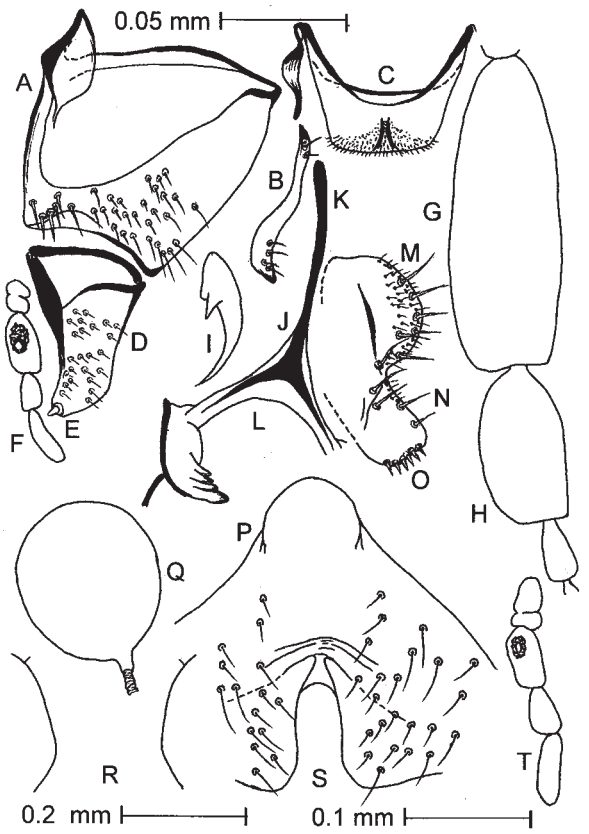

Fig. 2. *Gymnopais bifistulatus* Rubzov, 1955. Male (A–H): A – gonocoxite; B – gonopleurite; C – ventral plate; D – gonostylus; E – apical spine on gonostylus; F – maxillary palp; G – hind basitarsus; H – hind tarsomere II. Female (I–T): I – claw; J – genital fork; K – stem of genital fork; L – posterior cleft of genital fork; M – cercus; N – anal lobe; O – spiniform setae on lower blade of anal lobe; P – abdominal sternite VIII; Q – spermatheca; R – frons; S – hypogynal valves; T – maxillary palp. Scale bar: 0.2 mm = F, G, H, R, T; 0.1 mm = A, B, C, D, E, J, K, L, M, N, O, P, Q, S; 0.05 mm = I.

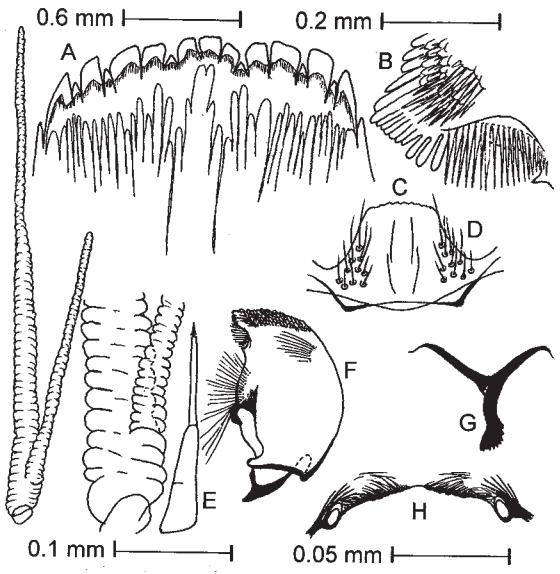

Fig. 3. *Gymnopais bifistulatus* Rubzov, 1955. Lectotype larva with pupal gill histoblasts (A–H): A – hypostomal teeth; B – mandibular teeth; C – hypostoma; D – sublateral setae on hypostoma; E – antenna; F – mandible; G – anal sclerite; H – posteroventral margin of head capsule. Pupa (I, J): I – gill; J – basal part of gill. Scale bar: 0.6 mm = I; 0.2 mm = C, D, F, G, H, J; 0.1 mm = E; 0.05 mm = A, B.

Larva. Length 5–6 mm. Body and head capsule yellow, head pattern distinct, dark yellow. Articles I+II of antennae 1.3–1.4 times as long as article III. Median and lateral hypostomal teeth about equal in length, frontal edge of hypostoma smoothly rounded; each side of hypostoma with 9–10 sublateral setae disposed in 3 rows. Apical end of mandibles transversely cut, flattened apical teeth relatively short, shorter than inner teeth; inner mandibular teeth 15–17; mandibular serration of 1 small notch. Posterior circlet of 84–86 rows with 14–16 hooklets in each row. Median branch of anal sclerite almost not widened and weakly serrated laterally in distal part, thornlets near anal sclerite not developed.

Pupa. Body length 3 mm. Gill of 2 moderately swollen filaments, slightly widened in basal part, lower filament 2–3 times as long and 2 times as wide as upper filament, filaments diverged near the base of gill; angle between basal parts of upper and lower filaments about 20°.

Lectotype. Larva (ZIN, slide 7311), Irkutsk Province, efflux of Zhilishche River, 29 July 1953, coll. I.A. Rubzov (designated by Yankovsky 1995: 13).

Additional material. 1 female, 1 male, (ZIN, slides 7312, 7313), 2 females, 1 male (ZIN, pinned), Irkutsk Province, efflux of Zhilishche Rivulet, 29 July 1953, coll. I.A. Rubzov; 2 larvae (ZIN, slides 17217, 17219), Khabarovsk Territory, Verhne-Bureinskiy District, Spirtak River (affluent of Niman River), 24 July 1963, coll. Shimanskiy; 1 larva with pupal gill histoblasts (ZIN, slide 17079), 2 larvae (ZIN, slides 17078, 17080), Khabarovsk Territory, affluent of Nimakan-Elga River, July – August 1963, coll. Shimanskiy.

Distribution. South of Eastern Siberia and Russian Far East, Mongolia (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

3. *Gymnopais dichopticus* Stone, 1949
(Figs. 4 and 5)

Gymnopais dichopticus Stone 1949: 261; Wood 1978: 1314, figs. 19, 20, 24, 27, 31, 33, 35, 45, 57, 61; Adler et al. 2004: 240, figs. 10.4, 10.5, 10.46, 10.87, 10.231, 10.513, 10.537, map 7.

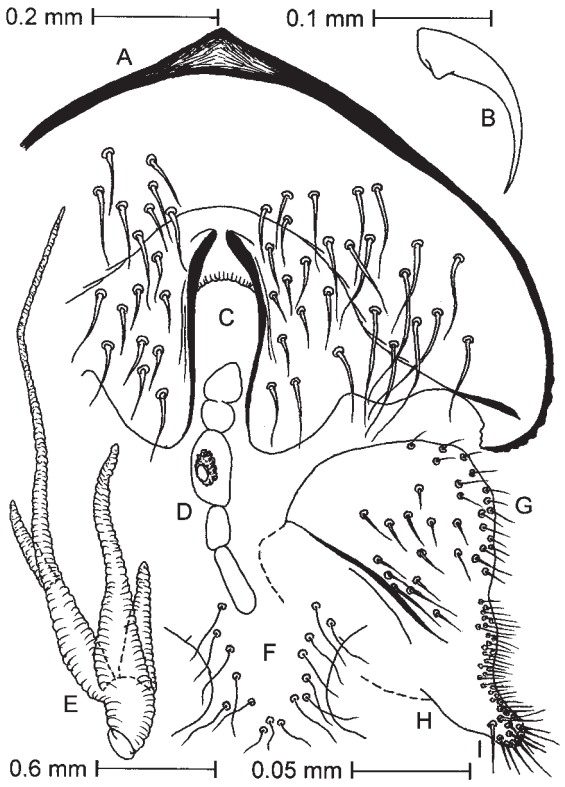

Fig. 4. *Gymnopais dichopticus* Stone, 1949. Pupa (female): A – abdominal sternite VIII; B – claw; C – hypogynal valves; D – maxillary palp; E – pupal gill; F – frons; G – cercus; H – anal lobe; I – spiniform setae on lower blade of anal lobe. Scale bar: 0.6 mm = E; 0.2 mm = D, F; 0.1 mm = A, C, G, H, I; 0.05 mm = B.

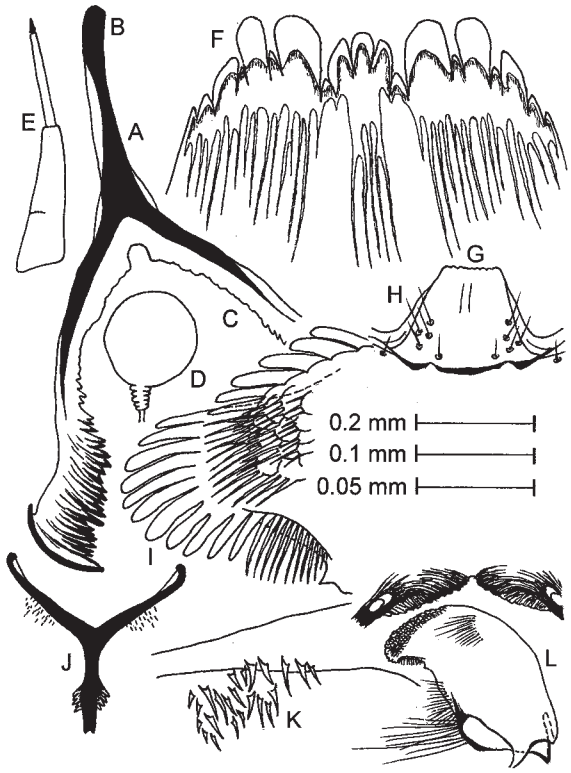

Fig. 5. *Gymnopais dichopticus* Stone, 1949. Pupa (female) (A–D): A – genital fork; B – stem of genital fork; C – posterior cleft of genital fork; D – spermatheca. Larva (E–M): E – antenna; F – hypostomal teeth; G – hypostoma; H – sublateral setae on hypostoma; I – mandibular teeth; J – anal sclerite; K – thornlets near anal sclerite; L – mandible; M – posteroventral margin of head capsule. Scale bar: 0.2 mm = G, H, J, L, M; 0.1 mm = A, B, C, D, E; 0.05 mm = F, I, K.

Description. *Male*. In the collection of ZIN males of this species are absent (characters see: Adler et al. 2004: fig. 10.231).

Female. Frons wide (height ⅔ of least width), with rare long sublateral hairs. Maxillary palpi relatively short and thick, palpomere V 1.5–1.6 times as short as palpomeres III+IV, sensory vesicle about ½ of length of palpomere III. Claws toothless. Abdominal sternite VIII moderately sclerotized, slightly protruding forwards. Hypogynal valves 1.5 times as long as middle part of sternite VIII, with long large hairs; anteromedial angles of valves distinctly sclerotized. Stem of genital fork 1.5 times as short as branches, branches weakly widened distally, posteromedial apodeme narrow, not widened, strongly serrated on medial edge; posterior cleft of genital fork about triangular, 1.2 times as wide as long. Anal lobes 2 times as high and 1.8 times as long as cerci. Anal lobes 3.5 times, cerci 1.2 times as high as long; lower blade of anal lobes with 10–12 long spiniform setae. Spermatheca small, with long trunk at base, its size 2 times less than width of posterior cleft of genital fork.

Larva. Articles I+II of antennae 1.5 times as long as article III. Median and lateral hypostomal teeth about equal in length, frontal edge of hypostoma even; each side of hypostoma with 5–6 sublateral setae disposed in 2 rows. Apical end of mandibles evidently rounded, flattened apical teeth long, equal to inner teeth; inner mandibular teeth 12–14; mandibular serration of 1 small notch. Posterior circlet of 106–108 rows with 13–15 hooklets in each row. Median branch of anal sclerite distinctly widened and serrated in distal part, 20–30 thornlets developed near anterior edge of lateral branches of anal sclerite.

Pupa. Gill of 4 filaments, 2 lower filaments long and thin, on common swollen trunk, 2 upper filaments short and distinctly swollen; angle between basal parts of upper and lower filaments very approximately about 30–45°.

Material. 2 females with pupal exuviae (ZIN, slides 10210, 10213), Alaska, 7 September 1948, coll.unknown; 2 larvae (ZIN, slides 10211, 10212), Alaska, 16 July 1948, coll.unknown.

Remarks. Holotype male with pupal exuviae was labeled: Alaska, Steese Hwy., mi. 19.1, north of Fairbanks, 14 September 1948, coll. unknown (Stone 1949). Specimens examined were collected in the type locality and were determined by author of species.

Distribution. North West Canada, USA (Alaska) (Crosskey and Howard 1997; Adler et al. 2004).

4. *Gymnopais frontatus* Yankovsky, 1982
(Figs. 6 and 7)

Gymnopais frontatus Yankovsky 1982: 160, fig. 1.
Gymnopais boreopacificus Yankovsky 1996: 113.

