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The Net-Winged Midges (Diptera: Blephariceridae) of the Russian Far East

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Abstract. A revision and synopsis of the Diptera: Blephariceridae of the Russian Far East is presented; it includes generic keys to all life stages. Constitutive characters supporting the monophyly of the genera *Bibiocephala* Osten-Sacken and *Agathon* von Röder are named. Genera *Philorus* Kellogg and *Blepharicera* Macquart are recorded from the Russian Far East for the first time. New species described are *Philorus levanidovae* sp. n., *Blepharicera parva* sp. n. and *Agathon setosus* sp. n. The number of species known from the Russian Far East rises to eight. *Agathon decorilarva* (Brodsky, 1954), *A. eoasiaticus* (Brodsky, 1954) and *Neohapalothrix manschukuensis* (Mannheims, 1938) are widespread, ranging west to Mongolia and Kazakhstan, respectively, and *A. decorilarva* east to Kamchatka. All species were compared with actual specimens of close relatives from Korea and Japan and are distinct from them, except perhaps *Bibiocephala maxima* Brodsky, 1954. In the case of *Bibiocephala*, the world fauna is compared and keys to all stages of the four nominal species are provided. *Agathon kawamurai* (Kitakami, 1950) from Korea, *A. ezoensis* (Kitakami, 1950) from Sakhalin and Hokkaido, and the Korean *Philorus chosenensis* Kitakami, 1931 are redescribed from lectotypes, which are here designated.

Key words. Taxonomy, faunistics, new species, lectotype designation, keys, Far East Asia

1. INTRODUCTION

The Blephariceridae of the Russian Far East were first studied by BRODSKY (1954) who named several taxa. Unfortunately, Brodsky was apparently unaware of several studies by S. Kitakami who published on the Blephariceridae of Japan, Taiwan, Korea, Sakhalin, and Manchuria, from 1931-1950, and of the description of a peculiar Manchurian species (MANNHEIMS 1938). Two of Brodsky's taxa proved in the meantime to be synonyms of species named from nearby countries in the above papers. The validity of the remaining nominal species needed confirmation.

BRODSKY´S collection is in the Zoological Museum, St. Petersburg, but not all of his specimens could be located. Kitakami's collection in Kyoto (KITAKAMI 1951: 70) is apparently lost. Very few specimens remain in the Otsu Hydrobiological Station of Kyoto University at Otsu (K.N. Satake, in lit. 1987); we were unable to study them. However, Kitakami gave specimens in alcohol, including syntypes, to the United States National Museum (Washington, D.C.) and to B. Mannheims (Museum Koenig, Bonn, Germany). This material has uniform printed labels, occasional additions in ink are all in the same style, probably in Kitakami's own hand. A typed page by Kitakami sent to Mannheims lists every individual specimen with place and date of collection. The list shows that specimens belonging to some particular species and kept in the same vial may nevertheless have been collected at different places or times, respectively. Similar information is not available for the material in USNM. Therefore, even though the Washington specimens are authentic Kitakami material, they are eligible as lectotypes only under certain conditions, mainly taxa named in Kitakami's last taxonomical paper (1950) where all available specimens were listed as equal syntypes.

NARTSHUK (1999) presented keys to the then known larvae and pupae of the entire Russian fauna, to species or genus, respectively, apparently largely relying on published information. Adults were not considered.

2. MATERIAL, COLLECTION SITES AND DEPOSITORIES

During three weeks in June 1998, net-winged midges were the specific target of fieldwork by the authors and several of their colleagues in Primorye and the Khabarovsk district; collecting and treatment of collected insects conformed with Russian legal regulations. Whenever possible, large samples were collected to permit safe association of different life stages by dissection of pharate specimens, and to give an idea of the population structure at the time of sampling, and perhaps of volitinism and phenology. This alcohol-preserved material provides also information on habitat preferences and species associations. To avoid frequent repetition, locality information is gathered in Table 1.

Additional material collected by workers of the Institute of Biology and Soil Science, Academy of Sciences, Vladivostok (IBSSAN), consists of many smaller samples, most from the same general area. Some data were already published (AREFINA 1995). We list this addi-

Table 1. List of localities successfully sampled for Blephariceridae by the authors during field work in Primorye and the Khabarovsk District, in June 1998; material housed in coll. P. Zwick. Coordinates were read from Tactical Pilot Charts (prepared and published by the Defense Mapping Agency Aerospace Center, St. Louis, Missouri, 1986) and are approximate

RFE01	43°24'E, 132°48'N; Primorje, Steklyanukha River, tributary of Shkotovka River, Sevy Gorbatov Klyuch, waterfalls and cascades accessible from logging road beyond Novaya Moskva, 11.06.1998 and 26.06.1998
RFE03	43°03'N, 133°17'E; Primorje, Vodopadnaja River nr Nikolayevka, E of Partizansk [43.08N, 133.09E], 12.06.1998
RFE04	43°05'N, 133°18'E; Primorje, small rocky tributary to RFE03, at forest edge, 12.06.1998
RFE04	43°05'N, 133°18'E; Primorje, small rocky tributary to RFE03, at forest edge, 12.06.1998
RFE06	43°25'N, 133°28'E; Primorje, Povorotny River NE Partizansk [43.08N, 133.09E], on road to Lazo, 12.06.1998
RFE06	43°25'N, 133°28'E; Primorje, Povorotny River NE Partizansk [43.08N, 133.09E], on road to Lazo, 12.06.1998
RFE07	43°29'N, 133°42'E; Primorje, Lazovka River 30 km W of Lazo[43.25N, 133.55E], 12.06.1998
RFE08	43°28'N, 133°44'E; Primorje, Lazovka River 25 km W of Lazo [43.25N, 133.55E], at bridge, 13.06.1998
RFE09	43°12'N, 133°15'E; Primorje, Kiyevka River, 5 km S of Lazo [43.25N, 133.55E], 13.06.1998
RFE10	43°35'N, 134°36'E; Primorje, upper course of Milogradovka River, 25 km NW Milogradovo, 13.06.1998
RFE10a	Primorje, small forest tributary to RFE10 in forest, 14.06.1998
RFE12	43°38'N, 134°20'E; Primorje, Ussuri River, upper course on logging track from Margaritovka, N of pass, near Nishni, 15.06.1998
RFE13	43°42'N, 133°58'E; Primorje, Krasnaya River, tributary of Ussuri near Beryozovi, 15.06.1998
RFE14	43°43'N, 133°53'E; Primorje, Pravaya Poperechka River S of Arkhipovka, 15.06.1998
RFE15	43°53'N, 133°55'E; Primorje, Izvilinka River at Izvilinka, near mouth into Ussuri, 15.06.1998
RFE16	44°19'N, 133°54'E; Primorje, Ussuri River 6 km SW Kamenka, 15.06.1998
RFE17	44°41'N, 134°04'E; Primorje, Zadovka River, tributary of Zhuralyovka River 10 km SW Samarka, 16.06.1998
RFE18	44°43'N, 134°08'E; Primorje, Zhuralyovka River (tributary of Ussuri) at Samarka, 16.06.1998
RFE19	44°50'N, 134°19'E; Primorje, Komisarovski River near Lesogorje, tributary of Otkosnaya River/ Ussuri, 16.06.1998
RFE20	44°57'N, 134°24'E; Primorje, Malinka River S of Pozhiga, 16.06.1998
RFE21	45°05'N, 134°32'E; Primorje, Malinovka River ESE of Pozhiga, 16.06.1998
RFE22	45°06'N, 134°43'E; Primorje, cold forest tributary to RFE21, 3 km upstream on logging track, 17.06.1998
RFE23	45°26'N, 134°35'E; Primorje, Orekhovka River near Marevka, tributary Malinovka, 17.06.1998
RFE24	45°27'N, 134°42'E; Primorje, small tributary to RFE23, about 5km on, near Polyany, 17.06.1998
RFE25	45°28'N, 135°00'E; Primorje, small upper course of Orekhovka River, near pass to Perevalnaja River, 17.06.1998
RFE26	45°29'N, 135°04'E; Primorje, small forest stream just N of pass, Rogaty River, tributary of upper Perevalnaja River, 17.06.1998
RFE27	45°32'N, 135°04'E; Primorje, Rudny River, larger tributary of upper Perevalnaja River, 17.06.1998

RFE28	45°38'N, 135°10'E; Primorje, Perevalnaja River, near mouth of Dorozhny River, 17.06.1998
RFE30	46°32'N, 134°53'E; Primorje, branch of Bikin River near ferry, 25 km E of Verkhny Pereval, 18.06.1998
RFE31	Primorje, unnamed small stream on road, much disturbed through building of new culvert, turbid, 19.06.1998
RFE33	46°41'N, 135°27'E; Primorje, Bikin River and major tributary near Soboliny, 19.06.1998
RFE34	46°43'N, 135°28'E; Primorje, Stolbovaya River above Soboliny, tributary of Bikin River, 19.06.1998
RFE35	46°45'N, 135°33'E; Primorje, Tahalo River, large tributary to Bikin River at bridge, 19.06.1998
RFE36	46°48'N, 135°38'E; Primorje, Maly Tahalo River, 20.06.1998
RFE37	47°12'N, 135°34'E; Khabarovsky Kraj, Ivanov River at large bridge, between Yushnyi and Metsa, 20.06.1998
RFE38	47°22'N, 135°37'E; Khabarovsky Kraj, Dolmi River at Dolmi, S tributary of Khor River, 20.06.1998
RFE39	47°33'N, 135°33'E; Khabarovsky Kraj, Matai River, 20.06.1998
RFE41	48°04'N, 136°23'E; Khabarovsky Kraj, upper course of Nemtu River on road from Sidima to Sukpai, 21.06.1998
RFE42	Khabarovsky Kraj, small tributary to RFE41, about 3 km towards Sukpai, 21.06.1998
RFE43	48°05'N, 136°33'E; Khabarovsky Kraj, Petin River, tributary of Nemtu/Khor River, 21.06.1998
RFE44	48°02'N, 136°44'E; Khabarovsky Kraj, tributary to Ku River, 21.06.1998
RFE45	48°02'N, 136°44'E; Khabarovsky Kraj, cascades of small cold spring-fed stream 100 m uphill from RFE 44, 21.06.1998
RFE46	48°01'N, 136°46'E; Khabarovsky Kraj, Ku River, upper course at first bridge on road Sidima-Sukpai, 21.06.1998
RFE47	47°56'N, 136°46'E; Khabarovsky Kraj, Khor River below Sukpai village, 21.06.1998
RFE48	47°59'N, 136°47'E; Khabarovsky Kraj, Sukpai River at Sukpai village, 22.06.1998
RFE49	48°00'N, 136°53'E; Khabarovsky Kraj, large tributary to Sukpai River, 22.06.1998
RFE49a	48°00'N, 136°53'E; Khabarovsky Kraj, tributary to large tributary of Sukpai River, 22.06.1998
RFE50	47°47'N, 136°55'E; Khabarovsky Kraj, Sukpai River upper course at dead end of road, 22.06.1998
RFE52	Khabarovsky Kraj, Avan River on main road Khabarovsk – Vladivostok, just N of Kotikovo [47°27'N, 134°37'E], 23.06.1998
RFE53	Primorje, Bolshaya Ussurka, immediately above Dalnerechensk [45.55N, 133.43E], 23.06.1998
RFE54	44°45'N, 131°43'E; Primorje, Poperechnaya River, small tributary to Molokanka River W of Lake Khanka, 24.06.1998
RFE55	44°45'N, 131°52'E; Primorje, tiny trickle, tributary to Komissarovka River, at old bridge, 24.06.1998 (Kommissarovo [44.59N, 131,.46E])
RFE56	44°45'N, 131°48'E; Primorje, Komissrovka River, at mouth of Reshetinka River, SE of the Pogranichny Ridge, 24.06.1998
RFE100	43°21'N, 131°38'E; Gryaznaya stream, waterfalls, 10.07.1998, T. Arefina & T. Tiunova

tional material under the respective species only if taxonomically important, or if originating from places distinctly outside the range sampled in 1998.

We were also given valuable comparative material from Mongolia (P. Surenkhorloo, Ulan Bataar), Kazakhstan (V. Devyatkov, Ust-Kamenogorsk) and Japan (S. Uchida, Toyota). All of these collections are presently kept at Schlitz in collection P. Zwick (PZ) and will eventually be deposited in a public museum.