Description. *Male*. Length about 3 mm. Head dichoptic. Sensory vesicle of maxillary palpi very large (near ½ of length of palpomere III, in other species ¼ or less). Scutum mat black, legs brown. Hind basitarsus moderately widened, 4.5–5.0 times as long as wide, hind tarsomere II of usual size, 3 times as short and 2 times as narrow as basitarsus, 3.5–4.0 times as long as wide. Conocoxites about equal in length to gonostyli; in ventral view length nearly equal to maximal width. Gonostyli moderately tapered distal-

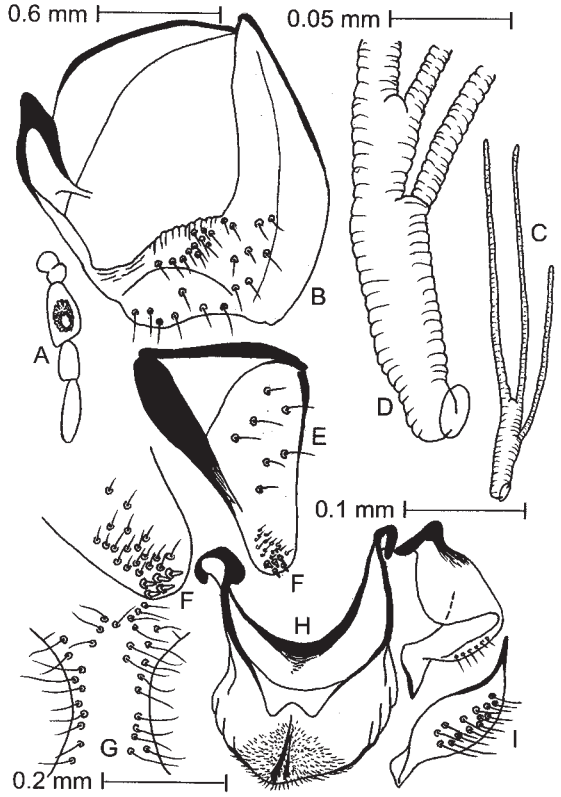

Fig. 6. *Gymnopais frontatus* Yankovsky, 1982. Holotype pupa (male): A – maxillar palp; B – gonocoxite; C – pupal gill; D – basal part of pupal gill; E – gonostylus; F – apical spines on gonostylus; G – frons; H – ventral plate; I – gonopleurite. Scale bar: 0.6 mm = C; 0.2 mm = A, D, G; 0.1 mm = B, E, H, I; 0.05 mm = F.

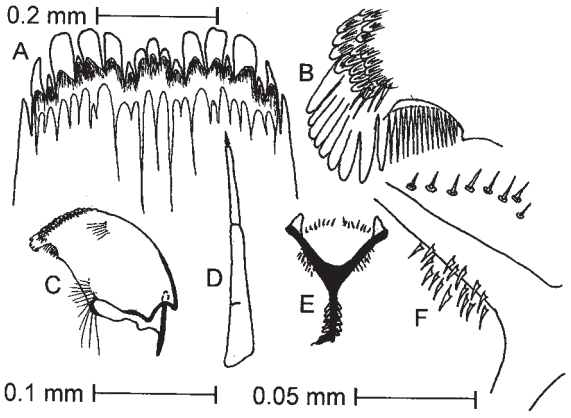

Fig. 7. *Gymnopais frontatus* Yankovsky, 1982. Paratype larva: A – hypostomal teeth; B – mandibular teeth; C – mandible; D – antenna; E – anal sclerite; F – thornlets near anal sclerite. Scale bar: 0.2 mm = C, E; 0.1 mm = d; 0.05 mm = A, B, F.

ly (width in basal part 1.5 times width in distal part), in ventral view 1.6–1.7 times as long as wide at base; apical spines 5 in 2 rows, also in distal part of gonostyli numerous strong spinules. Body of ventral plate moderately widened, 2 times as wide as long (ventral view), posterior edge convex, on lateral edges 2 large distinct wrinkles, medial keel distinctly developed. Gonopleurites with 13–15 long setae.

Female. Length about 3 mm. Frons wide (height equal to least width), dull black, with rare short hairs. Maxillary palpi relatively short and thick, palpomere V 2 times as short as palpomeres III+IV, palpomere III not widened; sensory vesicle about ⅓ of length of palpomere III. Scutum and legs black, with rare short hairs; abdomen brown black. Claws toothless. Abdominal sternite VIII very sclerotized, distinctly protruding forwards. Hypogynal valves equal in length to middle part of sternite VIII; anteromedial angles of valves rostriform, weakly sclerotized. Stem of genital fork equal in length to branches, branches moderately widened distally, posteromedial apodeme wide, not tapered, serrated but not sclerotized on medial edge; posterior cleft of genital fork wide, about oval, 3 times as wide as long. Anal lobes 1.3 times as high and 2 times as long as cerci. Anal lobes 2.5–3.0 times, cerci 2 times as high as long. Spermatheca 1.3 times as wide as long, without trunk at base. [Preparation of ♀ in bad condition, drawing *see:* Yankovsky 1982: 161, fig. 1].

Larva. Length 5–6 mm. Head capsule yellowish brown, head pattern distinct, dark. Body dirty white. Articles I+II of antennae 1.5 times longer than article III. Median hypostomal teeth slightly shorter than lateral teeth, frontal edge of hypostoma about smooth; each side of hypostoma with 9–10 sublateral setae disposed in 3 rows. Apical end of mandibles rounded, flattened apical teeth long, distinctly longer than inner teeth; inner mandibular teeth 14–16; mandibular serration of 1 weakly developed small notch. Posterior circlet of 116–120 rows with 12–16 hooklets in each row. Median branch of anal sclerite not widened but distinctly serrated laterally in distal part, thornlets near anal sclerite: 16–18 at anterior side, and 6–8 spiniform at posterior side of lateral branches.

Pupa. Body length 3 mm. Gill of 3 not swollen, but slightly widened in basal part filaments of about equal diameter, filaments II, III on thick common stem (5 times as long as wide), upper filament near 2

times as short as others, diverged immediately from trunk; angle between basal parts of upper and lower filaments about 20°.

Holotype. Male with pupal exuviae (ZIN, slide 21428), Kamchatka Peninsula, Dyakonovskiy Spring, affluent of Azhabachye Lake, 80 km W of Ust'-Kamchatsk, 12 August 1980, coll. A.V. Yankovsky.

Paratypes. 2 males with pupal exuviae (ZIN, slides 21429, 21443), 1 female with pupal exuviae (ZIN, slide 21430), 6 larvae with pupal gill histoblasts (ZIN, slides 21431, 21432, 21434, 21435, 21440, 21442), 5 larvae (ZIN, slides 21433, 21436–21438, 21441), same data.

Distribution. N of Russian Far East (Kamchatka) (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

5. *Gymnopais holopticus* Stone, 1949
(Fig. 8)

Gymnopais holopticus Stone 1949: 265; Wood 1978: 1312, figs. 13–16, 23, 26, 30, 32, 34, 41, 42, 44, 60; Adler et al. 2004: 241, figs. 4.10, 4.14, 4.18, 4.44, 4.49, 10.7, 10.8, 10.47, 10.90, 10.233, 10.516, 10.623, 10.684, map 10.

Description. *Male, female*. In the collection of ZIN males and females of this species are absent (characters *see:* Adler et al. 2004: fig. 10.233, 10.90).

Larva. Articles I+II of antennae 1.7 times as long as article III. Median and lateral hypostomal teeth equal in length, frontal edge of hypostoma even; each side of hypostoma with 7 sublateral setae disposed in 2 rows. Apical end of mandibles transversely cut, flattened apical teeth relatively short, shorter than inner teeth; inner mandibular teeth 14–16; mandibular serration of 2 small notch. Posterior circlet of 100–102 rows with 13–15 hooklets in each row. Median branch of anal sclerite moderately widened and serrated latreally, 30–35 thornlets developed near anterior side of lateral branches of anal sclerite.

Pupa. Gill of 2 moderately swollen long filaments, about equal in length, angle between basal parts of upper and lower filaments very approximately about 20–30°.

Material. 1 larva with pupal gill histoblasts (ZIN, slide 10208), 1 pupa (ZIN, slide 10209), Alaska, 17 August 1948, coll.unknown.

Remarks. Holotype male with pupal exuviae was labeled: Alaska, Steese Hwy., mi. 16.2, north of Fairbanks, 17 August 1948, coll. unknown (Stone 1949).

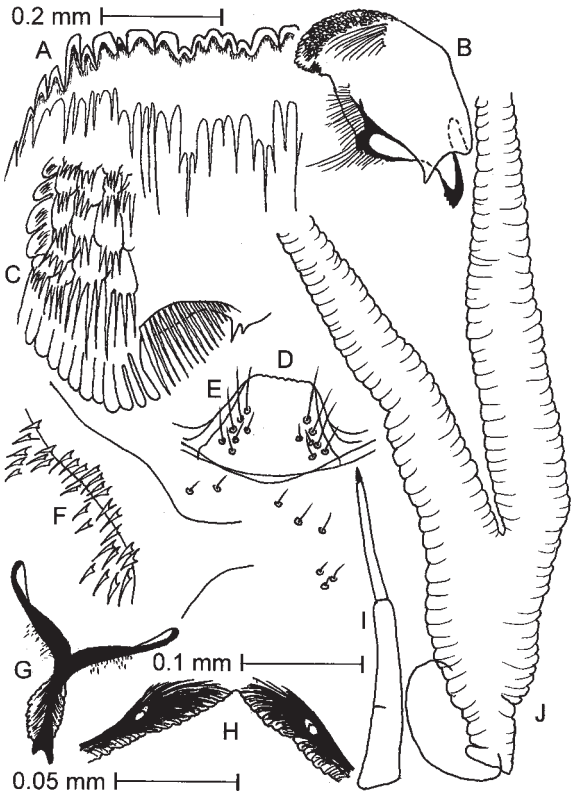

Fig. 8. *Gymnopais holopticus* Stone, 1949. Larva with pupal gill histoblasts (A–I): A – hypostomal teeth; B – mandible; C – mandibular teeth; D – hypostoma; E – sublateral setae on hypostoma; F – thornlets near anal sclerite; G – anal sclerite; H – posteroventral margin of head capsule; I – antenna. Pupa: J – basal part of gill. Scale bar: 0.2 mm = B, D, E, G, H, J; 0.1 mm = I; 0.05 mm = A, C, F.

Specimens examined were collected in the type locality and were determined by author of species.

Distribution. North West Canada, USA (Alaska) (Crosskey and Howard 1997; Adler et al. 2004).

6. *Gymnopais lindneri* Rubzov, 1963
(Figs. 9–11)

Gymnopais lindneri Rubzov 1963: 1, figs. 1–3.

Description. *Male*. Length 2.8–3.0 mm. Head dichoptic. Scutum and abdomen black, with thin short hairs. Legs wholly dark; hind basitarsus moderately widened, 4.5–5.0 times as long as wide, hind tarsomere II of usual size, 3 times as short and 2 times as narrow as basitarsus, 3.5–4.0 times as long as wide. Conocoxites equal in length or slightly longer than

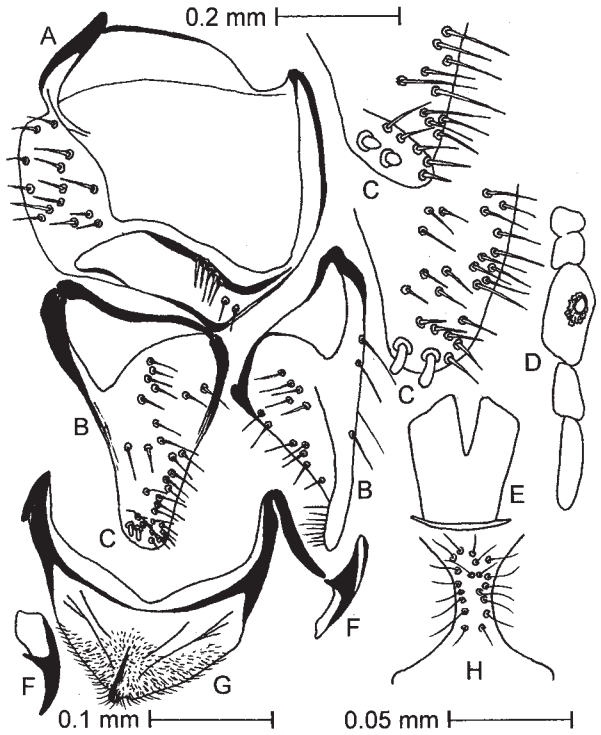

Fig. 9. *Gymnopais lindneri* Rubzov, 1963. Holotype male: A – gonocoxite; B – gonostylus; C – apical spines on gonostylus; D – maxillary palp; E – median sclerite; F – gonopleurite; G – ventral plate; H – frons. Scale bar: 0.2 mm = D, H; 0.1 mm = A, B, E, F, G; 0.05 mm = C.

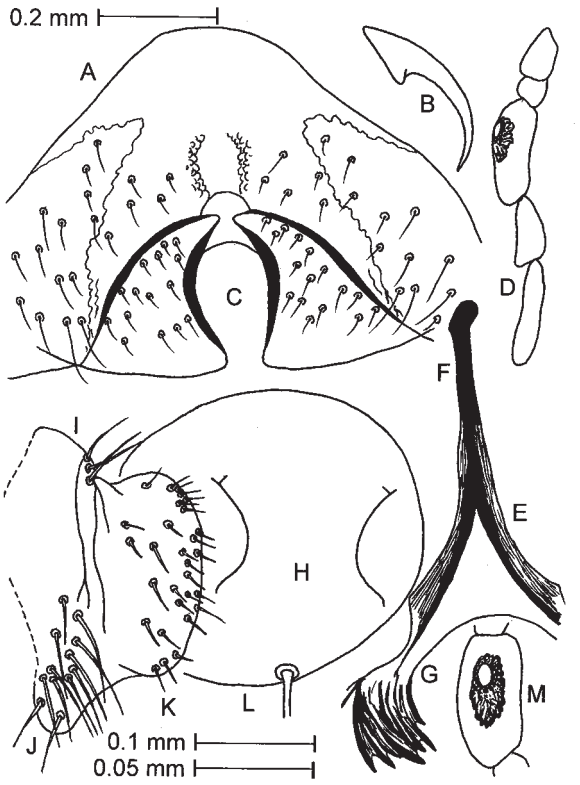

Fig. 10. *Gymnopais lindneri* Rubzov, 1963. Paratype female: A – abdominal sternite VIII; B – claw; C – hypogynal valves; D – maxillary palp; E – genital fork; F – stem of genital fork; G – posterior cleft of genital fork; H – frons; I – anal lobe; J – spiniform setae on lower blade of anal lobe; K – cercus; L – spermatheca; M – sensory vesicle of maxillary palp. Scale bar: 0.2 mm = D, H; 0.1 mm = A, C, E, F, G, I, J, K, L, M; 0.05 mm = B.

gonostyli; in ventral view length slightly less than maximal width. Gonostyli distinctly tapered distally (width in basal part 4 times width in distal part), in ventral view their length about equal width at base; apical spines 2. Body of ventral plate widened, 2 times as wide as long (ventral view), posterior edge convex, medial keel distinctly developed. Gonopleurites without setae.

Female. Length 3.2–3.5 mm. Frons very wide (height ⅔ of least width), black, with thin hairs on lateral parts. Maxillary palpi relatively long and thin, palpomere V 1.3 times as short as palpomeres III+IV, palpomere III about cylindrical, sensory vesicle near ½ of length of palpomere III. Scutum black, with rare short hairs; abdomen and legs brown black. Claws toothless. Abdominal sternite VIII distinctly sclerotized, not protruding forwards. Hypogynal valves slightly shorter than middle part of sternite VIII, with short hairs; anteromedial angles of valves distinctly sclerotized. Stem of genital fork 1.8–2.0 times as long as branches, branches widened distally, posteromedial apodeme wide, not tapered, strongly serrated and sclerotized on posterior edge; posterior cleft of genital fork about oval, 1.4–1.5 times as wide as long. Anal lobes 1.5 times as high and as short as cerci. Anal lobes 4 times, cerci 1.8–2.0 times as high as long; lower blade of anal lobes with 10–12 long spiniform setae. Spermatheca enormous, its size twice more than width of posterior cleft of genital fork, 1.2 times as wide as long, without trunk at base.

Larva. Length 6 mm. Head capsule black, body brown, head pattern hardly distinguishable. Articles I+II of antennae widened, 1.5–1.7 times as long as article III. Median hypostomal teeth slightly shorter than lateral teeth, frontal edge of hypostoma about even; each side of hypostoma with 6 sublateral setae disposed in 2 rows. Apical end of mandibles rounded, flattened apical teeth equal to inner teeth; inner

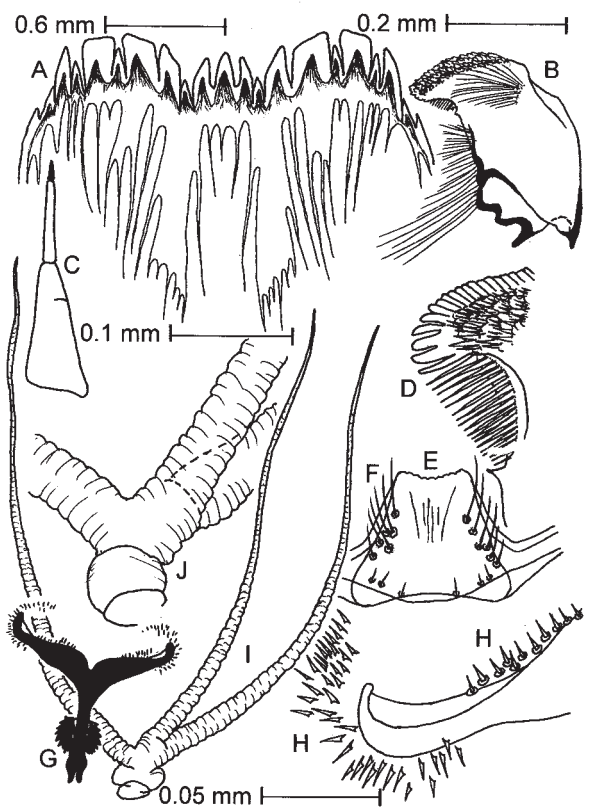

Fig. 11. *Gymnopais lindneri* Rubzov, 1963. Paratype larva with pupal gill histoblasts (A–H): A – hypostomal teeth; B – mandible; C – antenna; D – mandibular teeth; E – hypostoma; F – sublateral setae on hypostoma; G – anal sclerite; H – thornlets near anal sclerite. Paratype pupa (I, J): I – gill; J – basal part of gill. Scale bar: 0.6 mm = I; 0.2 mm = B, E, F, G, J; 0.1 mm = C; 0.05 mm = A, D, H.

mandibular teeth 15–17; mandibular serration of 1 small notch. Posterior circlet of about 120 rows with 16–18 hooklets in each row. Median branch of anal sclerite distinctly widened and serrated laterally in distal part, thornlets near anal sclerite: about 40 at posterior and lateral sides, and 10–12 spiniform at anterior side of lateral branches.

Pupa. Body length 3 mm. Gill of 3 filaments, moderately widened in basal part, near equal in length and diameter, filaments diverge immediately at base of gill; angle between basal parts of upper and lower filaments about 90°.

Holotype. Male with pupal exuviae (ZIN, slide 16090), Tuva, affluent of Samagaltaya River, 17 August 1962, coll. N.A.Violovitsh.

Paratypes. 1 larva with pupal gill histoblasts (ZIN, slide 16087), 1 female with pupal exuviae, 2 males with pupal exuviae (ZIN, slides 16088, 16089, 16091), same data; 1 pupa (ZIN, slide 17622), Tuva, II right affluent of Samagaltaya River, 18 July 1963, coll. N.A. Violovitsh.

Additional material. 1 pupa (ZIN, slide 16176), Tuva, spring in Tanu-Ola Mountain Range, 17 August 1962, coll. N.A. Violovich; 3 pupae (ZIN, pinned), Tuva, affluent of Samagaltaya River, 17 VIII 1962, coll. N.A. Violovich; 1 larva (ZIN, slide 17617), Tuva, source near middle current of Alam River, 31 July 1963, coll. N.A. Violovitsh; 1 male with pupal exuviae (ZIN, slide 19713), Yakutia, Ust'-Yanskiy District, Kular Settlment, Burgaat Spring, 4 August 1967, coll. E.I. Worobez; 1 female with pupal exuviae (ZIN, slide 19711), same locality, 7 August 1967, coll. E.I. Worobez; 1 larva with pupal gill histoblasts (ZIN, slide 21159), same locality, 25 July 1968, coll. E.I. Worobez; 1 female with pupal exuviae (ZIN, slide 21158), same locality, 1 August 1968, coll. E.I. Worobez.

Distribution. East Siberia (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

7. *Gymnopais rubzovi* Bobrova, 1967
(Fig. 12)

Gymnopais rubzovi Bobrova 1967: 884, fig. 1.

Description. *Male* and *female* unknown.

Larva. [Length 5–6 mm. Head capsule dark brown, head pattern distinct, body fallow (Bobrova 1967: 884, fig. 1)]. Articles I+II of antennae 2 times as long as article III. Median hypostomal teeth distinctly shorter than lateral teeth, frontal edge of hypostoma concave; each side of hypostoma with 5–6 sublateral setae (4 of them in about straight row). Apical end of mandibles transversely cut, flattened apical teeth relatively short, shorter than inner teeth; inner mandibular teeth 15–16; mandibular serration of 2 small notch. Posterior circlet of about 110–116 rows with 10–17 hooklets in each row. Median branch of anal sclerite distinctly widened and serrated laterally in distal part, thornlets near anal sclerite: 10–13 at anterior side, and 7–8 spiniform at posterior side of lateral branches.

Pupa. Gill of 4 dark brown filaments, upper filament 4–5 times shorter than others and wholly swollen, upper and lower filaments diverge immediately at base of gill, filaments II and III on common trunk

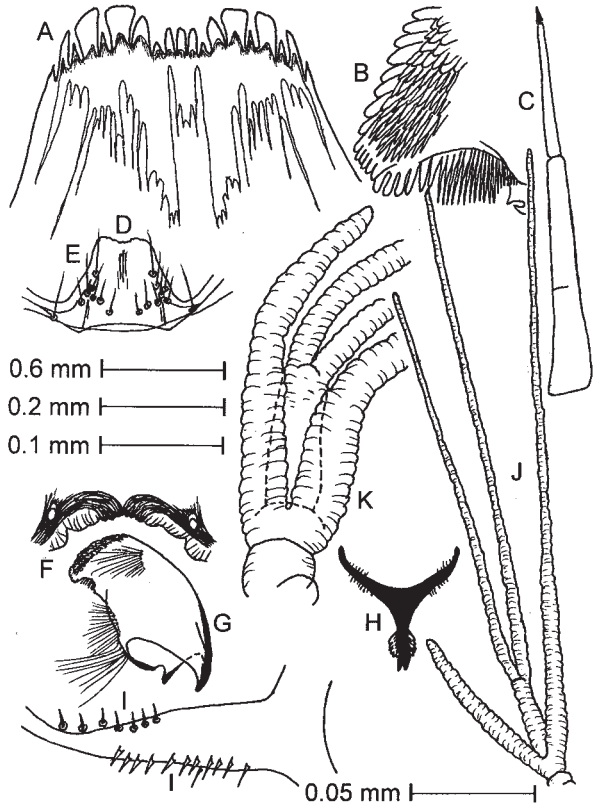

Fig. 12. *Gymnopais rubzovi* Bobrova, 1967. Larva with pupal gill histoblasts (A–I): A – hypostomal teeth; B – mandibular teeth; C – antenna; D – hypostoma; E – sublateral setae on hypostoma; F – posteroventral margin of head capsule; G – mandible; H – anal sclerite; I – thornlets near anal sclerite. Pupa (J, K): J – gill; K – basal part of gill. Scale bar: 0.6 mm = J; 0.2 mm = D, E, F, G, H, K; 0.1 mm = C; 0.05 mm = A, B, I.

(3 times as long as wide); angle between basal parts of upper and lower filaments about 45°.

Material. 3 larvae with pupal gill histoblasts (ZIN, slides 18912, 18913, 18914), 2 larvae (ZIN, slides 18785, 18786), Altai, affluent of Dzhumala River, 21 July 1964, coll. S.I. Bobrova; 1 pupa, 1 larva (ZIN, slides 20280, 20281), Mongolia, Bayan-Olgiy, stream, 25 August 1964, coll. unknown.

Remarks. Holotype larva with pupal gill histoblasts was labeled: ZIN, slide18785, [Altai], affluent of Dzhumala River, 21 July 1964, coll. S.I.Bobrova (Bobrova 1967: 886), but in the collection of the Zoological Institute this slide is absent. 2 larvae examined have the same label as holotype (only the numbers of slides insignificantly differ), also drawings of author (Bobrova 1967, fig. 1) closely resemble drawings of details of this species given in this paper (Fig. 12); it is very probable, that these 2 specimens are from the same sample with holotype.

Distribution. South Siberia (Altai), W Mongolia (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

8. *Gymnopais sexcornutus* Bodrova, 1975
(Fig. 13)

Gymnopais sexcornutus Bodrova 1975: 429, figs. 1–8.

Description. *Male* and *female* unknown.