Comparative material was borrowed from the following collections: SAWL – Sächsische Akademie der Wissenschaften zu Leipzig, Arbeitsgruppe Limnologie, Lengfeld, Germany; USNM – United States National Museum, Smithsonian Institution, Washington, D.C., USA; ZFMK – Zoologisches Forschungsinstitut und Museum Alexander Koenig, Bonn, Germany; ZIAS – Zoological Institute, Academy of Sciences, St. Petersburg, Russia

In lists of studied material, capital letters E, L, P stand for exuviae, larvae, and pupae, respectively. Larval instars 1-4 are identified by the respective numeral following the letter L.

3. KEY TO GENERA OF BLEPHARICERIDAE IN THE RUSSIAN FAR EAST

The Far East Russian fauna comprises five genera. Genus *Neohapalothrix* Kitakami is endemic to the eastern part of Asia, its closest relative being the European genus *Hapalothrix* Loew. The position of these genera in the family is doubtful – see under *Neohapalothrix* Kitakami. The other four genera belong to tribe Blepharicerini and exhibit amphi-Pacific disjunctions, with close relatives in western North America. In the Palaearctic Realm, *Bibiocephala* Osten-Sacken, *Agathon* von Röder and *Philorus* Kellogg are restricted to the eastern part of Asia, while *Blepharicera* Macquart is widespread in the northern hemisphere.

Adults

1 Branches of R on long fork (Figs. 1a-b) 2

1' Branches of R sessile, or from short fork (Figs. 1c-e) 3

2 An unconnected branch M_3 originating freely in wing membrane and ending in wing margin, and a basal crossvein between branches of M and Cu present (Figs. 1b) .... ***Philorus***

2' No unconnected vein in wing, no basal crossvein between M and Cu (Figs. 1a) .... ***Neohapalothrix***

3 R with three long branches, anterior branch ending in R_1 shortly before wing margin; basal crossvein between branches of M present (Fig. 1c) .... ***Bibiocephala***

3' R with two long branches; if a rudimentary anterior branch is present it ends in R_1 near base of latter and appears like an oblique crossvein forming a small triangular cell. Basal crossvein between branches of M present or absent (Figs. 1d, e) 4

4 Rudimentary branch R_2 delimiting small triangle present or absent; crossvein between M and Cu present (Fig. 1d) .... ***Agathon***

4' Neither rudimentary R_2 nor crossvein between M and Cu present (Fig. 1e) .... ***Blepharicera***

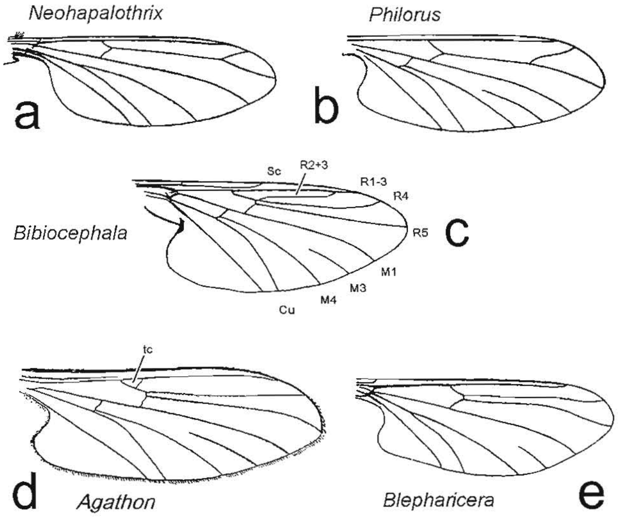

Fig. 1: Wing venation of Blephariceridae from the Russian Far East. a, *Neohapalothrix manschukuensis* (Mannheims) (after BRODSKY 1954); b, *Philorus asiaticus* Brodsky (after BRODSKY 1972); c, *Bibiocephala maxima* Brodsky (after BRODSKY 1954); d, *Agathon japonicus* (Alexander) (after KITAKAMI 1931); e, *Blepharicera asiatica* Brodsky (after BRODSKY 1976). Nomenclature of wing veins after HOGUE (1987); tc = triangular cell delimited on outside by R_{2+3}.

Pupae

1 Respiratory organs composed of four erect lamellae (Fig. 11); three or four pairs of abdominal adhesive organs 2

1' Respiratory lamellae in the form of short crests or flanges (Figs. 12d, e); three pairs of abdominal adhesive organs .... ***Philorus***

2 Respiratory lamellae resemble slender pointed triangles. Body cross-section approximately triangular, several abdominal tergites with median spines; four pairs of abdominal adhesive organs .... ***Neohapalothrix***

2' Respiratory lamellae tongue- or leaf-shaped, apices rounded; body cross-section rounded, regularly curved, no dorsal armature; three pairs of abdominal adhesive organs 3

3 Body highly domed, cross-section semicircular .... ***Bibiocephala***

3' Body moderately arched, cross-section lower than a half circle 4

4 All respiratory lamellae structurally similar, flexible. Dorsal surface matt, granulation strong, mesothorax with rugose zig-zag pattern .... ***Agathon***
4' Anterior and posterior respiratory lamellae hard, stiff, two inner ones soft. Dorsal surface shining, granulation fine and sparse, no zig-zag pattern on mesothorax .... ***Blepharicera***

Larvae (instars 2-4, with one to six filaments per gill)

1 Head capsule entire, posterior notches insignificant (Figs. 2a, c, 5) 2
1' Rear of head capsule laterally distinctly notched, usually deeply divided (to eye-spot; Fig. 12 f) 3
2 Antenna 2-segmented. Labrum sclerotized, forming part of a continuous prestomal ridge between left and right posterior mandibular articulations (Fig. 2b) .... ***Bibiocephala***
2' Antenna 3-segmented. Sclerotizations above mandibles extend between the two mandibular articulations on each side but are medially separated from each other by the soft labrum (Fig. 2c) ...... ***Agathon***
3 Body compact, abdominal segments lack "neck pieces". Highly convex, body cross-section triangular, dorsum of last instar with median row of spines. Two lateral pseudopods, both appressed to ground (L4), or single pseudopod forked (L3; Fig. 19e), or with knob (L2; Fig. 19d) .... ***Neohapalothrix***
3' Body not compact, abdominal segments 2-6 with narrow anterior portions (neck pieces), not highly arched, cross-section not triangular. Dorsal armature variable; if forming a median row it consists of blunt knobs or warts; dorsal pseudopods variable but never appressed to ground 4
4 Dorsal sensory pseudopod missing altogether, only ventral ambulatory pseudopod present (Figs. 16a, d). Dorsal armature, if any, consists of single blunt warts along midline .... ***Blepharicera***
4' Dorsal sensory pseudopod present, with dorsal process or erect spine; abdominal armature consisting of six structures per segment (Fig. 12 f) .... ***Philorus***

Larvae (first instar)

1 Dorsum with continuous transverse crests 2
1' Dorsum with transverse rows of separate erect little sclerites (Figs. 13, 19a, b) 3
2 Cephalic division with five crests, one on each thoracic and two on 1st abdominal segment .... ***Bibiocephala*** **and** ***Agathon***
2' Cephalic division with two crests (one on thorax, one on 1st abdominal segment) .... ***Blepharicera***
3 Dorsal sclerites are little triangular spikes arranged in transverse rows; cephalic division with four of these rows. Pseudopod with apical brush of slender setae (Fig. 13) .... ***Philorus***
3' Dorsal sclerites long and slender, band- or hair-like, in transverse rows; five of these on cephalic division. Pseudopod with group of retractile tiny hooks (Figs. 19a-c) .... ***Neohapalothrix***

4. TAXONOMY

4.1. Genus *Bibiocephala* Osten-Sacken, 1874

Bibiocephala Osten-Sacken, 1874. Type species: *Bibiocephala grandis* Osten-Sacken, 1874, by monotypy (OSTEN-SACKEN 1874: 564).

Amika Kitakami, 1950. Type species: *Liponeura infuscata* Matsumura, 1916, by original designation (KITAKAMI 1950: 37).

The genera *Bibiocephala* and *Agathon* were not separated by KITAKAMI (1931) but later he recognized their distinctness (KITAKAMI 1950). Unfortunately the nomenclature was confused; *Amika* Kitakami, 1950 is a synonym of the North American genus *Bibiocephala.* Kitakami erroneously used the latter name for what is in fact *Agathon.* Our present use of the name *Bibiocephala* is based on the redescription of the type species, *B. grandis* Osten- Sacken (HOGUE 1982) and conforms to the restricted use by HOGUE (1973, 1987) and ZWICK (1990, 1992).

Bibiocephala and *Agathon* differ from other northern hemisphere net-winged midges by characters in which they resemble the southern hemisphere Edwardsininae: undivided larval head capsule (Figs. 2a, c, 5); presence of a remnant of vein R_{2+3} (Figs. 1c, d), secondarily absent in individual species of *Agathon*; 4 visible growth zones of larval head capsule behind the cephalic sclerites, like in *Edwardsina* Alexander, 1920 (TONNOIR 1924; ZWICK 1977, fig. 22) and the Madagascan *Paulianina (Eupaulianina)* Stuckenberg, 1958 (STUCKENBERG 1958, fig. 28); *Philorus* also similar.

The first two agreements are undoubtedly plesiomorphic character expressions, the third probably so. Additional resemblances between *Bibiocephala, Agathon* and *Philorus* are difficult to interpret: dorsal larval pseudopods with erect outgrowth or process (Fig. 12f); in some species of *Agathon*, only a knob or angle remains; unique in the family; larval abdomen with six spines, sclerites or appendages standing in a characteristic arrangement (Figs. 8a, 12f); abdominal armatures are not uncommon in larvae of net-winged midges but in other taxa their arrangement differs.

In any case, the monophyly of the genera in question needs be established. As constituent apomorphies of genus *Bibiocephala* we accept the following characters:

Larva: Massive highly domed body (Fig. 2a). Mouth area forming a completely flat oral field surrounded in front by an essentially continuous triangular prestomal margin (Fig. 2b): Sides of prestomal margin formed by sclerotized arcs supporting mandibular articulations, the short transverse middle piece by the sclerotized, transversely folded labrum. Two setiform labral sensilla stand above, two below the sclerotized edge. In the groundplan of the family (for example, Fig.2c) the oral field is not flat and in front not surrounded by a continuous sclerotized prestomal margin because the labrum is largely soft and bulges forward and ventrad between the sclerotized arcs to its left and right which support the mandibular articulations. At the medial end, these sclerotized arcs turn dorsad towards the lower end of the median frontal sclerite.

Larva: Short stout lanciform or spatulate setae present on head in front of eyes, around antennal foramen, and on anterior corners of cephalic division (Fig. 5a; last instar only).

Pupa: Highly domed. Respiratory lamellae very large, often leafy.

Adult: Body unusually setose, especially males. Abdominal segment one fused to metathorax, tilted up, immobile; mobility of abdomen achieved via well developed membrane between abdominal segments one and 2.

♂: antenna short, compact; front femur arched; last tergite posteromedially sclerotized and spinulose.

♀: Pleuron and tergite 9 enlarged, both with fringe of dense, exceptionally long setae surrounding abdominal tip like a basket (see ZWICK 1990, fig. 1).

From the description by KITAKAMI (1931), the first instar larva of *Bibiocephala infuscata* has the full complement of transverse cuticular crests, that is, three thoracic and two abdominal ones on the cephalic division, and two each on the other abdominal segments. The pseudopod bears eversible hooklets.