Larva. [Length 5.0–5.5 mm. Head capsule nearly black, body fallow, head pattern distinct (Bodrova 1975: 429, fig. 4)]. Articles I+II of antennae 2 times as long as article III. Median hypostomal teeth very short, 2 times shorter than lateral teeth, frontal edge of hypostoma distinctly concaved; each side of hypostoma with 7 sublateral setae in 3 rows. Apical end of mandibles transversely cut, flattened apical teeth distinctly shorter than inner teeth; inner mandibular teeth 15–16; mandibular serration of 2 small notch.

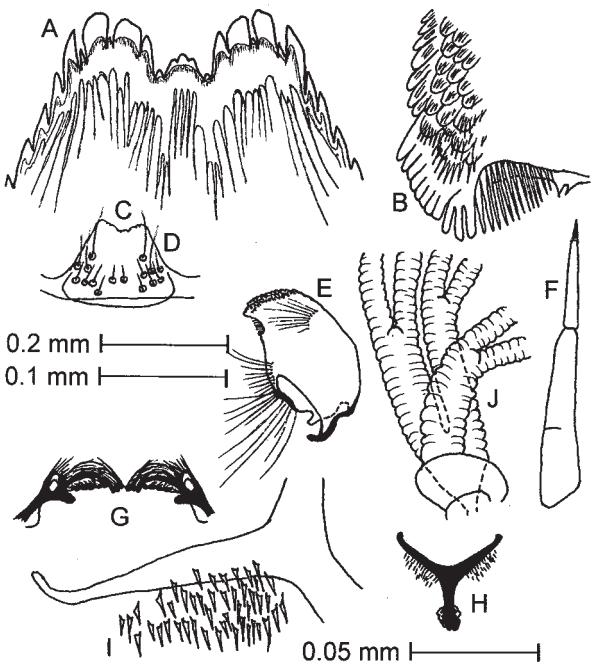

Fig. 13. *Gymnopais sexcornutus* Bodrova, 1975. Larva with pupal gill histoblasts: A – hypostomal teeth; B – mandibular teeth; C – hypostoma; D – sublateral setae on hypostoma; E – mandible; F – antenna; G – posteroventral margin of head capsule; H – anal sclerite; I – thornlets near anal sclerite; J – basal part of pupal gill histoblast. Scale bar: 0.2 mm = C, D, E, G, H, J; 0.1 mm = F; 0.05 mm = A, B, I.

Posterior circlet of about 120 rows with 14–18 hooklets in each row. Median branch of anal sclerite distinctly widened in distal part, near anterior side of lateral branches of anal sclerite numerous (40–50) thornlets in 3–4 rows.

Pupa. In the collection of ZIN only pupal gills in slides of 1 larva. Gill of 6 filaments, disposed on 3 trunks (2+2+2), trunks 3–4 times as long as wide; all trunks diverged near base of respiratory organ.

Material. 1 larva with pupal gill histoblasts (ZIN, slide 20610), Maritime [Primorskiy] Territory, Sikhote-Alin Mountains, 1 August 1970, coll. Yu.D. Bodrova.

Remarks. Holotype larva with pupal gill histoblasts was labeled: ZIN, slide 20578, [NW Maritime Territory], Meteorologov Spring, 1600 m above sea level, 1 VIII 1970, coll. Yu.D. Bodrova (Bodrova, 1975: 429), but in the collection of the Zoological Institute this slide is absent. Specimen examined has in principle the same label (only the number of slide insignificantly differs), also drawings of author (Bodrova 1975, figs. 1, 2, 3, 5, 7, 8) very closely resemble drawings of details of this species given in this paper (Fig. 13); it is very probable, that both specimens are from the same sample.

Distribution. South of Russian Far East (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

9. *Gymnopais trifistulatus* Rubzov, 1955
(Figs. 14 and 15)

Gymnopais trifistulatus Rubzov 1955: 333, figs. 4, 5; 1956: 190, figs. 40, 41; 1960: 130, figs. 38, 39.

Description. *Male*. Length 3.5 mm. Head holoptic. Scutum and abdomen black. Legs black; hind basitarsus moderately widened, 4.5–5.0 times as long as wide, hind tarsomere II of usual size, 3 times as short and 2 times as narrow as basitarsus, 3.5–4.0 times as long as wide. Conocoxites equal in length or slightly longer than gonostyli, in ventral view length equal to maximal width; in dorsal view gonocoxites with peculiar longitudinal lines. Gonostyli distinctly tapered distally (width in basal part 4 times width in distal part), in ventral view 1.5 times as long as wide at base; apical spines 2. Body of ventral plate moderately widened, 1.5–1.7 times as wide as long (ventral view), posterior edge convex, medial keel distinctly developed. Gonopleurites without setae.

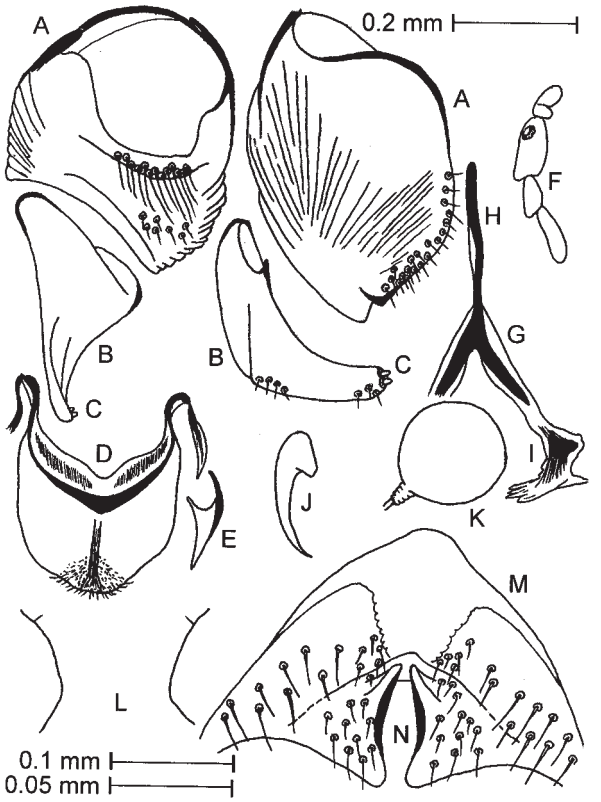

Fig. 14. *Gymnopais trifistulatus* Rubzov, 1955. Lectotype pupa (male) (A–E): A – gonocoxite; – gonostylus; C – apical spines on gonostylus; D – ventral plate; E – gonopleurite. Paralectotype pupa (female) (F – N): F – maxillary palp; G – genital fork; H – stem of genital fork; I – posterior cleft of genital fork; J – claw; K – spermatheca; L – frons; M – abdominal sternite VIII; N – hypogynal valves. Scale bar: 0.2 mm = F, L; 0.1 mm = A, B, C, D, E, G, H, I, K, M, N; 0.05 mm = J.

Female. Length 4.0–4.5 mm. Frons wide (height ¾ of least width), black, with thin sublateral hairs. Maxillary palpi relatively short, palpomere V about 2 times as short as palpomeres III+IV, palpomere III slightly flattened; sensory vesicle very small, less than ¼ of length of palpomere III. Scutum black, with rare rough hairs; abdomen and legs brown black. Claws toothless. Abdominal sternite VIII distinctly sclerotized, slightly protruding forwards. Hypogynal valves near equal in length to middle part of sternite VIII, with long hairs; anteromedial angles of valves distinctly sclerotized. Stem of genital fork slightly longer than branches, branches moderately widened distally, posteromedial apodeme tapered, not serrated but sclerotized on posterior edge; posterior cleft of genital fork about triangular, 1.2 times as long as wide. Anal lobes 1.5 times as high and 1.5 times as

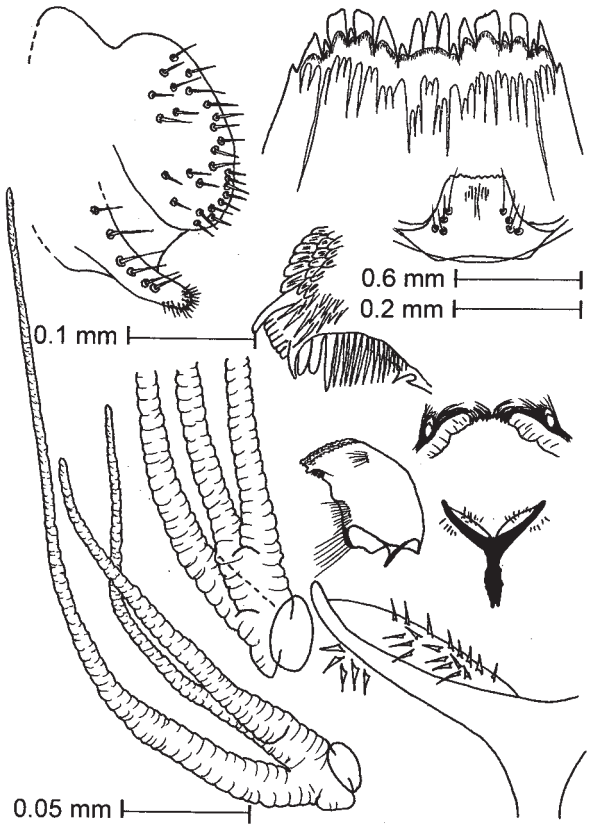

Fig. 15. *Gymnopais trifistulatus* Rubzov, 1955. Lectotype pupa (male) (A, B): A – gill; B – basal part of gill. Paralectotype pupa (female) (C–E): C – cercus; D – anal lobe; E – spiniform setae on lower blade of anal lobe. Larva with pupal gill histoblasts (F–): F – hypostomal teeth; G – hypostoma; H - sublateral setae on hypostoma; I – mandibular teeth; J – posteroventral margin of head capsule; K – mandible; L – anal sclerite; M – thornlets near anal sclerite. Scale bar: 0.6 mm = A; 0.2 mm = B, G, H, J, K, L; 0.1 mm = C, D, E; 0.05 mm = F, I, M.

short as cerci. Anal lobes 4 times, cerci 1.7 times as high as long; lower blade of anal lobes with 6 long spiniform setae. Spermatheca with long trunk at base, its size 1.2–1.3 times less than width of posterior cleft of genital fork.

Larva. Length 7–9 mm. Head capsule brown, head pattern hardly distinguishable; body dirty white, with brown transverse stripes. Articles I+II of antennae widened, 1.5 times as long as article III. Median and lateral hypostomal teeth about equal in length, frontal edge of hypostoma even; each side of hypostoma with 4 sublateral setae. Apical end of mandibles transversely cut, flattened apical teeth relatively short, shorter than inner teeth; inner mandibular teeth 15–16; mandibular serration of 2 small notch. Posterior circlet of about 140 rows with 12–18 hooklets in each row. Median branch of anal sclerite slightly widened and serrated laterally, thornlets near anal sclerite: 4–6 at anterior side, and 18–20 at posterior side of lateral branches.

Pupa. Body length 3 mm. Gill of 3 filaments moderately widened in basal part, lower filament 2 times as long as others, filaments I, II on very short trunk; angle between basal parts of upper and lower filaments about 20°.

Lectotype. Male with pupal exuviae (ZIN, slide 6503, terminalia in pinned slide 6502), Irkutsk Province, Bilchir River (affluent of Sagan-Ugun River), 17 August 1952, coll. Boldaruev.

Paralectotypes. 1 female with pupal exuviae (ZIN, slide 6494), 3 pupae (ZIN, slides 6493, 6497, 6706), same data.

Additional material. 2 pupae (males) (ZIN, pinned, terminalia and pupal gills in slides 6504, 6505 on same pins), Irkutsk Province, Bilchir River (affluent of Sagan-Ugun River), 17 August 1952, coll. Boldaruev; 1 larva with pupal gill histoblasts (ZIN, slide 17492), Taymyr Region, Dudinskiy District, Pokomokon River, 10 August 1962, coll. Z.V. Usova.

Remarks. In the original description of this species (Rubzv, 1955) type material was not designated. Here the lectotype and 4 paralectotypes are designated, the specimens labeled by author of species-name in collection as “holotype” and “paratypes” were used.

Distribution. East Siberia (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

Key to species of the genus *Gymnopais* Stone, 1949

Males (males of parthenogenetic *G. dichopticoides* Wood, 1978 and *G. holopticoides* Wood, 1978 do not exist; males of *G. rubzovi* Bobrova, 1967 and *G. sexcornutus* Bodrova, 1975 unknown)

1. Head dichoptic (wide frons between eyes); all eye facets about equal in size 2
– Head holoptic (eyes meeting medially); upper eye facets enlarged 5
2. Body of ventral plate (ventral view) about equal or slightly longer than wide . . . *G. fimbriatus* Wood, 1978
– Body of ventral plate (ventral view) 2.0–2.5 times as wide as long 3
3. Gonostyli moderately tapered distally (width in basal part 1.5 times width in distal part, ventral view); apical

spines 5 in 2 rows . . . . . *G. frontatus* Yankovsky, 1982 (Fig. 6)
– Gonostyli distinctly tapered distally (width in basal part 2.5–4.0 times width in distal part, ventral view); apical spines 2–3 4
4. Width of gonostyli in basal part 2.5 times width in distal part; apical spines 3 . . . . . .*G. dichopticus* Stone, 1949
– Width of gonostyli in basal part 4 times width in distal part; apical spines 2 ... *G. lindneri* Rubzov, 1963 (Fig. 9)
5. Hind basitarsus very widened, 2.7–3.0 times as long as wide, hind tarsomere II unusually large, 2 times as short and 1.2 times as narrow as basitarsus, 2 times as long as wide; apical spine 1 . . . . . *G. bifistulatus* Rubzov, 1955 (Fig. 2)
– Hind basitarsus moderately widened, 4.5–5.0 times as long as wide, hind tarsomere II of usual shape, 3 times as short and 2 times as narrow as basitarsus, 3.5–4.0 times as long as wide; apical spines 2 6
6. Gonocoxites with peculiar longitudinal lines dorsally; width of gonostyli in basal part 4 times width in distal part . . . . . .*G. trifistulatus* Rubzov, 1955 (Fig. 14)
– Gonocoxites without longitudinal lines dorsally; width of gonostyli in basal part 2.5–3.0 times width in distal part 7
7. Posterior edge of body of ventral plate about straight; gonopleurites with 2 long setae . . . . . .*G. andrei* Worobez, 1984 (Fig. 1)
– Posterior edge of body of ventral plate concave; gonopleurites without setae . . . . . .*G. holopticus* Stone, 1949

Females (females of *G. rubzovi* Bobrova, 1967 and *G. sexcornutus* Bodrova, 1975 unknown)

1. Palpomeres IV and V not distinctly separated, appearing fused . . . . . .*G. fimbriatus* Wood, 1978
– Palpomeres IV and V distinctly separated 2
2. Stem of genital fork 1.8–2.0 times as long as branches; spermatheca enormous, its size twice more than width of posterior cleft of genital fork . . . . . .*G. lindneri* Rubzov, 1963 (Fig. 10)
– Stem of genital fork from 1.5 times as short to 1.5 times as long as branches; size of spermatheca from about equal to 2.5 less than width of posterior cleft of genital fork 3
3. Claws with small but distinctly distinguishable basal tooth . . . . . .*G. bifistulatus* Rubzov, 1955 (Fig. 2)
– Claws toothless 4
4. Posterior cleft of genital fork very wide, 3 times as wide as long; spermatheca shortened, 1.3 times as wide as long, without trunk at base . . . . . *G. frontatus* Yankovsky, 1982
– Posterior cleft of genital fork from equal in width to 1.5 times as wide as long; spermatheca rounded, width about equal to length, with trunk at base 5
5. Stem of genital fork 1.5–1.6 times as long as branches . . . . . .*G. andrei* Worobez, 1984 (Fig. 1)
– Stem of genital fork equal or 1.5 times as short as branches 6
6. Stem of genital fork 1.5 times as short as branches . . . 7
– Length of stem of genital fork equal to length of branches 8
7. Widened distal part of genital fork branches 2.3 times as wide as long; posterior cleft of genital fork 1.2 times as wide as long; size of spermatheca 2 times less than width of posterior cleft of genital fork . . . . . *G. dichopticus* Stone, 1949 (Figs. 4, 5)
– Widened distal part of genital fork branches 1.5 times as wide as long; posterior cleft of genital fork 1.5 times as wide as long; size of spermatheca 2.5 times less than width of posterior cleft of genital fork . . . . . *G. dichopticoides* Wood, 1978
8. Hypogynal valves near equal in length to middle part of sternite VIII; anal lobes 1.5 times as high as cerci; anal lobes 4 times, cerci 1.7 times as high as long . . . . . .*G. trifistulatus* Rubzov, 1955 (Figs. 14, 15)
– Hypogynal valves 1.3 times as long as middle part of sternite VIII; anal lobes 2.3 times as high as cerci; anal lobes 2.5 times, cerci 1.2 times as high as long 9
9. Width of posterior cleft of genital fork about equal to length; spermatheca with very long trunk at base, its size 1.5 times less than width of posterior cleft of genital fork . . . . . *G. holopticus* Stone, 1949
– Posterior cleft of genital fork wide, about oval, 1.5 times as wide as long; spermatheca with trunk of moderate length at base, its size 2 times less than width of posterior cleft of genital fork . . . .*G. holopticoides* Wood, 1978

Larvae

1. Width of frontoclypeal apotome in posterior part 7–8 times width in middle part . . . . . *G. lindneri* Rubzov, 1963 (Fig. 11)
– Width of frontoclypeal apotome in posterior part 1.5–2.0 times width in middle part 2
2. Each side of hypostoma with numerous (more than 40) sublateral setae . . . . . *G. fimbriatus* Wood, 1978
– Each side of hypostoma with 3–10 sublateral setae . . . 3
3. Pupal gill histoblast of 2 filaments 4
– Pupal gill histoblast of 3–6 filaments 5
4. Each side of hypostoma with 7 sublateral setae in 2 rows; mandibular serration of 2 notches; posterior circlet of 100–102 rows of hooklets; near anterior side of lateral branches of anal sclerite 30–35 thornlets; gill filaments of equal length . . . . . *G. holopticus* Stone, 1949 (Fig. 8)
– Each side of hypostoma with 9–10 sublateral setae in 3 rows; mandibular serration of 1 notch; posterior circlet of 84–86 rows of hooklets; thornlets near anal sclerite absent; lower gill filament 2–3 times as long and 2 times

as wide as upper filament . . . . . *G. bifistulatus* Rubzov, 1955 (Fig. 3)
5. Pupal gill histoblast of 6 filaments . . . . . *G. sexcornutus* Bodrova, 1975 (Fig. 13)
– Pupal gill histoblast of 3–4 filaments 6
6. Pupal gill histoblast of 4 filaments 7
– Pupal gill histoblast of 3 filaments 8
7. Median and lateral hypostomal teeth about equal in length; apical end of mandibles evidently rounded; mandibular serration of 1 notch . . . . . *G. dichopticus* Stone, 1949 (Fig. 5)
– Median hypostomal teeth distinctly shorter than lateral teeth; apical end of mandibles transversely cut; mandibular serration of 2 small notch . . . . . *G. rubzovi* Bobrova, 1967 (Fig. 12)
8. Apical end of mandibles transversely cut; mandibular serration of 2 notch; posterior circlet of about 140 rows of hooklets . . . . . *G. trifistulatus* Rubzov, 1955 (Fig. 15)
– Apical end of mandibles rounded; mandibular serration of 1 notch; posterior circlet of 100–120 rows of hooklets 9
9. Median hypostomal teeth distinctly shorter than lateral teeth; each side of hypostoma with 2–3 sublateral setae; gill filaments of equal length . . . . . *G. andrei* Worobez, 1984
– Median and lateral hypostomal teeth about equal in length; each side of hypostoma with 5–10 sublateral setae; 1 or 2 gill filaments short 10
10. Each side of hypostoma with 9–10 sublateral setae disposed in 3 rows; posterior circlet of 116–120 rows of hooklets . . . . . *G. frontatus* Yankovsky, 1982 (Fig. 7)
– Each side of hypostoma with 5–7 sublateral setae disposed in 1–2 rows; posterior circlet of 100–108 rows of hooklets 11
11. Each side of hypostoma with 5 sublateral setae; posterior circlet of 106–108 rows of hooklets; medial branch of anal sclerite distinctly widened in distal part; upper gill filaments I, II short . . . *G. dichopticoides* Wood, 1978
– Each side of hypostoma with 7 sublateral setae; posterior circlet of 100–102 rows of hooklets; medial branch of anal sclerite not widened or slightly widened in distal part; upper gill filament I short . . . . . *G. holopticoides* Wood, 1978

Pupae

1. Gill of 6 filaments . . . . . *G. sexcornutus* Bodrova, 1975 (Fig. 13)
– Gill of 2–4 filaments 2
2. Gill of 2 filaments 3
– Gill of 3–4 filaments 4
3. Gill filaments of about equal length . . . . . *G. holopticus* Stone, 1949 (Fig. 8)
– Lower gill filament 2 times as long as upper filament . . . . . *G. bifistulatus* Rubzov, 1955 (Fig. 3)
4. Gill of 4 filaments 5
– Gill of 3 filaments 6
5. Upper gill filaments I, II very short and thickened . . . . . *G. dichopticus* Stone, 1949 (Fig. 4)
– Upper gill filament 3–4 times as short as 3 other, not very thickened . . . . . *G. rubzovi* Bobrova, 1967 (Fig. 12)
6. Upper gill filaments I, II very thickened . . . . . *G. dichopticoides* Wood, 1978
– Upper gill filaments I, II not very thickened 7
7. Angle between basal parts of upper and lower filaments about 90° . . . . . *G. lindneri* Rubzov, 1963 (Fig. 11)
– Angle between basal parts of upper and lower filaments 20–30° 8
8. Gill filaments approximately equal in length . . . . . *G. andrei* Worobez, 1984
– Gill filaments distinctly not equal in length 9
9. Upper gill filaments I, II 2 times as short as filament III . . . . . *G. trifistulatus* Rubzov, 1955 (Fig. 15)
– Upper gill filament 1.7–2.0 times as short as filaments II, III 10
10. Lower gill filaments II, III on thick common stem (5 times as long as wide), upper filament 2 times as short as others, diverges immediately from trunk . . . . . *G. frontatus* Yankovsky, 1982 (Fig. 6)
– Lower gill filament diverges immediately from common stem, upper filament slightly shorter than others, diverges in evident distance from the base of common trunk 11
11. On IV, V abdominal sternites 12, on VI, VII sternites 10 hooks . . . . . *G. holopticoides* Wood, 1978
– On IV, V abdominal sternites 6, on VI sternite 4, on VII sternite 2 hooks . . . . . *G. fimbriatus* Wood, 1978

Genus *Twinnia* Stone et Jamnback, 1955

Twinnia Stone and Jamnback 1955: 18; Rubzov 1956: 844; 1960: 122; Wood 1978: 1308; Rubzov and Yankovsky 1984: 27; 1988: 115; Crosskey and Howard 1997: 25; Yankovsky 2002: 124; Adler et al. 2004: 241.

Type-species. *Twinnia tibblesi* Stone et Jamnback, 1955, by original designation.

Diagnosis. *Imago*. Antennae of 9 articles. Proboscis slightly shorter than clypeus. Body black or dark-gray, with short, erect hairs; scutum with black, silvery or golden hairs, without silvery reflecting spots. Thorax slightly arched. Wings slightly wrinkled, vein Rs bifurcated, veins R1 and C with hairs only, basal radial cell ⅓ of wing length. Legs black, brownish black or brown. Calcipala absent or very small, pointed; pedisulcus absent. Fore basitarsi thin, cylindrical.

Male. Head always holoptic, about equal in width to thorax. Hind basitarsi widened (3.5–4.5 times as

long as wide). Gonocoxites from equal in length to 1.3–1.4 times as long as gonostyli, about equal in length to maximal wide (ventral view). Gonostyli narrowed distally (width in basal part 1.4–3.0 times width in distal part), 1.5–1.8 times as long as maximal wide (ventral view), armed with 1 apical spine. Body of ventral plate lamellate, 1.2 –2.5 times as wide as long, with moderate medial keel. Gonopleurites short, narrow, without setae. Median sclerite 3.0–7.5 times as long as wide in middle part, bifurcated ⅓–¼ of length.

Female. Mouthparts of bloodsucking type, laciniae and mandibles with teeth (very rarely not of bloodsucking type, without teeth); palpomere V from equal in length to 1.3 times as short as palpomeres III+IV. Claws toothless. Hypogynal valves simple, about triangular (very rarely obliquely cut in distal part), from 1.5 times as short to equal in length to middle part of abdominal sternite VIII, anteromedial angles of valves not rostriform. Stem of genital fork not widened (rarely slightly widened) distally, from 1.7 times as short to 1.6 times as long as branches, branches with well developed posteromedial apodeme, anterolateral apodeme absent. Anal lobes and cerci distinctly separated by membranous zone; anal lobes 1.4–1.7 times as high, and from equal in length to 1.5 times as long as cerci. Anal lobes 2.0–3.3 times, cerci 1.5–2.0 times as high as long; lower blade of anal lobe with 10–20 large spiniform setae. Spermatheca wider than long, without trunk at base; surface with wrinkled or crumpled pattern and large smooth unpigmented area around duct.