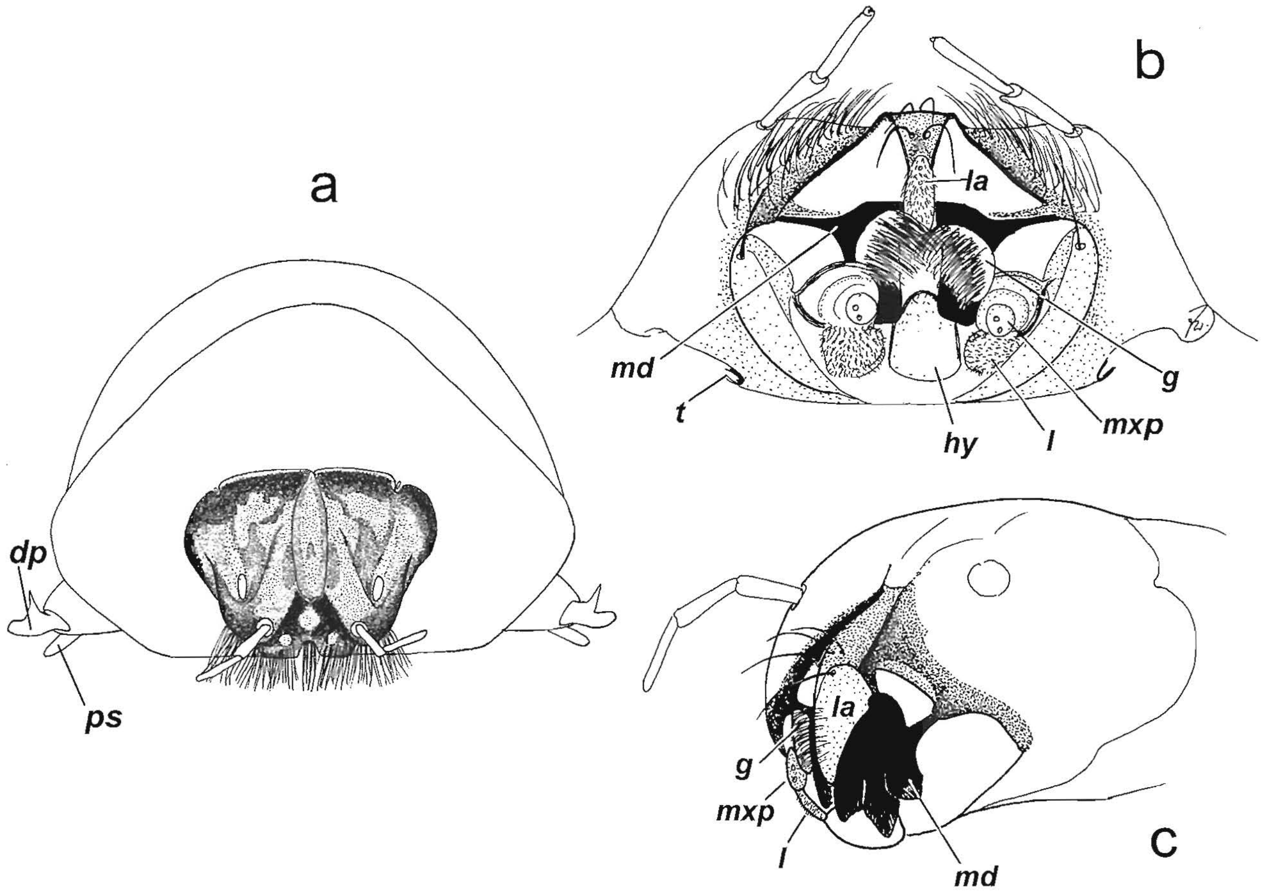

Fig. 2: a, *Bibiocephala grandis* Osten-Sacken, frontal view of last instar larva; b, *B. maxima* Brodsky, ventral view of head; c, *Agathon eoasiaticus* Brodsky, oblique frontolateral view of cephalic division, left antenna and maxilla removed. dp, dorsal pseudopod; g, galea; hy, hypopharynx; l, lacinia; la, labrum; md, mandible; mxp, maxillary palpus; ps, ventral pseudopod; t, tentorial invagination.

Nearctic *Bibiocephala* belong to a single species, *B. grandis* Osten-Sacken, 1874, which is widespread in western North America (HOGUE 1982). The number of Asian species is uncertain, see under *B. komaensis* Kitakami, 1950. We studied abundant material of *B. maxima, B. infuscata, B. grandis* as well as some larvae of *B. komaensis*. We summarise our knowledge in keys, which replace formal descriptions of the previously unknown larva of *B. maxima.* Keys also contain supplementary details on adults and pupae. There are excellent figures of male genitalia of *B. grandis* (HOGUE 1982, reprinted 1987) and of *B. infuscata* (KITAKAMI 1937), but dististyle structure of *B. maxima* in the existing figure (BRODSKY 1954) is confusing. We draw and compare the closely related Asian species (Figs. 3, 4), mainly to facilitate a decision on possible synonymy between *B. komaensis* and *B. maxima,* should fresh Korean material become available.

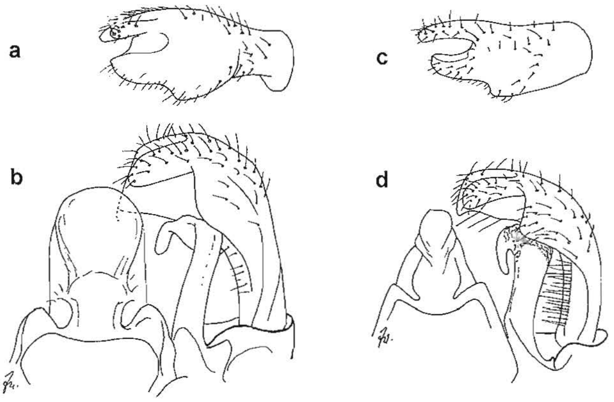

Fig. 3: *Bibiocephala infuscata* (a, b) and *B. maxima* (c, d). a, c, apical views of left dististyle; b, d, left dististyle and apex of tegmen in dorsal view. All to same scale.

4.1.1. Key to all known *Bibiocephala*-species

Adult males (*B. komaensis* (Kitakami) not known)

1 Hypopygium elongated, its anteroventral margin positioned much in front of anterior margin of tergite 9; anterior lobe of dististyle strongly spinose; inner dististyle with erect basal lobe on outside and simple band-shaped apex which is gently curved back; inner hypopygial sclerites partly rotated, penis filaments prolonged .... ***B. grandis*** Osten-Sacken

1' Hypopygium not elongated, anteroventral margin level with anterior margin of tergite 9; anterior lobe of dististyle finely pubescent; inner dististyle without basal lobe; inner hypopygial sclerites and penis filaments of normal length 2

2 Dististyle with massive apex, ventral lobe wide. In apical view, ventral lobe flat, much narrower than plump dorsal lobe; notch between lobes shallow, triangular (Figs. 3a, b). Apex of inner dististyle narrow, ribbon-like. Tegmen with broadly rounded spoon-shaped apex .... ***B. infuscata*** (Matsumura)

2' Dististyle slender, both lobes slender and narrow; in apical view, notch between them deeply U-shaped. Apex of inner dististyle narrow and pointed, semicircularly curved (Figs. 3c, d), surface before bend with curved rugosities. Apex of tegmen narrowed, tongue-shaped .... ***B. maxima*** Brodsky

Adult females (*B. komaensis* (Kitakami) not known)

1 Eyes almost meeting on vertex, ocelli on raised turret. Antenna shorter than head, beaded, flagellar segments two and following as long as wide, distal ones may be wider than long. Oviscapt ventrally with several large setae on bulging base, in addition to fine trichomes; laterodistal corners obtuse; paramedian tips with falcate sensilla barely visible in ventral view. Lobes covering dorsal side of oviscapt short, broadly divided, covered with stiff trichomes about as long as width of lobe (Fig. 4a). Seminal receptacles larger than oviscapt, basally gradually narrowed, coiled, eventually blending into long narrow duct .... ***B. grandis*** Osten-Sacken

1' Eyes widely separate on vertex, no ocellar turret. Antenna variable. Oviscapt without setae, only with fine trichomes; paramedian tips of oviscapt long, often partly visible in ventral view. Lobes covering dorsal side of oviscapt narrowly separated, stiff trichomes brush-like, much longer than width of lobe. Receptacles sharply set off against their short ducts (Figs. 4b, c) 2

2 Antenna longer than head plus rostrum, setiform, flagellar segments longer than wide. Laterodistal corners of oviscapt obtuse (Fig. 4c, d). Receptacles pyriform, about twice as long as oviscapt, surface of receptacles everywhere with fine pale punctures .... ***B. infuscata*** (Matsumura)

2' Antenna short, subuliform, basal flagellar segments wider than distal ones, only first flagellar segment longer than wide. Oviscapt with prominent laterodistal corners. Receptacles oval, about as long as oviscapt, (Fig. 4b) pale punctures only in basal half, distal half with fine dark trichomes inside .... ***B. maxima*** Brodsky

Pupae

1 Gills normal, the lamellae diverge only slightly; granula on pupal dorsum spinous .... ***B. grandis*** Osten-Sacken

1' Gill lamellae diverge strongly; pupal granula rounded 2

2 Gill lamellae spread out widely, slightly curled, suggesting a cabbage leaf. Wide margins of lamellae pale, covered with visible plastron .... ***B. infuscata*** (Matsumura)

2' Gill lamellae divergent but in regular alignment, one behind the other. Lamellae smooth, not curled, uniformly dark and shining, no plastron .... **B. maxima** Brodsky and **B. komaensis** (Kitakami)

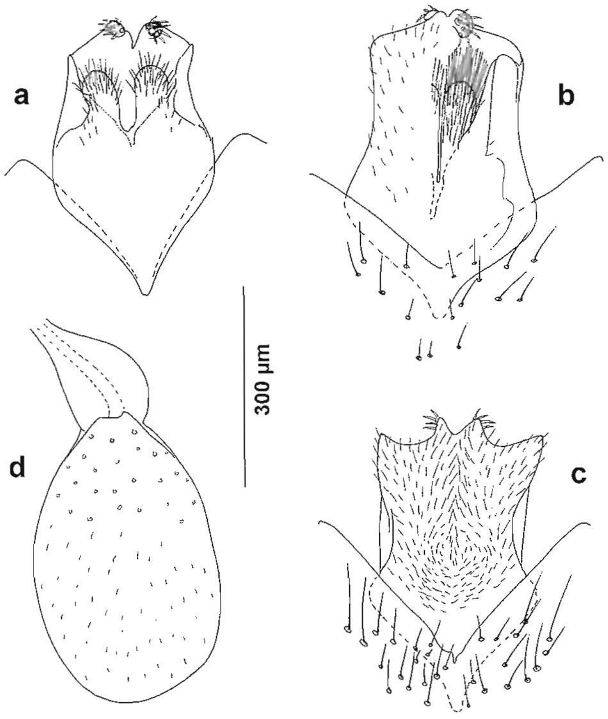

Fig. 4: *Bibiocephala* spp., oviscapts (a-c) and seminal receptacle (d), all to same scale. a, *B. grandis*, dorsal view of oviscapt; b, *B. infuscata*, combined ventral (left) and dorsal views (right) of oviscapt; c, d, *B. maxima*, ventral view of oviscapt and one of the two lateral receptacles.

Larvae (only last instar specimens with five to six gill filaments per tuft)

1 Six gill filaments per tuft; peristomal margin medially notched (labrum shorter than laterally adjacent areas; Fig. 2a); dorsal pseudopods slender and long, directed obliquely backward; ventral face laterally from suckers with heavy dark spine-like setae; dorsal face with flat sclerotized glossy calluses .... **B. grandis** Osten-Sacken

1' Five gill filaments per tuft; peristomal margin entire (Fig. 2b); dorsal pseudopods short, pointing sideways; ventral face laterally from suckers with short pilosity; dorsal face variable 2

2 Distinct sclerotized warts or calluses on dorsum; distal antennal segment little longer than basal one. Labrum with several long setae in addition to four normal setiform sensilla . **B. infuscata** (Matsumura) (*B. infuscata minor* Kitakami, 1931 is said to differ from *B. infuscata* by paler pigmentation and smaller size. *Bibiocephala jezoensis* (Matsumura), 1931, from Hokkaido was synonymized with *B. infuscata* (Zwick 1990). Largest species of genus).

2' No dorsal sclerotizations but sometimes low unsclerotized swellings present; labrum only with the normal four setiform sensilla; antenna variable 3

3 Distal antennal segment littler longer than basal one .... **B. maxima** Brodsky

3' Distal antennal segment almost twice as long as basal one .... **B. komaensis** (Kitakami)

4.1.2. *Bibiocephala maxima* Brodsky, 1954

(Figs. 1c, 3c, d, 4c, d, 5)

Bibiocephala maxima Brodsky, 1954 (BRODSKY 1954: 229)

Our specimens from the entire known range match the description of *B. maxima* Brodsky, 1954 and we did not study types. Unfortunately, BRODSKY (1954) compared *B. maxima* only with Nearctic *Bibiocephala. Bibiocephala maxima* occupies a vast range, from Kazakhstan and the Altai mountains to the Ayano-Mayski Region on the coast of the Sea of Okhotsk. Its southernmost Russian localities are not far from North Korea and Manchuria from where *B. komaensis* was recorded (see below). *Bibiocephala maxima* has clear to faintly tinged wings; despite its name it is smaller than *B. infuscata.*

Material (See Table 1; all in PZ). RFE03, 16 E; RFE06, 1♀, 49P, 6E; RFE08, Russian Far East, Primorje, Lazovka r. 25 km W of Lazo, at bridge, 13.06.1998: 1E; RFE09, 4E; RFE10, 2E; RFE14, 36P, 8E; RFE15, 3♂, 28P, 72E, 2L; RFE16, 4P, 2E; RFE21, 56♂, 3♀, 16 P, 31E; RFE27, 2♀; RFE28, 2♂, 1♀, 6E; RFE33, 2E; RFE35, 1♀, 1E; RFE38, 2E; RFE39, 2E; RFE40, 1♂; RFE41, 56♂, 3♀, 170P, 22E; RFE42, 8♂, 1♀; RFE47, 7♂, 14♀, 2P, 20E; RFE48, 2♂, 1♀, 6E; RFE49, 2P; RFE50, 48P, 2E, 1L4. Russian Far East: Ayano-Mayski Region, Aldoma R., 11/12.8.1999, M&T Tiunov, 2E. Khabarovsk Territory: Ochotsky Region, River Kuchtui, 10 km above mouth, 30.06.1999, 10.3°C, M.&T. Tiunov, 16♂, 1♀, 38P, 1L4.