Larva. Cephalic apotome narrow, tapered posteriorly. Labral fans absent. Boundary between articles I and II of antennae hardly distinguishable, their common length from slightly longer to 2 times length of article III. Hypostoma with broad flat teeth; each side of hypostoma with 2–4 sublateral setae. Postgenal cleft absent. On outer surface of distal part of mandibles 3–6 large spine-like setae; apical mandibular teeth flat, apical end rounded; inner mandibular teeth 7–10, above main row of inner teeth additional row of 3–10 small teeth; mandibular serration of 3 sharp notches. Anal sclerite Y-shaped. Abdominal posterior circlet of 66–76 rows with 10–12 hooklets in each row, thornlets near anal sclerite absent. Rectal organ of 3 simple lobes.

Pupa. Respiratory organ (gills) of 14–16 thin filaments on 2–3 swollen trunks; angle between basal parts of upper and lower stems 60–120°. Spine combs on abdominal tergites absent. Cocoon unshaped, friable, partly or wholly covers pupal body.

Distribution. Holarctic.

Species included. *T. cannibora* Ono, 1977 (PA), *T. changbaiensis* Sun, 1994 (PA), *T. hirticornis* Wood, 1978 (NA), *T. hydroides* (Novák, 1956) (PA), *T. japonensis* Rubzov, 1960 (PA), *T. magadensis* Rubzov, 1973 (PA), *T. nova* (Dyar et Shannon, 1927) (NA), *T. sedecimfistulata* (Rubzov, 1955) (PA), *T. subtibbelesi* Ono, 1980 (PA), *T. tibblesi* Stone et Jamnback, 1955 (NA). [PA – Palaearctic, NA – Nearctic].

1. *Twinia hydroides* (Novák, 1956)
(Figs. 16 and 17)

Gymnopais hydroides Novák 1956: 226, fig. 3; Rubzov 1956: 845, fig. 424; 1960: 126, fig. 36.
Twinnia tatrensis Novák 1959: 366.

Description. *Male*. Length about 4 mm. Scutum velvet black, with rare erect black hairs. Legs brown, tarsi black. Hind basitarsus slightly swollen (4 times as long as wide). Gonocoxites 1.3–1.4 times as long as gonostyli, in ventral view their length equal to maximal width. Gonostyli slightly narrowed distally (width in basal part 1.4 width in distal part), in ventral view 1.5 times as long as wide at base. Body of ventral plate 1.4 times as wide as long (ventral view). Median sclerite 7.0–7.5 times as long as wide in middle part.

Female. Length near 4 mm. Frons relatively narrow (least width ½ of height). Body and legs wholly black, scutum with black hairs. Palpomere V equal in length or slightly shorter then palpomeres III+IV, sensory vesicle relatively small, about ¼ of length of palpomere III. Abdominal sternite VIII distinctly sclerotized, moderately protruding forwards. Hypogynal valves about triangular, with rare short hairs, 1.5–1.7 times as short as middle part of sternite VIII, medial edges moderately sclerotized. Stem of genital fork 1.3–1.4 times as long as branches, branches very widened distally, posteromedial apodeme distinctly sclerotized, its posterior edge serrated; posterior cleft of genital fork rounded, 1.3 times as wide as long. Anal lobes 1.7 times as high and 1.5 times as long as cerci. Anal lobes 2 times, cerci 1.8 times as high as long; lower blade of anal lobe with 10–12 large spiniform setae. Spermatheca 1.5 times as wide as long, surface with distinct crumpled pattern.

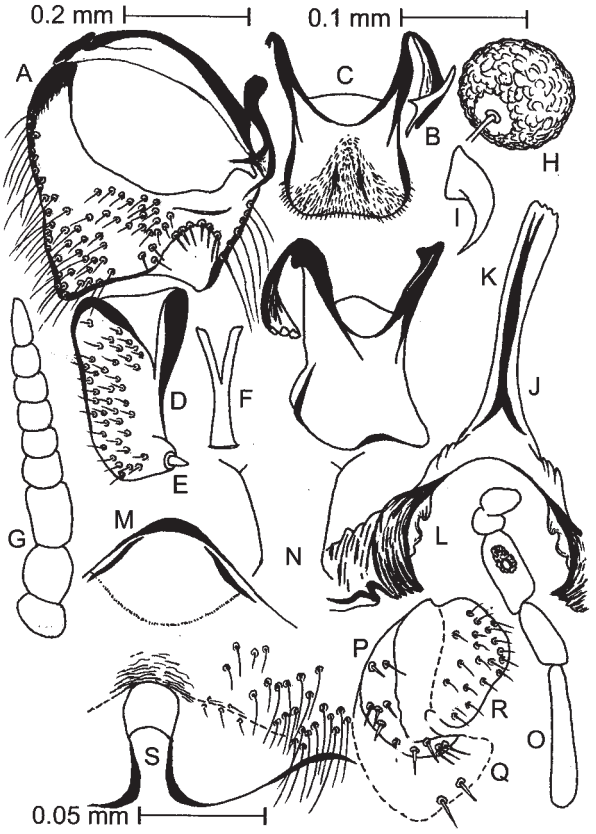

Fig. 16. *Twinnia hydroides* (Novák, 1956). Pupa (male) (A–G): A – gonocoxite; B – gonopleurite; C – ventral plate; D – gonostylus; E – apical spine of gonostylus; F – median sclerite; G – antenna. Pupa (female) (H–S): H – spermatheca; I – claw; J – genital fork; K – stem of genital fork; L – posterior cleft of genital fork; M – abdominal sternite VIII; N – frons; O – maxillar palp; P – anal lobe; Q – spiniform setae on lower blade of anal lobe; R – cercus; S – hypogynal valves. Scale bar: 0.2 mm = G, N, O; 0.1 mm = A, B, C, D, E, F, H, J, K, L, M, P, Q, R, S; 0.05 mm = I.

Fig. 17. *Twinnia hydroides* (Novák, 1956). Pupa (male): A – hind basitarsus. Larva with pupal gill histoblasts (B–H): B – hypostomal teeth; C – hypostoma; D – sublateral setae on hypostoma; E – anal sclerite; F – posteroventral margin of head capsule; G – mandibular teeth; H – antenna. Pupa: I – gill. Scale bar: 0.6 mm = I; 0.2 mm = A, C, D, E, F; 0.1 mm = H; 0.05 mm = B, G.

Larva. Length about 8 mm. Head capsule black, body gray. Articles I+II of antennae widened, 2 times as long as article III. Medial hypostomal teeth shorter than lateral teeth; anterior edge of hypostoma very sclerotized; each side of hypostoma with 2 sublateral setae. On outer apical surface of mandibles 5–6 large long setae. Posterior circlet of 72–76 rows with 9–10 hooklets in each row. Medial branch of anal sclerite distinctly widened and serrated laterally.

Pupa. Length about 5 mm. 14 thin filaments of pupal gill on 3 swollen stems (6+4+4), stems about equal in length; angle between basal parts of upper and lower stems about 120°. Cocoon unshaped, friable, partly or wholly covers pupal body.

Material. 1 male with pupal exuviae (ZIN, slide 9384), 1 larva, 1 larva with pupal gill histoblasts (ZIN, slides 9385, 9386), Bohemia [Czech Rep.], Svoboda, 15 May 1956, coll. V. Novák; 1 pupa with larval head capsule (ZIN, slide 11259), Czechoslovakia, Furkot[sk]á Zlomisica Dol[ina]., V[ysoké] Tatry, 27–28 June 1957 (det. as *tatrensis)*, coll. V. Novák; 1 male, 1 male with pupal exuviae (ZIN, slides 13245, 13249), 1 female,1 female with pupal exuviae (ZIN, slides 13247, 13243), 1 pupa (ZIN, slide 13248), 1 larva (ZIN, slide 13246), 1 pupa (ZIN, pinned), Poland, Tatry, "Murowanec", Vaksmundska Valley, 2 August 1959, coll. W. Zwolski; 1 larva (ZIN, slide 13234), Poland, Tatry, small spring, 2 August 1959, coll. W. Zwolski; 1 male with pupal exuviae, 1 female with pupal exuviae, 1 larva with pupal gill histoblasts (ZIN, slides 13238, 13239, 13242), 3 pupae (ZIN,

pinned), Poland, Tatry, Jaworzinka Valley, 9 June 1960, coll. W. Zwolski; 1 male (ZIN, pinned, terminalia in slide 10962 on same pin), Radnai Havas [Hungary ?], 1923, coll. Pávay.

Remarks. Material examined includes specimens of all developmental phases, 1 male with pupal exuviae and 2 larvae (1 of them with pupal gill histoblasts) (slides 9384, 9385, 9386), collected in type locality and determined by author of species.

Distribution. Central Europe (Austria, Czech Republic, Germany, Italy, Poland, Slovakia, Switzerland) (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky, 2002).

2. *Twinnia magadensis* Rubzov, 1973
(Fig. 18)

Twinnia magadensis Rubzov 1973: 120, fig. 1.

Description. *Males, larvae* and *pupae* unknown.

Female. Length 3 mm. Frons moderately narrow (least width ⅔ of height). Body black, scutum with dim bright (not silvery) spots on outer margin, with short adjacent silvery hairs, abdomen black. Legs wholly brownish black. Palpomere V equal in length to palpomeres III+IV, sensory vesicle relatively large, about ½ of length of palpomere III. Abdominal sternite VIII distinctly sclerotized, not protruding forwards. Hypogynal valves about triangular, with rare short hairs, about equal in length to middle part of sternite VIII, medial edges weakly sclerotized. Stem of genital fork 1.5–1.6 times as long as branches, branches moderately widened distally, posteromedial apodeme distinctly sclerotized, its posterior edge very serrated; posterior cleft of genital fork widened, about triangular, 1.7–1.8 times as wide as long. Anal lobes near equal in length and 1.7 times as high as cerci. Anal lobes 3.3 times, cerci 1.8 times as high as long; lower blade of anal lobe with 18–20 large spiniform setae. Spermatheca 1.5 times as wide as long, surface with distinct wrinkled pattern.

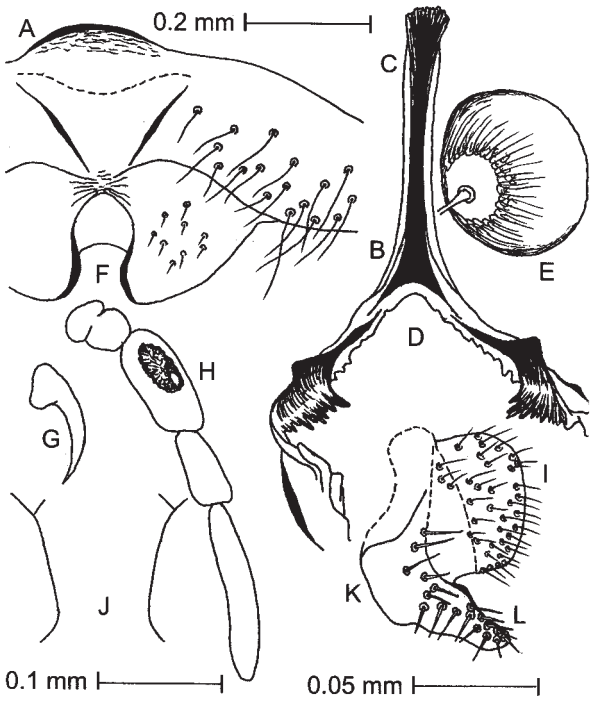

Fig. 18. *Twinnia magadensis* Rubzov, 1973. Holotype female: A – abdominal sternite VIII; B – genital fork, C – stem of genital fork; D – posterior cleft of genital fork; E – spermatheca; F – hypogynal valves; G – claw; H – maxillary palp; I – cercus; J – frons; K – anal lobe; L – spiniform setae on lower blade of anal lobe. Scale bar: 0.2 mm = H, J; 0.1 mm = A, B, C, D, E, F, I, K, L; 0.05 mm = G.

Holotype. Female holotype (ZIN, pinned, details in slide 20453 on same pin), [Magadan Province], Sokol, 56 km N of Magadan, 24 August 1966, coll. K.B. Gorodkov.

Paratype. 1 female (ZIN, pinned, details in slide 20452 on same pin), same data.

Distribution. North of Russian Far East (Rubzov and Yankovsky, 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

3. *Twinnia nova* (Dyar et Shannon, 1927)
(Fig. 19)

Prosimulium novum Dyar et Shannon 1927: 5, figs. 14,15; Wood 1978: 1308, figs. 2, 4, 7, 11, 48, 50, 56; Adler et al. 2004: 242, figs. 10.12, 10.21, 10.92, 10.235, 10.540, map 12.

Twinnia biclavata Shewell 1959: 686.

Description. *Male, larva, pupa*. In the collection of ZIN males, larvae and pupae of this species are absent (characters *see:* Adler et al. 2004: fig. 10.21, 10.235, 10.540).

Female. In collection of ZIN 2 females (in slides only fragments of genitalia and head) (*see also:* Adler et al. 2004: fig. 92). Frons moderately wide (least width slightly less than height). Sensory vesicle relatively large, about ½ of length of palpomere III. Stem of genital fork 1.4–1.5 times as long as branches, branches moderately widened distally, posteromedial apodeme weakly sclerotized, its posterior edge serrated; posterior cleft of genital fork widened, about triangular, 2 times as wide as long. Anal lobes rela-

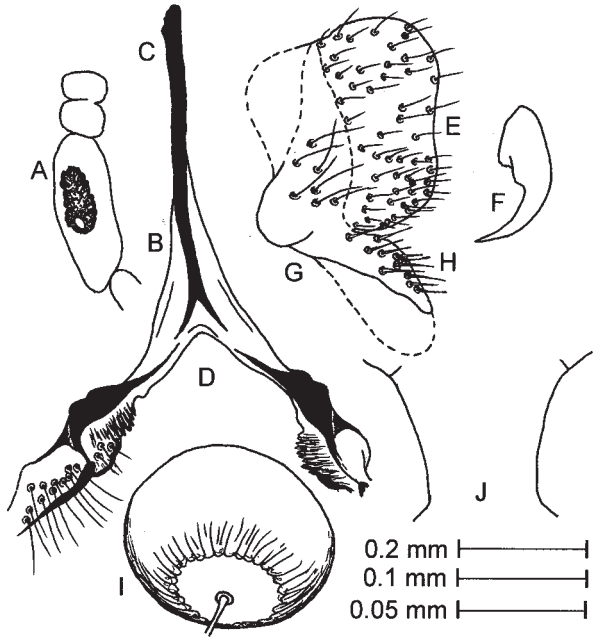

Fig. 19. *Twinnia nova* (Dyar et Shannon, 1927). Female: A – sensory vesicle of maxillary palp; B – genital fork; C – stem of genital fork; D – posterior cleft of genital fork; E – cercus; F – claw; G – anal lobe; H – spiniform setae of lower blade of anal lobe; I – spermatheca; J – frons. Scale bar: 0.2 mm = J; 0.1 mm = A, B, C, D, E, G, H, I; 0.05 mm = F.

tively short, 1.4 times as high and 1.2 times as short as cerci. Anal lobes 2.7 times, cerci 2 times as high as long; lower blade of anal lobe with 10–12 large spiniform setae. Spermatheca 1.5–1.6 times as wide as long, surface with distinct wrinkled pattern.

Material. 1 female (ZIN, pinned, details in slide 10861 on same pin), [USA, Montana], N Fork Ranger Station, Glacier Nat[ional]. Park Mont[ana]., 16 June 1926, coll. H.G. Dyar; 1 female (ZIN, pinned), same locality, 31 May 1926, coll. H.G. Dyar.

Remarks. Lectotype female (designated by Wood 1978: 1308) was labeled: Montana, Glacier Co, Glacier National Park, 4 July 1921, coll. H.G. Dyar. Specimens examined were collected in the type locality and were determined by one of the authors of the species.

Distribution. South West Canada, NW USA (Crosskey and Howard 1997; Adler et al. 2004).

4. *Twinnia sedecimfistulata* (Rubzov, 1955)
(Figs. 20 and 21)

Gymnopais 16-fistulatus Rubzov 1955: 332, fig. 3.

Gymnopais sedecimfistulatus Rubzov 1956: 189, figs. 38, 39; 1960: 124, figs. 34, 35.

Description. *Male*. Length about 2.8 mm. Scutum velvet black, with erect black hairs. Legs brown, tarsi black. Hind basitarsus slightly swollen (4.2–4.5 times as long as wide). Gonocoxites about equal in length or slightly longer than gonostyli, in ventral view their length equal to maximal width. Gonostyli narrowed distally (width in basal part 3.0 width in distal part), in ventral view 1.8 times as long as wide at base. Body of ventral plate 2.5 times as wide as long (ventral view). Median sclerite 3 times as long as wide in middle part.

Female. Length near 3 mm. Frons moderately narrow (least width ⅔ of height). Body and legs wholly black, scutum with long golden hairs. Palpomere V 1.3 times as short as palpomeres III+IV, sensory vesicle relatively large, about ½ of length of palpomere III.

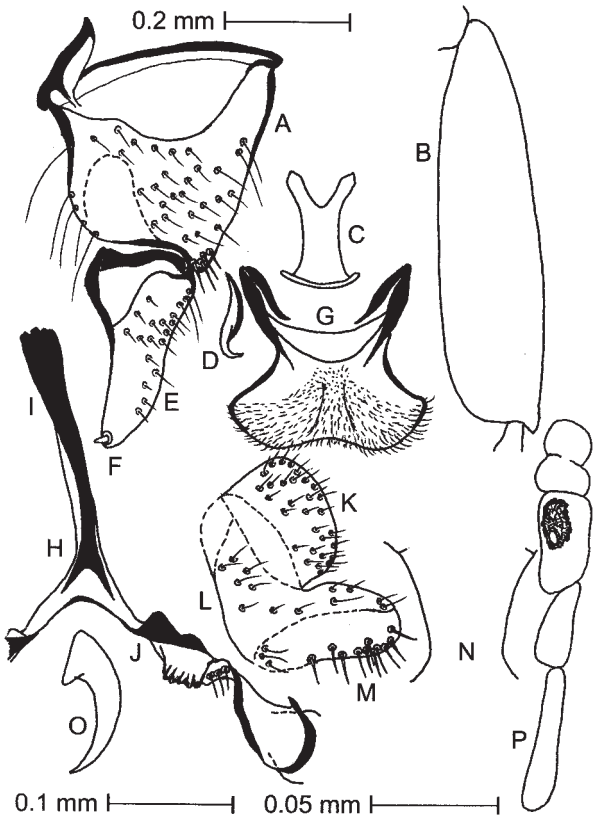

Fig. 20. *Twinnia sedecimfistulata* (Rubzov, 1955). Male (A–G): A – gonocoxite; B – hind basitarsus; C – median sclerite; D – gonopleurite; E – gonostylus; F – apical spine on gonostylus; G – ventral plate. Paralectotype pupa (female) (H–P): H – genital fork; I – stem of genital fork; J – posterior cleft of genital fork; K – cercus; L – anal lobe; M – spiniform setae on lower blade of anal lobe; N – frons; O – claw; P – maxillary palp. Scale bar: 0.2 mm = B, N, P; 0.1 mm = A, C, D, E, F, G, H, I, J, K, L, M; 0.05 mm = O.

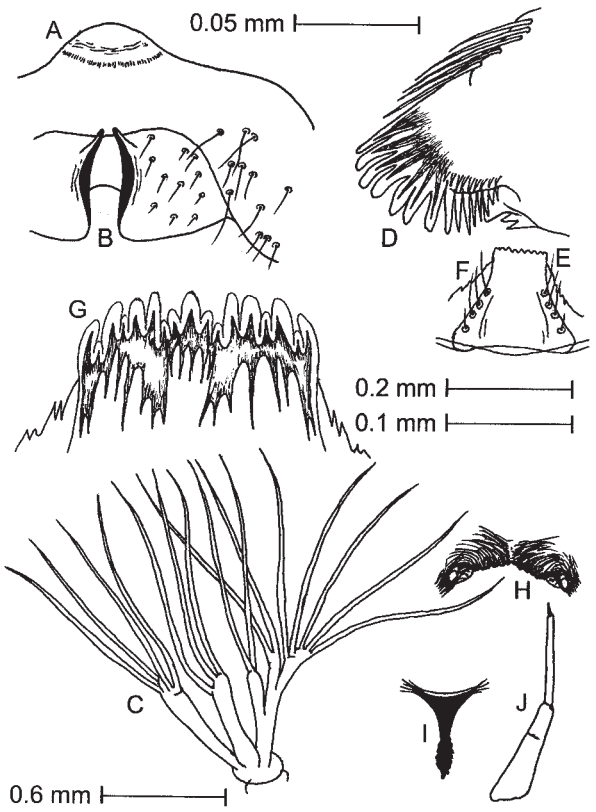

Fig. 21. *Twinnia sedecimfistulata* (Rubzov, 1955). Paralectotype pupa (female) (A–C): A – abdominal sternite VIII; B – hypogynal valves; C – gill. Lectotype larva with pupal gill histoblasts (D–J): D – mandibular teeth; E – hypostoma; F – sublateral setae on hypostoma; G – hypostomal teeth; H – posteroventral margin of head capsule; I – anal sclerite; J – antenna. Scale bar: 0.6 mm = C; 0.2 mm = E, F, H, I; 0.1 mm = A, B, J; 0.05 mm = D, G.

Abdominal sternite VIII weakly sclerotized, slightly protruding forwards. Hypogynal valves about triangular, with rare short hairs, about equal in length to middle part of sternite VIII, medial edges distinctly sclerotized. Stem of genital fork slightly longer than branches, branches moderately widened distally, posteromedial apodeme weakly sclerotized, its posterior edge serrated, distally of apodeme 3 large setae; posterior cleft of genital fork about triangular, very wide, 2.3–2.5 times as wide as long. Anal lobes short, 1.6–1.7 times as high and about equal in length to cerci. Anal lobes 2.5 times, cerci 1.5 times as high as long; lower blade of anal lobe with 10–12 large spiniform setae.

Larva. Length 5.0–5.5 mm. Head capsule brown, body bright yellow. Articles I+II of antennae widened, slightly longer than article III. Medial hypostomal teeth about equal in length to lateral teeth; anterior edge of hypostoma weakly sclerotized; each side of hypostoma with 4 sublateral setae. On outer apical surface of mandibles 4–5 large long setae. Posterior circlet of 66–68 rows with 10–12 hooklets in each row. Medial branch of anal sclerite slightly widened and serrated laterally.

Pupa. Length about 3 mm. 16 thin filaments of pupal gill on 3 swollen stems [(2+2+5)+3+4], upper stem longer than others; angle between basal parts of upper and lower stems about 60°. Cocoon unshaped, friable, partly or wholly covers pupal abdomen.

Lectotype. Larva with pupal gill histoblasts (ZIN, slide 7450), Irkutsk Province, M[alye] Koty River, 25 August 1953, coll. I.A. Rubzov (designated by Yankovsky, 1995: 47).

Paralectotype. 1 female with pupal exuviae and larval head capsule (ZIN, slide 7491), Irkutsk Province, B[olshye] Koty River, 26 August 1953, coll. I.A. Rubzov (designated by Yankovsky 1995: 47).

Additional material. 1 pupal gill histoblast (ZIN, slide 7454), Irkutsk Province, M[alye] Koty River, 25 July 1953, coll. I.A. Rubzov; 1 male (ZIN, slide 8816), Irkutsk Province, affluent of B[olshye] Koty River, 18 August 1955, coll. K.K. Prokofyeva; 1 female (ZIN, slide 13611), Irkutsk Province, Korshunikha, 1 July 1960, coll. unknown; 1 female (ZIN, slide 21565), Irkutsk Province, Kachugskiy District, Kozlova Village, 10 September 1965, coll. Z.S. Dariychuk; 1 female (ZIN, slide 21566), Irkutsk Province, Ust'-Kutskiy District, Narasovo Village, 23 June 1966, coll. Z.S. Dariychuk.

Distribution. South East Siberia (Rubzov and Yankovsky 1984, 1988; Crosskey and Howard 1997; Yankovsky 2002).