Kazakhstan, surroundings of Ust Kamenogorsk [49°58'N, 82°36'E], V. Devyatkov (PZ): River Kurchum, 25.9.2002, 1 L3, 1L4; mouth of River Khamir (tributary of River Bukhtarma), 11.6.2003, 4♂, 1(♂).

Mongolia: Selenge, Khonin Nuga [49°05'260N, 107°17'440E], Eroo River, 21.VI.2003, P. Surenkhorloo, 1 pharate ♀, 8 pupal exuviae (PZ); Turgen-Gol [50°05'18"N, 91°37'50"E], 20.8.1997 and 17.8.1999, 8 L2, 22 L3, 4 L4, W. Horn & M. Paul, 27.8.1999 (SAWL); Tesiyn Gol [49°39'29"N, 95°43'47"E], W. Horn & M. Paul, 27.8.1999, 2 L3 (SAWL).

Larvae of *B. maxima* undergo considerable change during development. Second and 3rd instar specimens have six short dorsal spines on each abdominal segment, their arrangement is the same as the dorsal calluses in *B. infuscata*, or of spines in *Agathon* spp. Last instar larvae of *B. maxima* lack dorsal sclerotizations, but spatulate setae on the fore body become important. A few larvae collected in autumn looked very unfamiliar because they are freshly moulted, their gut still empty, and body not fully extended. In this condition, spatulate setae on head capsule and corners of prothorax stand close together and appear large, in comparison with the trunk; in places, the true body contour is veiled by setae (Figs. 5a, b). By spring, larvae accumulate much biomass whereby the body becomes extended, the head is pushed forward and downward; general shape is strikingly different from autumn specimens. Spatulate setae on fore body stand widely separate and appear tiny against extended body, remaining easily unnoticed. Figure 5c shows the single extended last instar larva not yet in prepupal condition that we have seen (Mongolian specimen); shape of its fore body resembles *B. infuscata*. In prepupae, corners of cephalic division are effaced, because of further body extension. Some Far Eastern last instar larvae look slightly variegated. They are light brown with anterior portions of several body divisions darker brown.

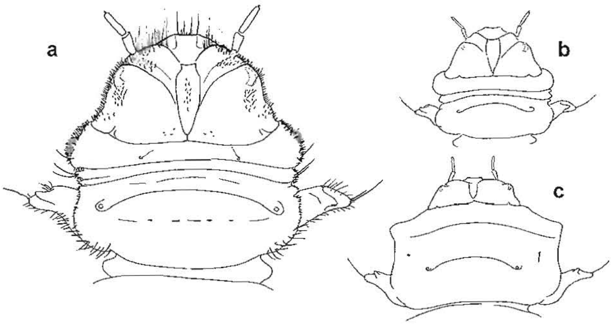

Fig. 5: *Bibiocephala maxima*, cephalic division of Mongolian last instar larvae. a, freshly moulted specimen showing arrangement of spatulate setae; b, same specimen, at same scale as specimen with extended fore body (c).

Biological notes. Larvae and pupae of *B. maxima* live on the underside of stones under which current rushes through and are never found on the upper side; the preferred larval habitat of *B. grandis* is similar (HOGUE 1982). *Bibiocephala maxima* emerges earlier than other net-winged midges in the Russian Far East. In early June, at several places, only fragments of pupal exuviae were left. Elsewhere there were many adults and pupae, but altogether only two prepupae were still found in June. The few earlier instars we saw were collected in autumn. Apparently the life cycle resembles *B. infuscata*, which hatches from eggs in autumn and overwinters in the 4th larval instar (KITAKAMI 1950). Hibernation of *B. maxima* larvae takes place under harsh environmental conditions. For example, winter temperatures are below -30°C near the Mongolian Turgen Gol, and a gauging station 25 km upstream from the sample site records no measurable discharge between December and March. The river bottom consists of coarse gravel with large near-surface interstitial spaces that may have contained flowing water also in winter (M. PAUL, pers. comm.).

HOGUE (1982) suggested that *B. grandis* might overwinter as eggs or very small larvae. However, the species probably has the same life cycle as the Asian congeners because large numbers of inactive, closely aggregated last instar larvae but no other life stage were collected immediately after snowmelt, in May, in the lower St. Vrain River, Colorado, and in several streams near Provo, Utah (P. Zwick). Indeed, 4th instar larvae were collected through the winter in Oregon, and even beneath winter ice in the Canadian Rockies (G.W. COURTNEY, pers. comm.).

Adult males resting in vegetation did not hang down from it like most other Blephariceridae. They often sat on grass stems, head up, grasping the support with all six legs. Because of the long hind legs, the body strongly diverged from the grass stem. Large swarms of only males were observed at Malinovka River with binoculars, in the morning and in the afternoon. Swarms were over land, 3-6 m above ground, above or on the sunny side of riparian willow bushes (*Salix* sp.). Specimens kept distances of 40-90 cm between each other, flying quietly in a floating manner. The front legs were held obliquely up and back between the wings, over the thorax, with the tarsal tips curved forward; short middle and very long hind legs hung down. Males that came close or other insects flying into the swarm, for example a fly (Calliphoridae), were rapidly approached from below by some swarm member and chased away.

At evening dusk, numerous males were noticed flying over swiftly and smoothly flowing sections of the upper Nemtu River. They flew upstream for short distances, then dropped back again. Various pale insects emerging from the river, mainly small Ephemeroptera and Plecoptera: Chloroperlidae were well visible under the low light conditions. Many of them suddenly changed direction of flight, or dropped abruptly. When caught with a net, the pale insect had each time been seized by a fully pigmented male *Bibiocephala*. In two cases, however, the pale specimen was a freshly emerged *Bibiocephala* female. It appears that males emerge before females and catch these for copula, upon evening emergence. Where and for how long females live is unknown. We saw only few females, either at emergence, or spent and dying between stones on the shore of River Khor, below Sukpai.

Distribution. *Bibiocephala maxima* was first described from the Altai. It occurs even further west, near Ust-Kamenogorsk. It is also widespread and common in the Russian Far East. The new Mongolian records fit in well. ZASYPKINA & RYABUKHIN (2001) report unidentified larvae of *Bibiocephala* from further northeast than the area sampled by us.

4.1.3. *Bibiocephala komaensis* (Kitakami, 1950)

Amika komaensis Kitakami, 1950 (KITAKAMI 1950: 41).

Material. *B. komaensis*: 1 last instar larva, Korea, Ryeongha, Hamgyeongbuk-do (= Reika, N. Korea), 12.6.1936, leg. Kawamura. In the same vial are also 1L2, 1L3, Hakugan, N. Korea, 6.9.1940, leg. Kitakami (ZFMK); all three specimens are syntypes. 1 specimen of each larval instar, syntypes (no locality data; USNM).

We were unable to borrow a larval syntype (Reika, N. Korea, leg. Kawamura 13.VI.1936) kept in Otsu Hydrobiological Station of Kyoto University (K. N. SATAKE 1988, pers. comm.). These few larvae seem to be all of the still remaining syntypes; we designate no lectotype.

In the very old material we cannot assess slight differences in body surface colour and gills between *B. infuscata* and *B. komaensis* which Kitakami mentioned. In the last instar, the long distal antennal segment distinguishes *B. komaensis* from *B. infuscata* (KITAKAMI 1950), and also from *B. maxima*. Details of the mouth region agree with *B. maxima*, and differ from *B. infuscata*. Pupal exuviae of *B. komaensis* agree with *B. maxima*, by Kitakami's description; material is not available. Larval instars 2 and 3 lack dorsal spines, which are present in *B. maxima*; however, we saw few specimens.

Whether *B. komaensis* is really distinct from *B. maxima* cannot be decided in the absence of pupae and especially of adults of *B. komaensis*. The case of the two nominal species might resemble the species pairs *Agathon eoasiaticus* – *A. kawamurai*, *Philorus levanidovae* – *P. chosenensis,* and *Blepharicera parva* – *B. yamasakii*, see below.

4.2. Genus *Agathon* von Röder, 1890

Agathon von Röder, 1890. Type species: *Agathon elegantulus* von Röder, 1890: l.c.: 232 (VON RÖDER 1890: 230).

Apomorphies supporting the monophyly of *Agathon* are found in the male genitalia: long widely separate male cerci connected only by a transverse basal bar (e.g., Fig. 6a). Mostly, cerci are slender straight rods although there is some variation in detail. For example, in *A. elegantulus* cerci are curved mediad and apically narrowed (see figures in HOGUE 1973, 1987). In *A. setosus* sp. n. and *A. aylmeri* (Garrett, 1923) (Nearctic) their slightly enlarged apices are gently turned ventrad, etc. Vesica with transverse apodeme, not a vertical one, as normal.

Agathon was in the past confused with *Bibiocephala* because a remnant of wing vein R_2 is retained in some species; it lacks in others. However, aberrant specimens occur in either group; they have a remnant of R_2 in one wing only.

All Asian species are closely related and similar to the Nearctic type species. Outer dististyle bifid, shorter dorsal branch arises basally and may end before, or extend over, subapical modifications on dorsal face of ventral branch. In *A. elegantulus* and almost all other species a subterminal process or fold extends variably far across ventral branch so that a pocket or depression is formed between fold and apex proper (Figs. 7c, d, 9c, d, g). Inner dististyle very wide, a largely membraneous foliaceous structure (Figs 6a, 9h).

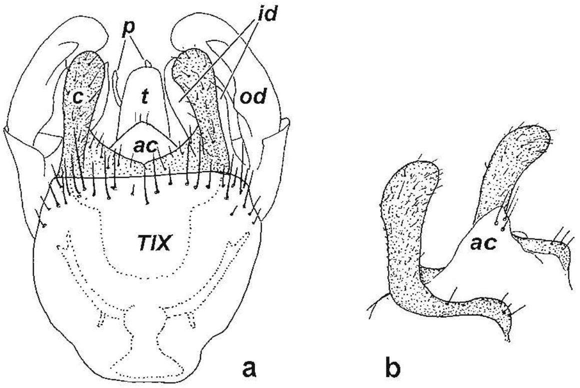

Fig. 6: *Agathon setosus* sp. n. a, male genitalia in dorsal view; b, cerci and anal cone in oblique posterior view from left side, to show connection of cerci to sclerites supporting anal pouch. ac, anal cone; c, cercus; TIX, tergite 9; p, paramere tips; t, tegmen; id, inner dististyle; od, outer dististyle.

The above diagnosis does not apply to *A. comstocki* (Kellogg, 1903) and *A. doanei* (Kellogg, 1900) whose relationship remains doubtful. The genus *Agathon* requires further study; its relations with *Asioreas* Brodsky in the Altai and Himalaya will be discussed separately (ZWICK, in preparation).

Each lobe of the female oviscapt bears distally a broad spinuliferous dorsal callus (not narrow and finger-shaped like in *Bibiocephala*). Three spheroid to pyriform receptacles, basal half with tiny puncture-like pale spots, are sharply set off against short straight ducts. As usual, the median receptacle is more slender than the lateral ones.

We name a new species, raising the number of Russian species to four, all of which are found also in the Far East. The Russian species have closely similar relatives in Korea and Japan, respectively (KITAKAMI 1931, 1950) with which they were previously never compared. We have carefully compared these species and considered the Russian taxa are valid.

Several large samples contained also first instar larvae, which by their association with later instars, can preliminarily be assigned to *A. decorilarva* and *A. eoasiaticus*, respectively. We noticed no specific differences and none to distinguish them from first instar larvae of *Bibiocephala*.