Key to species of the genus *Twinnia* (information on *T. changbaiensis* Sun, 1994 is insufficient and this species is not included in the key)

Males (males of *T. magadensis* Rubzov, 1973 unknown)

1. Width of body of ventral plate equal or slightly less than length (ventral view) . . . *T. japonensis* Rubzov, 1960
– Body of ventral plate 1.4–2.5 times as wide as long (ventral view) 2
2. Gonocoxites about equal in length or slightly longer than gonostyli 3
– Gonocoxites 1.4–2.0 times as long as gonostyli 5
3. Body of ventral plate 2.5 times as wide as long; median sclerite 3 times as long as wide in middle part . . . . . *T. sedecimfistulata* (Rubzov, 1955) (Fig. 20)

– Body of ventral plate 1.4–1.5 times as wide as long; median sclerite less than 1.5 times as long as wide in middle part 4
4. Gonostyli in ventral view 2 times as long as wide at base; lateral edges of body of ventral plate concave . . . . . *T. nova* (Dyar et Shannon, 1927)
– Gonostyli in ventral view 2.3 times as long as wide at base; lateral edges of body of ventral plate convex . . . . . *T. cannibora* Ono, 1977
5. Gonostyli moderately narrowed distally (width in basal part 2 width in distal part), 2 times as long as wide at base . . . . . *T. subtibbelesi* Ono, 1980
– Gonostyli slightly narrowed distally (width in basal part 1.4–1.7 width in distal part), 1.5 times as long as wide at base 6
6. Body of ventral plate 2 times as wide as long; length of median sclerite less than width in middle part . . . . . *T. hirticornis* Wood, 1978
– Body of ventral plate 1.4–1.5 times as wide as long; length of median sclerite more than width in middle part 7
7. Width of gonostyli in basal part 1.4 width in distal part; median sclerite 7.0–7.5 times as long as wide in middle part . . . . . *T. hydroides* (Novák, 1956) (Figs. 16, 17)
– Width of gonostyli in basal part 1.7 width in distal part; median sclerite 2–3 times as long as wide in middle part . . . . . *T. tibblesi* Stone et Jamnback, 1955

Females

1. Mouthparts not of bloodsucking type, laciniae and mandibles without teeth . . . . . *T. tibblesi* Stone et Jamnback, 1955
– Mouthparts of bloodsucking type, laciniae and mandibles with teeth 2
2. Hypogynal valves obliquely cut in distal part; stem of genital fork 1.5–1.7 times as short as branches . . . . . *T. subtibbelesi* Ono, 1980
– Hypogynal valves about triangular; stem of genital fork from equal in length to 1.6 times as long as branches 3
3. Hypogynal valves 1.5–1.7 times as short as middle part of sternite VIII . . . *T. hydroides* (Novák, 1956) (Fig. 16)
– Hypogynal valves about equal in length to middle part of sternite VIII 4
4. Lower blade of anal lobe with 18–20 large spiniform setae . . . . . *T. magadensis* Rubzov, 1973 (Fig. 18)
– Lower blade of anal lobe with 5–12 large spiniform setae 5
5. Stem of genital fork slightly longer than branches; posterior cleft of genital fork very wide, 2.3–2.5 times as wide as long; cerci 1.5 times as high as long . . . . . *T. sedecimfistulata* (Rubzov, 1955) (Figs. 20, 21)
– Stem of genital fork 1.3–1.5 times as long as branches; posterior cleft of genital fork not very wide, from equal in width to 2 times as wide as long; cerci 2 times as high as long 6
6. Posteromedial apodeme of branches of genital fork not serrated, with prominent angles; anal lobes 3.2 times as high as long, 1.7 times as high as cerci . . . . . *T. hirticornis* Wood, 1978
– Posteromedial apodeme of branches of genital fork distinctly serrated, without prominent angles; anal lobes 2.0–2.7 times as high as long, 1.3–1.4 times as high as cerci 7
7. Width of posterior cleft of genital fork about equal to length; anal lobes 2.0 times as high as long, 1.4 times as long as cerci . . . . . *T. cannibora* Ono, 1977
– Posterior cleft of genital fork 1.7–2.0 times as wide as long; anal lobes 2.5–2.7 times as high as long, about equal in length to cerci 8
8. Abdominal sternite VIII weakly sclerotized, slightly protruding forwards; posterior cleft of genital fork 2.0 times as wide as long; spermatheca 1.5 times as wide as long . . . . . *T. nova* (Dyar et Shannon, 1927) (Fig. 19)
– Abdominal sternite VIII distinctly sclerotized and protruding forwards; posterior cleft of genital fork 1.7 times as wide as long; spermatheca 2 times as wide as long . . . . . *T. japonensis* Rubzov, 1960

Larvae (larvae of *T. japonensis* Rubzov, 1960 and *T. magadensis* Rubzov, 1973 unknown)

Now it is difficult to find constant morphological characters for separating the larvae of Nearctic and Japanese species of *Twinnia*, and here we are forced to use partly the characters of species distribution (*see also the same cases in:* Wood 1978: 1300; Adler et al. 2004: 210).

1. Nearctic 2
– Palaearctic 4
2. East of Great Plains . . . . . *T. tibblesi* Stone et Jamnback, 1955
– West of Great Plains 3
3. Pupal gill histoblast with at least 1 pair of filaments on each basal trunk arising from common stem . . . . . *T. hirticornis* Wood, 1978
– Pupal gill histoblast with filament arising independently on basal trunks . . . . . *T. nova* (Dyar et Shannon, 1927)
4. Japan 5
– Other territories 6
5. Length 7.2–7.5 mm; posterior circlet of 74–76 rows with 12–14 hooklets in each row; medial branch of anal sclerite widened laterally . . . . *T. subtibbelesi* Ono, 1980
– Length 5–6 mm; posterior circlet of 78–80 rows with 8 hooklets in each row; medial branch of anal sclerite not widened laterally . . . . . *T. cannibora* Ono, 1977
6. Length 8 mm; body grey; articles I+II of antennae 2 times as long as article III; each side of hypostoma with 2 sublateral setae; posterior circlet of 72–76 rows; pupal

gill histoblast of 14 filaments . . . . . *T. hydroides* (Novák, 1956) (Fig. 17)
– Length 5.0–5.5 mm; body bright yellow; articles I+II of antennae slightly longer than article III; each side of hypostoma with 4 sublateral setae; posterior circlet of 66–68 rows; pupal gill histoblast of 16 filaments . . . . . *T. sedecimfistulata* (Rubzov, 1955) (Fig. 21)

Pupae (pupae of *T. magadensis* Rubzov, 1973 unknown)

1. Gill of 14 filaments . . . . . *T. hydroides* (Novák, 1956) (Fig. 17)
– Gill of 16 filaments 2
2. Angle between basal parts of upper and lower gill trunks about 120° . . . . . *T. tibblesi* Stone et Jamnback, 1955
– Angle between basal parts of upper and lower gill trunks 60–90° 3
3. Gill filaments on 2 thick trunks 4
– Gill filaments on 3 thick trunks 5
4. Gill with at least 1 pair of filaments on each basal trunk arising from common stem; filaments 2.0–2.3 times as long as trunks . . . . . *T. hirticornis* Wood, 1978
– Gill with filament arising independently on basal trunks; filaments about equal in length or slightly longer than trunks . . . . . *T. nova* (Dyar et Shannon, 1927)
5. Angle between basal parts of upper and lower gill trunks about 90° 6
– Angle between basal parts of upper and lower gill trunks about 60° 7
6. Upper gill trunk (with 8 filaments) 2 times as long as trunks II, III . . . . . *T. cannibora* Ono, 1977
– All 3 gill trunks of about equal length . . . . . *T. subtibbelesi* Ono, 1980
7. Median gill trunk 3 times as short as trunks I, III . . . . . *T. japonensis* Rubzov, 1960
– All 3 gill trunks of about equal length . . . . . *T. sedecimfistulata* (Rubzov, 1955) (Fig. 21)

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REFERENCES

Adler P.H., Currie D.C. and Wood D.M. 2004. The Black Flies (Simuliidae) of North America. Cornell University Press, Ithaca, London, 941 p.

Bobrova S.D. 1967. A new species of black fly from the genus *Gymnopais* (Diptera, Simuliidae) from Altai. *Entomologicheskoye Obozreniye,* **46**(4): 884–886. [In Russian]

Bodrova Yu.D. 1975. A new species of black flies (Diptera, Simuliidae) from Primorskiy Territory. *Entomologicheskoye Obozreniye,* **54**(2)**:** 429–431. [In Russian]

Chubareva L.A. and Petrova N.A. 1981. A new genus of black flies (Diptera, Simuluudae) from Tajikistan. *Entomologicheskoye Obozreniye,* **60**(4): 898–900. [In Russian]

Crosskey R.W. 1987. An annotated list of the world black flies (Diptera: Simuliidae). In: K.C.Kim and R.W. Merritt (Eds.). Black flies: ecology, population management, and annotated world list. Pennsylvania State University, University Park: 425–520.

Crosskey R.W. 1990. The natural history of blackflies. John Wiley, Chichester, U.K., 711 p.

Crosskey R.W. and Howard T.M. 1997. A new taxonomic and geographical inventory of world blackflies (Diptera: Simuliisdae). Natural History Museum, London, 144 p.

Currie D.C. and Grimaldi D. 2000. A new black fly (Diptera: Simuliidae) genus from mid Cretaceous (Turonian) amber of New Jersey. In: D. Grimaldi (Ed.). Studies on fossils in amber, with particular reference to the Cretaceous of New Jersey. Backhuys Publishers, Leiden, 473–485.

Dyar H.G. and Shannon R.C. 1927. The North American two-winged flies of the family Simuliidae. *Proceedings of the United States National Museum,* **69**(10): 1–54.

Enderlein G. 1929. Neue Arten des Simuliidengenus *Cnetha* (Dipt.). *Wiener Entomologische Zeitung,* **46**(2): 73–78.

Kalugina N.S. 1991. New Mesozoan Simuliidae and Leptoconopidae and the origin of bloodsucking in Nematocera. *Paleontologicheskiy Zhurnal,* **1**: 69–80. [In Russian]

Novák V. 1956. Příspěvek k poznání muchniček (Simuliidae, Diptera) ČSR. *Věstník Československé Společnosti Zoologické,* **20**(3): 224–248.

Novák V. 1959. Dalšínová muchnička podčeledi Gymnopaidinae z ČSR, *Twinnia tatrensis* sp.n. (Diptera, Simuliidae). *Časopis Československé Společnosti Entomologické,* **56**(4): 364–367.

Rubzov I.A. 1955. Peculiar new species of black flies (Diptera, Simuliidae) from Eastern Siberia. *Entomologicheskoye Obozreniye,* **34** (2): 323–339. [In Russian]

Rubzov I.A. 1956. Moshki (sem. Simuliidae) [Blackflies (fam. Simuliidae)]. Fauna SSSR, 6 (6). Second Edition. Akademiya Nauk SSSR, Moscow, Leningrad, 860 p. [In Russian]

Rubzov I.A. 1960. 14.Simuliidae (Melusinidae). In: E. Lindner (Ed.). Die Fliegen der paläarktische Region (III). E. Schweizerbart'sche Verlagsbuchhandlung, Stuttgart, Lieferung, **204**: 97–160.

Rubzov I.A. 1963. Eine neue Art aus der Unterfamilie Gymnopaidinae (Simuliidae, Dipt.). *Stuttgarter Beiträge zur Naturkunde,* **123**: 1–7.

Rubzov I.A. 1973. New and little known species of black flies (Diptera, Simuliidae). *New and little known species of Siberian fauna,* **7**: 120–128. [In Russian]

Rubzov I.A. and Yankovsky A.V. 1984. Opredelitel' rodov moshek Palearktiki [A key for the identification of blackfly genera of Palaearctic]. Nauka, Leningrad, 176 p. [In Russian]

Rubzov I.A. and Yankovsky A.V. 1988. Family Simuliidae. In: Á. Soós and L. Papp (Eds.). Catalogue of Palaearctic Diptera, 3. Akadémiai Kiadó, Budapest: 114–186.

Shewell G.E. 1959. New Canadian black flies (Diptera: Simuliidae). III. *Canadian Entomologist,* **91**: 686–697.

Stone A. 1949. A new genus of Simuliidae from Alaska (Diptera). *Proceedings of the Entomological Society of Washington,* **51**(6): 260–267.

Stone A. and Jamnback H.A. 1955. The blackflies of New York State (Diptera: Simuliidae). *New York State Museum Bulletin,* **349**: 1–144.

Sun Y. 1994. Black flies in most part of North China. Liaoning, China: 35–38. [In Chinese]

Wood D.M. 1978. Taxonomy of the Nearctic species of *Twinnia* and *Gymnopais* (Diptera: Simuliidae) and a discussion of the ancestry of the Simuliidae. *Canadian Entomologist,* **110**(12): 1297–1337.

Worobez E.I. 1984. On new species of black flies (Diptera, Simuliidae) from Yakutia and on taxonomic position of *Gomphpostilbia chomustachi* Worobez. *Clenistonogiye i gelminty (New and little known species of Siberian fauna),* **17**: 74–82. [In Russian]

Yankovsky A.V. 1982. A new species of black flies *Gymnopais frontatus* sp. n. from Kamchatka (Simuliidae). *Parazitologiya,* **16**(2): 160–162. [In Russian]

Yankovsky A.V. 1993. A review of the system of blackflies (Diptera, Simuliidae) on the suprageneric level. *Parazitologicheskiy Sbornik,* **37**: 203–217. [In Russian]

Yankovsky A.V. 1995. Fam. Simuliidae Newman. In: A.V. Yankovsky and K.N.Ulyanov (Compilers). Katalog tipovykh ekzemplyarov kollektsii Zoologicheskogo Instituta RAN [Catalogue of type specimens in the collection of the Zoological Institute, Russian Academy of Sciences]. Diptera. 5. Simuliidae, Culicidae. Russian Academy of Sciences, Zoological Institute, Saint Petersburg: 6–61. [In Russian]

Yankovsky A.V. 2002 (2003). Opredelitel' moshek (Diptera: Simuliidae) Rossii i sopredelnykh territoriy (byvshego SSSR) [A key for the identification of blackflies (Diptera: Simuliidae) of Russia and adjacent countries (former USSR)]. Saint Petersburg State University, Saint Petersburg, 570 p. [In Russian]

Zhang J.F. 1986. Some fossil insects from the Jurassic of northern Hebei, China. The paleontology and Stratigraphy of Shandong, Beijing, 95 p. [In Chinese]

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