4.2.1. Keys to *Agathon* species known or expected from the Russian Far East

Adult males (Keys to females not attempted)

1 Dististyle almost entire, dorsal lobe appears only as a subapical tooth (Fig. 6a) .... ***A. setosus*** sp. n.
1' Dististyle deeply divided into dorsal and ventral lobes, ventral one longer 2
2 Dorsal lobe extends to or over subterminal tooth or crest on ventral lobe of slender dististyle 3
2' Dorsal lobe of dististyle short, strong transverse crest across ventral lobe exposed. Ventral lobe apically very wide, transversely truncate (Fig. 9g) .... ***A. ezoensis*** (Kitakami)
3 Ventral lobe of dististyle dorsally with subapical tooth (Fig. 7c) .... ***A. decorilarva*** Brodsky
3' A subapical crest extends across dorsal face of ventral lobe of dististyle (Fig. 9c) .... ***A. eoasiaticus*** Brodsky, ***A. kawamurai*** (Kitakami)

Pupae

1 Outer respiratory lamellae rounded with narrow base (racket-shaped), respiratory organs prostrate (Figs. 11a-c) .... ***A. setosus*** sp. n.
1' Respiratory organs erect, lamellae slender, tongue-shaped 2
2 Anterior end of pupa in dorsal view regularly truncate to rounded, cephalic sclerite not recessed between lateral lobes of pronotum .... ***A. decorilarva*** Brodsky
2' Anterior end of pupa in dorsal view with cephalic sclerite recessed between anteriorly projecting lateral lobes of pronotum .... ***A. eoasiaticus*** Brodsky, ***A. ezoensis*** (Kitakami), ***A. kawamurai*** (Kitakami)

Larvae (final instar)

1 No spines or pointed granules on dorsum, only long soft setae on sides of body present (Fig. 8d) .... ***A. setosus*** sp. n.
1' Larval dorsum with pointed granules or long spines 2
2 Six long erect spines on each abdominal segment (Fig. 8a) .... ***A. decorilarva*** Brodsky
2' Dorsal armature consists of pointed granules not or hardly higher than width at base, and/or transverse rows of erect spinules 3
3 Six well developed granules or short spines per abdominal segment (Fig. 8b); no rows of spinules. Thorax with single short spinule row immediately behind cephalic sclerites. Dorsal pseudopods with blunt dorsal knee .... ***A. eoasiaticus*** Brodsky
3' Abdominal segments with two spinule rows, among which dorsal warts may or may not be distinct (Fig. 8c). Thorax with more spinule rows 4
4 Three thoracic spinule rows (N. Korea) .... ***A. kawamurai*** (Kitakami)
4' Two thoracic spinule rows (Hokkaido, Sakhalin, Iturup I.) .... ***A. ezoensis*** (Kitakami)

4.2.2. *Agathon decorilarva* (Brodsky, 1954) (Figs. 7, 8a)

Bibiocephala decorilarva Brodsky, 1954 (BRODSKY 1954: 236).

Material. *Agathon decorilarva* was described from syntypes from: "Altaj: r. Yan-Tsili; r. Korbu; r. Kokschi; r. Bolschoj Korbu; r. Abakan; S. Primorje: r. Sitsa; Pigarejeva gorge in St. Tigrovaja; Sutsan, r. Kamen; r. Kuatru, Kuretski Mts". We studied some larval syntypes (ZIAS) labelled: *Bibiocephala decorilarva* sp. n. det. K. Brodskii // [illegible abbreviation] 64 [illegible abbreviation] 78.

The species is common and widespread in rhithral streams in the Russian Far East, see also ZASYPKINA & RYABUKHIN (2001). Material from localities in Table 1 (all in PZ): RFE04, 1P; RFE06, 7P, 7L4; RFE07, 57P, 11L4; RFE08, 21P, 2L4; RFE09, 1P; RFE12, 6E, 23L4, 28L3; RFE13, 55L4; RFE14, 17P, 22L4, 1L3; RFE15, 17P, 23L4, 1L3; RFE16, 1L4; RFE17, 2♂, 1♀, 131P, 59E, 8L4 ; RFE18, 8P; RFE19, 50P; RFE20, 41P, 10E, 2L4; RFE21, 60P, 1L4; RFE22, 1♂, 10P, 10L4; RFE25, 1♂, 1P, 14L4; RFE26, 6P, 5E, 1L4; RFE27, 1♂, 50P, 6E, 23L4; RFE28, 3♂, 1♀; RFE28, 52P, 18E, 1L4; RFE33, 18P, 4E, 1L4; RFE34, 1P; RFE36, 16P, 10L4, 1L3; RFE37, 21P, 3E, 2L4; RFE38, 1P; RFE41, 4♂, 80P, 65L4; RFE42, ca. 20P, 4L4; RFE43, 1P, 5L4; RFE44, 64L4; RFE45, 1L4, 11L3, 118L2, 1L1; RFE46, 41L4, 24L3; RFE49, 18P, 52L4, 10L3; RFE49a, 10L4, 5L3; RFE50, 2P, 8L4, 2L3.

Additional material from the Russian Far East (PZ): Amur River Basin, I.M. Levanidova: Ali River, 23.07.1959, 10L, 8P; Iski River, 02.07.1961, 4L. Magadan Territory, Makarchenko: Dukcha River, 7, 9.7.1979, 99L; 23.07.1979, 8L; Motyklejka River [Motyklejka 59°34'N, 148°38'E], 13,14.7.1977, 17L; Ulakan River, 17.07.1977, 6P, 2L. Ayano-Mayski Region [Ayan 56°27'N, 138°10'E], M&T Tiunov: Uika River 1 km upstream of mouth, 21.-26.7.1999, 11L4, 14-15.8.1999, 9P; Ulujkan River, Lantar River basin, 29.07.1999, 19P, 8L4, 1L3; Aldoma River, 11/12.8.1999, 12♂, 8♀, 22P; Lantar River, 2.5 km upstream from mouth, 28.07.1999, 2♂, 1♀, 28P, 2L4.

Kamchatka, I.M. Levanidova (PZ): Kirpichnaya River, 18.7.1968, 11P, 4E; River Ewpitwajam (Lake Palanskoje), 18.8.1963, 6P, 9E; nameless stream near village Zhupanova, 20.07.1964, 1L; Talalayevka River, 04.08.1972, Nikolayeva, 1L.

Descriptive notes. BRODSKY (1954) described all stages and both sexes. He compared *A. decorilarva* with three Japanese species, *A. japonicus* (Alexander, 1922), *A. montana* (Kitakami, 1931), and *A. bispina* (Kitakami, 1931), none of which is really similar. We establish distinctness of *A. decorilarva* from several much more similar Japanese species that were not considered by BRODSKY (1954).

Adult. R_2 present. Spur formula 0.0.2 in both sexes. Spurs on hind tibia very unequal in size.

Male (Figs. 7a, c, d): Eyes widely separate, upper section little developed. Rostrum shorter than head height. Antenna short, with 14 segments, terminal one not longer than penultimate and only slightly constricted. Genitalia slender, outer dististyle with narrow apex and incurved tip; subterminal fold short, almost tooth-like. Dorsal branch of dististyle curved, extends to close to subterminal fold.

Female (Figs. 7b, e): Eyes large, narrowly separate, upper section fully developed. Antenna even shorter than in male, barely reaching tip of rostrum. Rostrum only as long as head height but fully developed. Oviscapt with slightly concave sides and tongue-shaped distal lobes; spermathecae subspherical to ovoid.

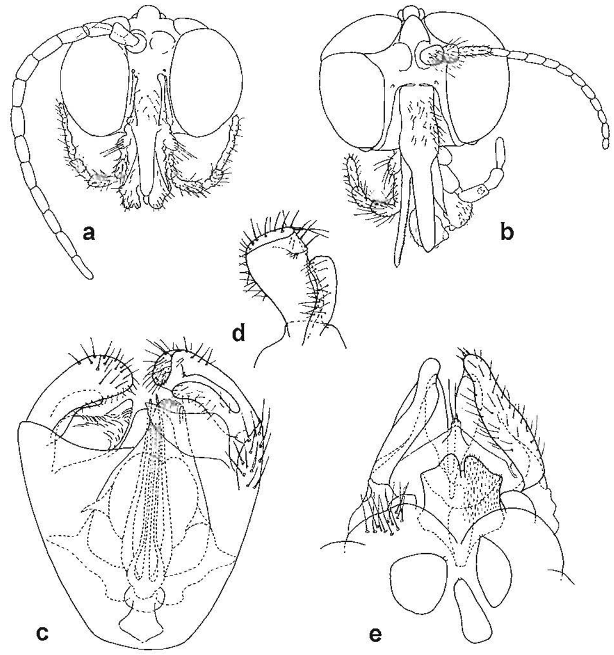

Fig. 7: *Agathon decorilarva*. a, b, head of pharate male and female , respectively; c, male hypopygium (tergite 9 and cerci removed); d, oblique dorsal view of left outer dististyle; e, female terminalia. Not to scale.

Pupa. Typical of genus, zig-zag pattern across thorax. Very similar to *A. eoasiaticus* (see BRODSKY 1954: figs. 4/6+7), respiratory lamellae less than twice as long as wide at base, lamellae set in an oblique row so that opposite first lamellae are wide apart while lamellae 4 are closer together, their slightly recurved tips meet, or almost so. Bases of lamellae on the outside terminating in integument as simple straight lines. The endpoints of the four lamellae lie on a slightly convex line because lamellae 2 and 3 project slightly further sideways than lamellae 1 and 2. Cephalic sclerite not distinctly recessed between fore leg sheaths.

Larva. Long erect spines, anterior ones longer and closer together than posterior ones (Fig. 8a). Lateral ones on segment seven smaller, about half the length of dorsal ones. Integument very variably contrastingly patterned, from mainly yellow to mainly dark. Also spines (all or only some) dark or yellow. Head capsule variably patterned in yellow and dark, often an extended pale center near anterior end of median frontal sclerite, lateral frontal sclerites with distinct yellow eye-brow-like mark above oblique suture. However, head capsule may also be almost completely black. Ventral pseudopods slender, with narrow recurved apex, posterior margin distinctly concave. Dorsal pseudopods slender, with erect narrow pointed subterminal outgrowth on narrow tip of pseudopod.

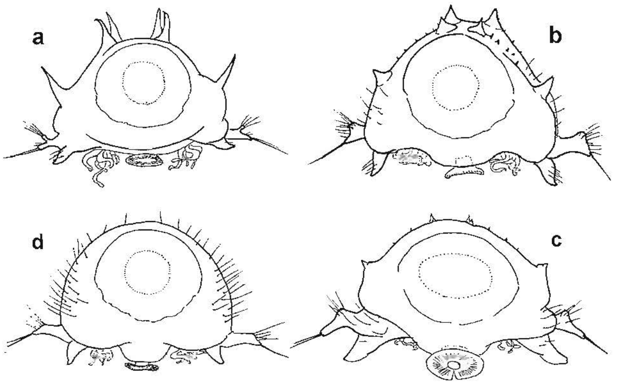

Fig. 8: *Agathon* ssp., cross-sections through larvae, 3rd abdominal segment from behind, diagrammatic. a, *A. decorilarva*; b, *A. eoasiaticus*; c, *A. ezoensis*; d, *A. setosus*. Not to scale.

Comparisons. *Agathon decorilarva* is a close relative of (but certainly distinct from) two Japanese species whose larvae also have long erect spines and sharply angled dorsal pseudopods. *Agathon bilobatoides* (Kitakami, 1931) has only the four central spines large. It also possesses additional transverse rows of abdominal thornlets, also three rows on the thorax. The subterminal fold on the male dististyle is long, standing in an oblique position. The pupal gill lamellae are closely packed, all semicircularly curved towards middle, with tips of opposite organs meeting. *Agathon longispinus* (Kitakami, 1931) has the median spines on the larval abdominal segments 2 and 3 connected by a transverse bar-like socket, and lateral spines on segment 7 are tiny, much shorter than on the other segments. Pupal lamellae more slender than in *A. decorilarva* (>3 times longer than wide at base), divergent, from 1st to 4th successively more curved and directed medially, tips of 4th lamellae meeting. Male with long antenna (reminding one of *A. eoasiaticus*), dorsal branch of male dististyle short, with strongly widened apex.

In the Russian Far East, *A. decorilarva* and *A. eoasiaticus* often coexist; pupae can be distinguished by the relative length of the cephalic sclerite versus leg sheaths. This character can no longer be assessed in pupal exuviae which can, however, be identified by the shape and position of the outer endpoints of the four respiratory lamellae.

4.2.3. *Agathon eoasiaticus* (Brodsky, 1954)
(Figs. 2c, 8b, 9)

Bibiocephala eoasiatica Brodsky, 1954 (BRODSKY 1954: 234).

Material. We identified the species from the description and saw no types. We did not find the species at the type locality ("St. Tigrovaja, tributary of r. Sitsa; Pigarejeva gorge") but Stations RFE01 and RFE03 are close to it: RFE01, 11.06.1998, 330L4, 25L3; 26.06.1998, 3 ♂, 322P, 15E, 79L4, 12L3; RFE09, 1L4, 1L3; RFE10a, 7P, 5E; RFE12, 1L4, 2L3; RFE15, 1♂, 3♀, 1P, 4E; RFE19, 3P, 3E; RFE20, 4P, 1E; RFE21, 1L2; RFE22, 3♂, 2♀, 225P, 9E, 20L4; RFE24, 1♀, 1P, 2E; RFE25, 2♀, 2E; RFE27, 3♀, 1P, 2E; RFE28, 1P; RFE31, 10♂, 3♀, 129P, 14E, 8L4; RFE33, 1♀, 1P, 3E; RFE34, 4♂, 1♀, 134P, 20E, 5L4; RFE36, 28P, 23E; RFE37, 6P, 12E, 1L2, 1L1; RFE41, 5♂, 3♀, 2P, 94P, 7E, 22L4; RFE42, 22P, 5L4; RFE44, 38L4; RFE49, 92P, 27L4; RFE49a, 1P, 15L4; RFE54, 12P, 8E; RFE55, 9♀,1E, 1L4 (all in PZ).

Mongolia, Selenge, Mandal, leg. P. Surenkhorloo (PZ): Khonin Nuga [49°05'260N, 107°17'440E], Tsagaan Chubut River, 30.VI.2003, numerous L3, L4, 8 P. Bar-Chuluut River [48°58'638N, 106°57'013E], 13.VII.2003, 6P (incl. 3♂). Bar-Chuluut River [48°58'368N, 106°59'564E], 4.VIII.2003, 2♂, 2♀. Eroo River near confluence with small tributary [49°05'260N, 107°17'440E], 01.VII.2003, 2 L4. Ataa River, 18.VII.2003, 56P (incl. pharate ♂♂), 3Ex, 3L4, 1L3 (all in PZ).

Adult. Previously unknown. R_2 present. Spur formula 0.2.2 (females) and 0.0.2 (males). Spurs on hind tibia unequal in size, those on female middle leg minute, not easily seen.

Male (Figs. 9a, c, d): Antenna more than twice as long as head with rostrum, individual flagellar segments long, last one strongly bottle shaped. Genitalia compact, hypopygium rounded. Distal edge of dorsal dististyle wider than in *A. decorilarva*, truncate, prominent subterminal fold across ¾ of dististyle width. Fold hidden by longer, slightly club-shaped dorsal branch of dististyle.

Female (Figs. 9b, e): Very similar to *A. decorilarva*, rostrum and antenna slightly longer. Oviscapt appears slightly more elongate but is not distinctive. Receptacles subspherical to ovoid.

Pupa. Resembles *A. decorilarva*, but cephalic sclerite distinctly recessed between leg sheaths. Bases of lamellae terminating in integument as simple straight lines. On outside, endpoints of lamellae 2-4 lie in straight line while lamella 1 projects distinctly further sideways and ends in small backwardly turned hook.

Larva. Short brown or yellow spines on pale sockets (Fig. 8b), or only distinct cones on abdominal segments, sometimes two or three small cones together instead of spine. Anterior spines or cones higher and more widely apart than posterior ones. Integument greyish, not contrastingly patterned. Head capsule with pale center near lower end of median frontal sclerite, remainder amber to dark brown; oblique suture across lateral frontal sclerites sometimes apparent as pale narrow line. Thornlets in transverse rows, tiny, but of variable expression; all abdominal and three thoracic rows may be present. Dorsal pseudopod plump, with obtuse rectangular knee instead of a dorsal process.

Comparisons. *Agathon eoasiaticus*, the Korean *A. kawamurai* (Kitakami, 1950), and the Japanese *A. ezoensis* (Kitakami, 1950) and *A. bispinus* (Kitakami, 1931) are similar. The last is from Honshu and not available to us; only larvae and pupae were described.

Male genitalia of *A. ezoensis* are distinct (see below) but those of *A. kawamurai* are not. Females (all with large upper portions of eyes, with large reddish ommatidia) and pupae are so similar that in view of the limited material available of the Japanese and Korean species, we attempt no distinction.

Larvae can be distinguished by the dorsal armature of thornlets and spiny warts. KITAKAMI (1950) used presence/absence and number of transverse rows of thornlets on thoracic and abdominal segments and the relative size of six dorsal warts to distinguish the taxa. In *A. eoasiaticus,* the six dorsal warts are all larger than the thornlets, the anteromedian pair being largest. In the other species (Fig. 8c; *A. ezoensis*), at best the lateral warts are distinct while the dorsal ones are effaced and barely larger than spinules in the transverse rows. However, *A. eoasiaticus* varies, both within and between samples. There may be 0-3 rows of thornlets on the thorax, and none, indistinct, or two distinct rows on the abdomen. The main warts may be prominent and stand by themselves, or be less distinct from adjacent thornlets. Warts may have several points each, or essentially consist of a closely set group of thornlets. The distinction of larvae remains therefore provisional until more material of the relatives of *A. eoasiaticus* becomes available.

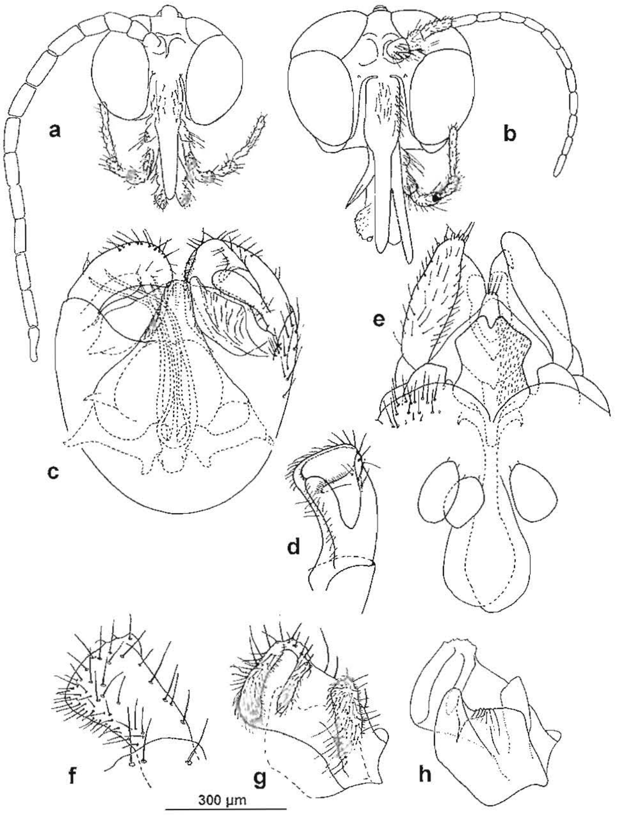

Fig. 9: *Agathon eoasiaticus*. a, b, head of pharate male and female, respectively; c, male hypopygium (tergite 9 and cerci removed); d, dorsal view of left outer dististyle; e, female terminalia. *A. ezoensis*. f, g, left outer dististyle in ventral and dorsal views; h, same as g, inner dististyle added. Not to scale.

4.2.4. *Agathon kawamurai* (Kitakami, 1950)

Bibiocephala kawamurai kawamurai Kitakami, 1950 (KITAKAMI 1950: 44).

Material. *Bibiocephala kawamurai kawamurai* Kit., 1♂ (lectotype, here designated), 1♀, 2P (genitalia of pharate ♂ on slide), 2L4 (paralectotypes, here designated), Korea, Baekam, Hamgyeongbuk-do (= "N. Korea, Hakugan"), 23.VII.1939 (ZFMK); additional paralectotypes; 1♂, 1♀, 2P, 2L4 (one lacking cephalic division) (USNM).

Taxonomy. KITAKAMI (1950) suggested "perhaps we can expect this species in Manchuria". Male genitalia do not differ from *A. eoasiaticus*. The nominal taxa may nevertheless be distinct because the rostrum of *A. kawamurai* attains not even head height. *Agathon eoasiaticus* (Fig. 9a) has also longer antennae than *A. kawamurai*. Larvae of *A. kawamurai* have the full set of transverse rows of prominent thornlets among which dorsal warts are indistinct. However, larval armature of *A. eoasiaticus* is variable. The variation of the widespread *A. eoasiaticus* may eventually be found to encompass the structural variants presently distinguished as *A. kawamurai*, which would become the valid name.

Comments. KITAKAMI (1950) made no distinction between specimens known to him, which therefore are all equal syntypes. Consequently, the specimens in USNM must have type status, even though their precise collection data are unknown. We have not seen syntypes from Ryeongha, Hamgyeongbuk-do (= Reika) in North Korea in Otsu Hydrobiological Station: 2L3, 2L2, 12.VI.1936 (Kawamura) and 1♂, 1♀, 2P, 2L4, 22.VII.1939 (Kitakami).

4.2.5. *Agathon ezoensis* (Kitakami, 1950) (Figs. 9f-h)

Bibiocephala kawamurai ezoensis Kitakami, 1950 (KITAKAMI 1950: 46).

Material. *Bibiocephala kawamurai ezoensis* Kit., 1♂ (lectotype, here designated) 2P (paralectotypes) [Takinozawa, S. Saghalien, 20.VII.1936]; 2L4 (paralectotypes) [Sôunkyo, Hokkaido, 25.VII.1936] (ZFMK). Additional paralectotypes without locality data: 1♂, 1P, 2L4 (USNM).

Additional material (PZ): Kuriles, Southeastern Iturup Isl.: Usach waterfall, 29.07.1998, T. Arefina & V. Teslenko, 1♀, 10P, 6L4, 1L3; unnamed stream with waterfall nr Usach waterfall, 29.7.1998, T. Arefina, 4♂, 1♀, 3P.

Very similar to *A. eoasiaticus* but R_2 normally absent. However one of the males in USNM and also one from Iturup Island have a remnant of R_2 in one wing.

Male genitalia (Figs. 9f-h) distinguished by outer dististyles with very wide apex and a short dorsal branch not closely appressed to larger ventral branch. Subterminal transverse fold across ventral branch of dististyle long, prominent, and exposed. Its caudal edge curves mediad and connects to apical edge, the curved connection projecting distinctly beyond general contour of dististyle. Inner dististyle wide, medial part distinctly elongated and projecting.

Presently females not separable from *A. eoasiaticus* by external characters because lack of R_2 in *A. ezoensis* is no reliable difference. Receptacles not examined. For pupae and larvae (Fig. 8c), see under *A. eoasiaticus*.

Remarks. Like *A. kawamurai*, this taxon was named from many syntypes from several localities in Hokkaido and on Sakhalin, between which no distinction was made in the description; therefore, the specimens in USNM are syntypes even though locality data are missing. The locality information for the specimens in ZFMK (in square brackets) is from the list that accompanies KITAKAMI'S material in coll. MANNHEIMS.

4.2.6. *Agathon setosus* sp. n. (Figs. 6, 10, 11)

Material. Russian Far East: Holotype (pharate ♂), paratypes (6 pharate ♂, 2 pharate ♀, 9P), [2773] Primorje, Sikhote-Alin, Edinka River, 10.08.1979, leg. Timoshkin. (Presently in PZ, will eventually be deposited in a museum).

Additional material: Primorje, Sikhote-Alin, Ada River, Bikin River basin, 22.07.1979, 4L, leg. Timoshkin. – Magadanskaya obl., Talok Stream at Susuman Town, Kolyma River basin, leg. Samokhvalov, 10.4.1982, 17 L; Khabarovskii krai, Basilii Stream, Tumnin River basin, 16.7.1997, leg. Tiunov, 1L. Mongolia, Selenge, [49°05'260N, 107°17'440E], Eroo River near confluence with small tributary, 01.VII.2003, P. Surenkhorloo, 5P, 8L4 (including prepupae) (all in PZ).

Adult. Adults apparently similar to previous species in size, venation, and colour; details unknown because only pharate specimens are available. Spur formula 0.0.1 in both sexes, both with small, widely separate eyes (Figs. 10a, b). Upper eye portion distinct but only small part of total eye area and not larger-facetted than lower part. Female with, male without functional mandibles and serrate hypopharynx. Antenna and palpus slender, much like *A. eoasiaticus*.

Male genitalia (Fig. 10c): Widely separate, long and slender cercus (Fig. 6) distally slightly enlarged and gently curved ventrad. Outer dististyle slender and narrow, with faint mediobasal swelling. Dorsal branch fused to ventral one over most of length, free tip resembles subapical tooth on ventral branch. Apex of ventral branch appearing simple because transverse fold practically apical, vertical fold separating it from ventral face visible only in apical view. Inner dististyle slender, more sclerotized and narrower than in relatives.

Female genitalia (Fig. 10d) similar to other species, oviscapt appears shorter and stouter. Seminal receptacles distinctly pyriform.

Pupa (Fig. 11). General shape normal except respiratory organs prostrate, less raised than in majority of species, extending distinctly further forward than long sheaths of fore legs which include wide straight front margin of cephalic sclerite between them. Outer lamellae racket-shaped, base narrower than distal part, stiff and shiny, distinctly wider than soft medial lamellae. Mesonotum with strong zig-zag folds. Dorsal granulation of metathorax and abdomen strong in middle, increasingly finer towards sides, lateral granules only 1/4 size of middorsal ones.

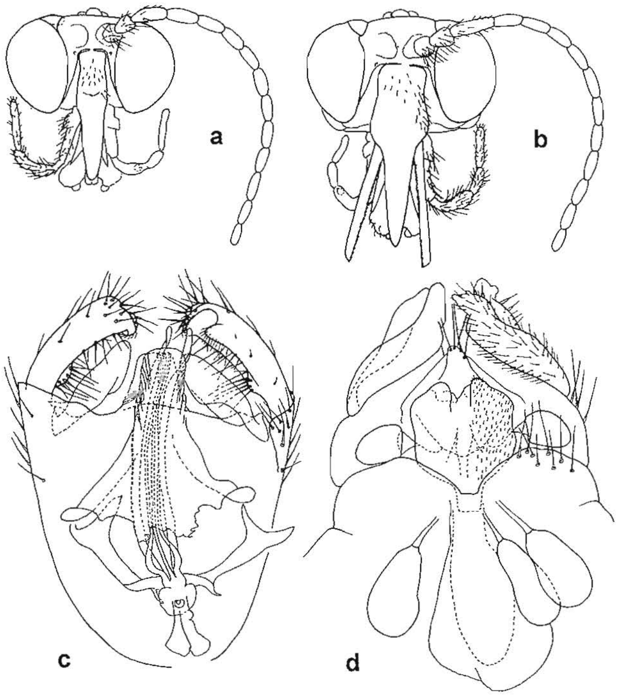

Fig. 10: *Agathon setosus* sp. n. a, b, head of pharate male and female respectively; c, male hypopygium (tergite 9 and cerci removed); d, female terminalia. Not to scale.

Larva. General shape resembles relatives. Cephalic sclerites amber, triangle above mandibles black, brown seams along anterior tentorial invaginations and along outer edges of medial and lateral frontal sclerites. Medial frontal sclerites additionally with faint traces of two usual brown longitudinal lines. Antenna 3-segmented. Body naked except long flexible setae arising from distinct insertion points, mainly on posterior segment halves. Ventral pseudopods simple, dorsal ones almost simple, only faint angle in dorsal contour (Fig. 8d).

Comparisons. The male genitalia are exceptional because the dorsal branch of the dististyle is not a freely projecting finger. Apex of outer dististyle and relatively narrow inner dististyle also unique. Pupa distinctive through its prostrate respiratory organs with stiff rounded outer lamellae much wider than median ones. Larva unusual in having long slender erect fine setae, instead of the usual cones, spines or stout thornlets. At first glance, larva appears naked and insofar resembles *A. montanus* (Kitakami, 1931) from Japan which, however, has prominently angled pseudopods. In particular, its exposed pseudopod 7 is so positioned that it resembles a backwardly bent knee. In contrast, pseudopods of A. setosus are almost simple.

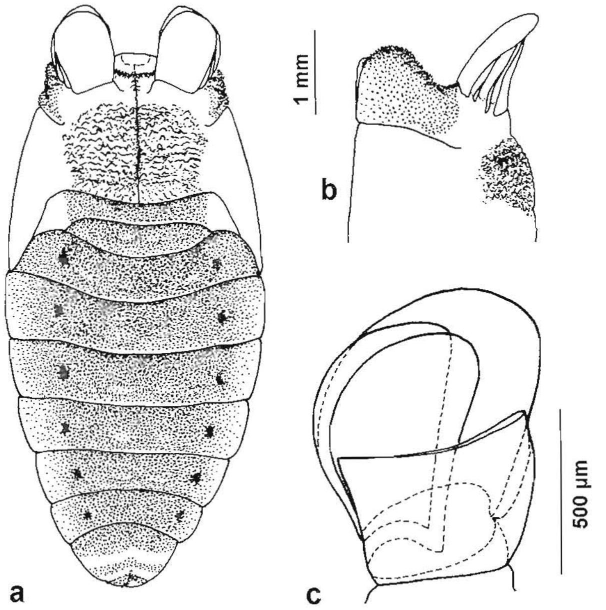

Fig. 11: *Agathon setosus* sp. n. a, pupa in dorsal view; b, front end seen from left side; c, left respiratory organ, lamella 4 partly cut to expose lamellae two and 3. Figures a and b to same scale.

4.3. Genus *Philorus* Kellogg, 1903

Philorus Kellogg, 1903 (KELLOGG 1903: 199). Type species: *Blepharocera yosemite* (Osten-Sacken, 1877), by subsequent designation of Coquillett, 1910 (COQUILLETT 1910: 588).

The phylogenetic relations of *Philorus* among Blephariceridni are doubtful because the genus still shares presumably primitive characters with *Bibiocephala* and *Agathon*; see under *Bibiocephala*. At the same time, the radial vein is more reduced (two short branches on a long stalk, instead of long independent branches) than in other Blephariceridni, supporting monophyly of genus *Philorus*. The pupal respiratory organ of four low, widely divergent lamellae is another obvious apomorphy.

The genus comprises almost 25 species from mainland Asia (south to Assam and west to Tian Shan), Japan, and western North America. Grouping of included species is not yet generally clear. However, the new Russian species clearly belongs to a monophyletic group distinguished by: lateral digitiform appendages on male tergite 9; male with extremely short ventral bridge from which the bag-like, uncrested vesica extends freely forward; pupal respiratory organs medially touching, lamellae very low, crest-like, divergent.

The name *Euliponeura* Tonnoir, 1930 would be available for this group which comprises *P. asiaticus* Brodsky, 1972, *P. assamensis* (Tonnoir, 1930), *P. chosenensis* Kitakami, 1931, *P. horai* (Tonnoir, 1930), *P. longirostris* Kitakami, 1931, *P. minor* Kitakami, 1931; not all of the three characters listed above are known for each included species. Recognising *Euliponeura* would turn the genus *Philorus* paraphyletic because the last two apomorphic characters in the above list are shared by *P. vividis* Kitakami, 1931 (ZWICK, 1997a). A complete phylogenetic analysis of the genus must be performed before any formal change of taxonomic status of included groups.

4.3.1. *Philorus levanidovae* sp. n. (Figs. 12, 13)

Material: Holotype pharate ♂, paratypes 1 pharate ♂, 2 pharate ♀, 4♂, 8♀ plus 4L1, 18L2, 35L3, 16P, 3E (some on slides) without type status: Russian Far East, Khasanski Region, Gryaznaya stream, Kravtsovski Cascades, 12. and 17.07.1998, T. Tiunova and T. Arefina (presently in PZ).

Additional material: Russian Far East, Primorje, small tributary to Vodopadnaja River at forest edge nr Nikolayevka, E of Partizansk, 12.06.1998, 5L1, 13L2, 8L3, 20L4 (PZ).

Adult. General structure, especially wing venation, typical of genus. Small, wing length: ♂ 5.5 mm, ♀ 7.5 mm. Pale, dorsal aspect of head, thorax and abdomen light brown, antennal flagellum and male genitalia brown, remainder yellowish.

Eyes widely separate, a tiny elongate-oval portion of eye towards ocelli more reddish, more finely facetted than the rest from which it is not set off by line of separation. Ocelli on flat wide frons, not raised on turret. Antenna with 13 segments, the 11 flagellar segments elongate and asymmetrical: dorsal contour straight with short seta at base, ventral side with distinct basoventral swelling.

Several structures sexually dimorphic. Antenna: each segment about 2.8-3.2 times as long as maximum width in males, 2.6-2.8 times in females (pharate specimens). Last segment 3.7x longer than wide in males, but similar to other segments in females. Mouthparts: rostrum of male shorter than height of head, no mandibles, no serrate hypopharynx. Palpus of ♂ short, segment four with prominent subterminal swelling, segment five long, whip-like, bare except some setae on convex face. Female rostrum slightly longer than height of head, with serrate hypopharynx and mandibles, mandibles longer than labrum. Palpus of ♀ generally similar to male but much longer. Scattered lateral setae along base of labrum in female, male without. Legs long and slender, unmodified. Tibial spurs hairy, spur formula 0.0.1 in males, 0.0.2 in females, spurs on hind tibia very unequal.

Male genitalia (Figs. 12a, b): Epandrium transverse, broad, setose, particularly strong setae bordering concave rear edge. Cercus simple, conical, setose, proctiger with two setae projecting below. Hypopygium transverse and short, distal margin in middle slightly triangular. On either side of dorsal face of gonocoxite arises sclerotized erect finger with strong apico-medial setation. Outer dististyle profoundly bilobed. Dorsal branch with blunt setose medial projection at base, apex of branch slender, bent anteromediad, with strong apical spines. Ventral branch largely soft, surface covered with microtrichia, rough. From an apical oval lobe with few large ventral setae hangs dorsally flat but ventrally keeled appendage. Band-shaped medial edge of appendage with microtrichia, semicircular lateral portion with hyaline outwardly directed spicules. Inner dististyle slender in form of dorsally hooked rod. Tegmen not apparent. Inner sclerites: ventral bridge shallow, vesica in form of oval sac without apodeme; three subequal penis filaments. Parameres longer and wider than penis filaments, apically widened, canal distinct, with funnel-shaped apical opening.

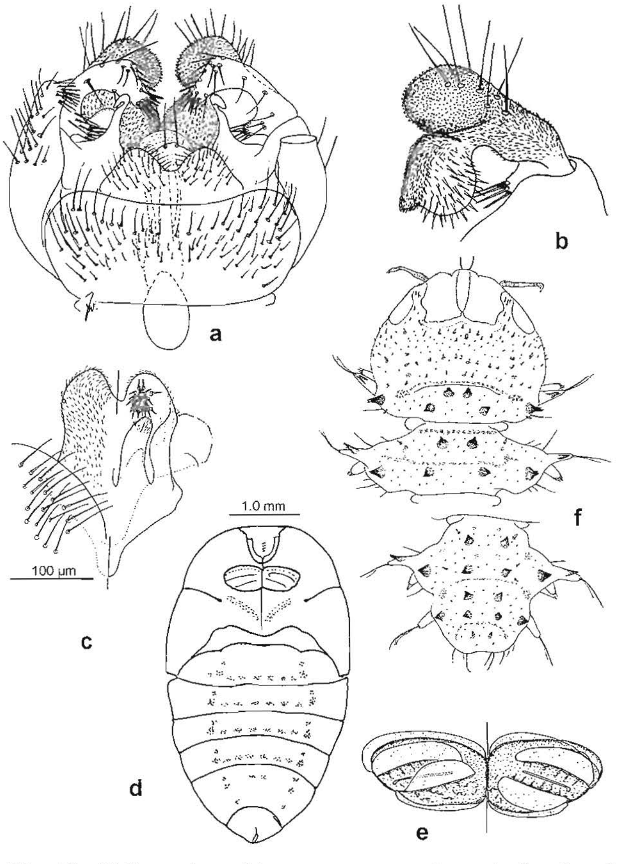

Fig. 12: *Philorus levanidovae* sp. n. a, male genitalia, dorsal view, left finger-shaped process cut; b, right dististyle, ventral view; c, female oviscapt; ventral view to the left, dorsal view to the right of the interrupted vertical line; the single curved spine on the side of one oviscapt lobe is apparently abnormal; d, pupa, dorsal view; e, pupal respiratory organs, dorsal view; slide preparation, position of lamellae caused by pressure of cover slip; f, last instar larvae, anterior and posterior body portions, dorsal views.

Female genitalia (Fig. 12c): Sternite 9 forms two semicircular lateral lobes with long setation including tongue-shaped base of oviscapt between them. Oviscapt plump, lobes rounded, separated by U-shaped notch. Microtrichia on ventral oviscapt face arranged in regular curved lines, middle strip bare. Dorsal face of each oviscapt lobe with about 15 grouped stout short curved setae just beyond apex of tongue-shaped process originating at oviscapt base; apex of process with slender microtrichia. Three pyriform spermathecae with short simple ducts.

Pupa. 4.7-6.5 mm long, flat. Pale brown. Granulation exceedingly fine and pale. Contour ovoid, front blunt, little wider than rear (Fig. 12d). Respiratory organs meeting medially, lamellae reduced to shallow crests. Outer lamellae form a low transparent rim around rough and partly wrinkled respiratory field. Slightly higher soft central lamellae 2 and 3 differ in length and distance from margin (Fig. 12e). Straight, open spiracular slit separating central lamellae; outer end of slit terminating in visible spiracular pore.

Larva. Last instar up to 7.5 mm long (Fig. 12f). Cephalic sclerites distinctly divided. Antenna about as long as cephalic sclerites, with long pale median zone. Antenna 2-segmented, separated by long ill-defined articular membrane. Sometimes, dark basal segment with narrow pale zone in middle, antenna then seemingly 3-segmented. Thoracic segmentation indistinct because segmental transverse rows of little erect spines on cephalic body division are irregular and somewhat obscured by numerous additional spinules. Abdominal tergites 1-6 with six pointed cones, each with several small spines at top. Two paramedian cones anteriorly, the other four widely spaced in posterior transverse line. Additionally, a pointed projection on elongate dorsal feeler situated above simple pseudopod. Segment 7 lacking pseudopod as well as cone on dorsal feeler. Remnant of tergite 8 with two small raised warts. Posterior margin of anal body division shallowly bilobed. Ventral face typical, six suckers, six pairs of gill tufts, five filaments in each; four rectal papillae surrounding last sucker from behind. Gills are so positioned that they are not normally visible in dorsal view. Lobes of rear body edge with shiny medially divided sclerite band. Instars 3 and 2 similar, with three and one gill filament per tuft, respectively. Cephalic sclerites in instars 1-3 with distinct posterior growth zones.

First instar larva (Fig. 13). No gills; rectal papillae present. Elongate egg burster on median frontal sclerite. Body surface finely wrinkled and with tiny flat cuticular spikes arranged in transverse slightly raised lines, crest-like. Long crest on only two of three thoracic segments and on abdominal segments 1-7. This long crest also includes pair of tiny cone-shaped and minute hairlike sensilla (tergal and subtergal sensilla, HOGUE 1978). Laterally, crest ends on small hump with 2-3 stronger spines above pseudopod (probably tergopleural sensilla of HOGUE 1978). Abdominal segments 1-7 additionally with short anterior crest lacking sensilla. Rudimentary segments 8 and following without crests and sensilla. Base of pseudopod with two, rarely three spines and tiny hair sensillum. Distally, each pseudopod with single very long seta and about 12 transparent rearward directed slender spines. Length of spines in each group increases from front to rear.

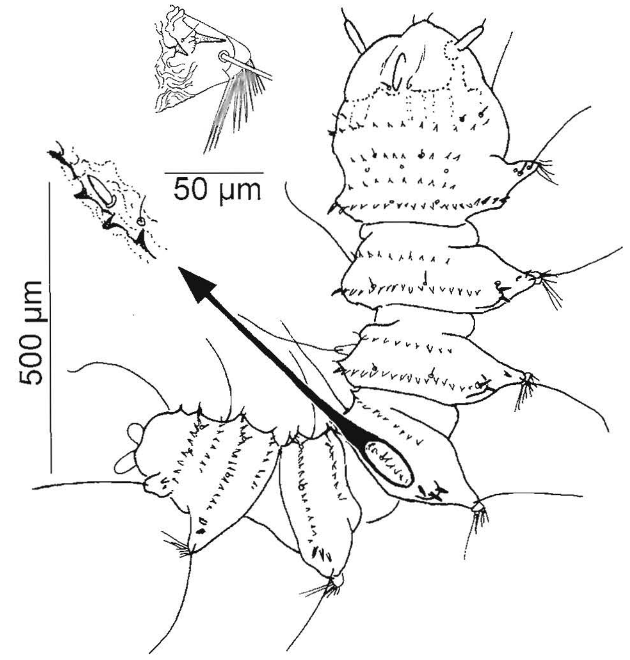

Fig. 13: *Philorus levanidovae* sp. n., first instar larva, dorsal view. Habitus with enlarged insets of dorsolateral armature and of apex of pseudopod (large seta clipped).

Comparisons. Because larvae of *P. levanidovae* and *P. chosenensis* cannot presently be distinguished, specimens from a tributary to Vodopadnaja River are tentatively assigned to *P. levanidovae* which is the sister-species of *P. chosenensis* Kitakami from Middle Korea; see there for distinction of males and pupae. Members of the so-called *Euliponeura*-group and *P. vividis* Kitakami have very similar pupae with medially meeting respiratory organs with low, crest-like lamellae and a spiracular slit with visible spiracular pore. Larvae of this group have similar dorsal armature; Japanese species are distinguished by forwardly shifted gills visible in dorsal view.

First instar larvae of *P. levanidovae* agree with *P. vividis* (KITAKAMI 1931, fig. 2) and *P. taiwanensis* Kitakami (KITAKAMI 1941b, fig. 2), but figures of the latter two species are not sufficiently detailed to compare integumental ornamentation.

Habitat. Kravtsovka stream flows in a narrow canyon shaded by forest; it forms many rapids and cascades. *Philorus levanidovae* was the only species of Blephariceridae found in the stream, larvae and pupae were collected from the hygropetric zone on big boulders, only a few larvae were found on pebbles in the main flow. Adults were swept from riverside vegetation. The small tributary to Vodopadnaja River flows in the shade of the forest edge; the collecting site was a few meters before the stream enters the Vodopadnaya River. Specimens were fully submerged in the main flow of the streamlet in which there were no other Blephariceridae. Conversely, no specimen of *P. levanidovae* was taken at a few meters distance in the fast-flowing unshaded Vodopadnaja river where *Agathon, Bibiocephala* and *Blepharicera* were common. The simultaneous presence of all life stages may suggest several overlapping generations, like in *P. chosenensis.*

Etymology. We are pleased to name this new Russian species in the honour of the late Dr. Iya M. LEVANIDOVA, Vladivostok, much admired pioneer scientist and grand old lady of Far East Russian freshwater research.

4.3.2. *Philorus chosenensis* Kitakami, 1931

Philorus chosenensis Kitakami, 1931 (KITAKAMI 1931: 93); 1950 (KITAKAMI 1950: 64, figs. 40-43).

Material. Lectotype (present designation) adult male, paralectotypes 1 pupa, 1 last instar larva (ZFMK); syntypes from Mt. Geumgang, Gangwon-do (= "Mt. Kongo"), Middle Korea, 25.VII.1939. – Additional material: 1 adult male, 1 pupa, 1 last instar larva (USNM), authentic material identified by Kitakami, possible syntypes.

P. chosenensis is thermophilic, hygropetric and plurivoltine (KITAKAMI 1950). The species is very similar to *P. levanidovae;* we saw no females. Males can be distinguished by the genitalia; Kitakami's figure is correct but too small to recognize details and consequently we provide a new illustration (Fig. 14). The above specimens appear to be all that still exist from Kitakami's collection and those that are definite syntypes are here designated as lectotype and paralectotypes, respectively. Only characters distinguishing *P. chosenensis* from *P. levanidovae* sp. n. are redescribed.

Adult. Male genitalia (Fig. 14): Dorsal branch of outer dististyle with broad but very blunt basal projection; apex short, rounded, not overhanging. Apex of ventral branch flat, resembling curved ribbon whose microsculpture changes from basal microtrichia to apical spinules but medial and lateral faces are similar. Inner dististyle sinuous, apex curved mediad, not dorsad. Penis of male in USNM is erect; parameres with small ovoid terminal section, enlargement being in parasagittal plane.

Pupa. Similar to *P. levanidovae* except fine but dark and distinct granulation.

Larva. Similar to *P. levanidovae*, no distinctive characters known.

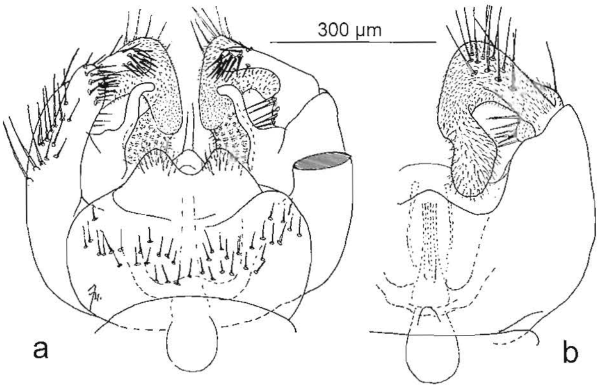

Fig. 14: *Philorus chosenensis* Kitakami, male lectotype. a, genitalia, dorsal view, left finger-shaped process cut; b, same, right half, ventral view.

4.4. Genus *Blepharicera* Macquart, 1843

Blepharicera Macquart, 1843 (MACQUART 1843: 61). Type species: *Blepharicera limbipennis* Macquart, 1843, by monotypy, a junior synonym of *Asthenia fasciata* Westwood, 1842.

Blepharicera is the most widespread genus of the family. It falls into several species groups (ZWICK 1990, ZWICK & ZWICK 1998) of which only the *fasciata*-group occurs in East Asia. The single species from the Russian Far East is new to science.

4.4.1. *Blepharicera parva* sp. n. (Figs. 15, 16)

Material. Holotype, 1 pharate ♂, paratypes 5 pharate ♂, 9 ♀, River Manoma, basin River Anjui [a tributary of Amur River], leg. Arefina & Tiunova, 28.07.1996; the same sample also includes 31 P, 30 L3 & L4 which have no status as syntypes (leg. IBSSAN; presently in PZ). Additional material: RFE03, 115 L1-L4; RFE09, 25L1, 67L2, 85L3, 137L4, 34P; RFE56, 42 L2-L4 (incl. prepupae); RFE10, 4 L1-L3; RFE21, 9 L1-L2; RFE28, 1 L2, 1L3; RFE37, 1 L3; RFE48, 39 L1-L3; RFE54, 29 L2-L4 (incl. prepupae) (all in PZ).

Primorje: Lazovskii Reservation, Lazovka River near vill. Lazo, leg. Vshivkova, 05.07.1978, 4L (IBP>PZ); 08.07.1979, 2P, 1L (IBP>PZ). Lazovsky Reserve, Kievka River, 04.08.1985, leg. Gostyukhina, 5L, 2P; 13.06.1998, leg. Arefina, 72L, 2P (IBSSAN). Ussuri River Basin, Zubkin Stream, 27.07.1992, leg. Tiunova, 1L (IBSSAN). Ussuri River near mouth of Izvilinka River, 08.08.1979, leg. Levanidova, 10L (IBSSAN). Ussuri-Bolshaya Ussurka River Basin, Perevalnaya Stream, 06.08.1997, leg. Tiunova, 4L, 2P (IBSSAN). Yedinka River (middle part), 14.08.1986, leg. Korionov, 3L, 7P (IBSSAN). Narva River (lower part), 02.08.1987, leg. Teslenko, 4L, 3P; 14.08.1994, leg. Arefina, 2L, 9P; Sikhote-Alin Reserve, Bystraya Stream, 02.08.1997, leg. Tiunova, 7L, 10P (IBSSAN).

Khabarovsk Territory: Iski River, 12.08.1959, leg. Levanidova, 5P, 3L (IBSSAN). Bikin River Basin near mouth of Omorochka Stream, 30.07.1995, leg. Tiunova, 1♀ (IBSSAN). Bikin River Basin, Klyuchevaya Stream, 28.07.1995, leg. Tiunova, 1L (IBSSAN). Bikin River Basin, Zeva River (upper part), 17.07.1995, leg. Tiunova, 1L (IBSSAN). Bikin River Basin, Zeva River, near Beriozovaya Stream, 24.07.1995, leg. Tiunova, 10L, 8P (IBSSAN). Bolshekhekhtsirsky Reserve, Ussuri River Basin, Bychikha Stream (15.5° C), 22.06.1958, leg. Levanidova, 4L, 1P (♀) (IBSSAN) (all in PZ).

A typical *Blepharicera*. Adults available only as pharate specimens; dimensions, pigmentation and details of wing therefore unknown.

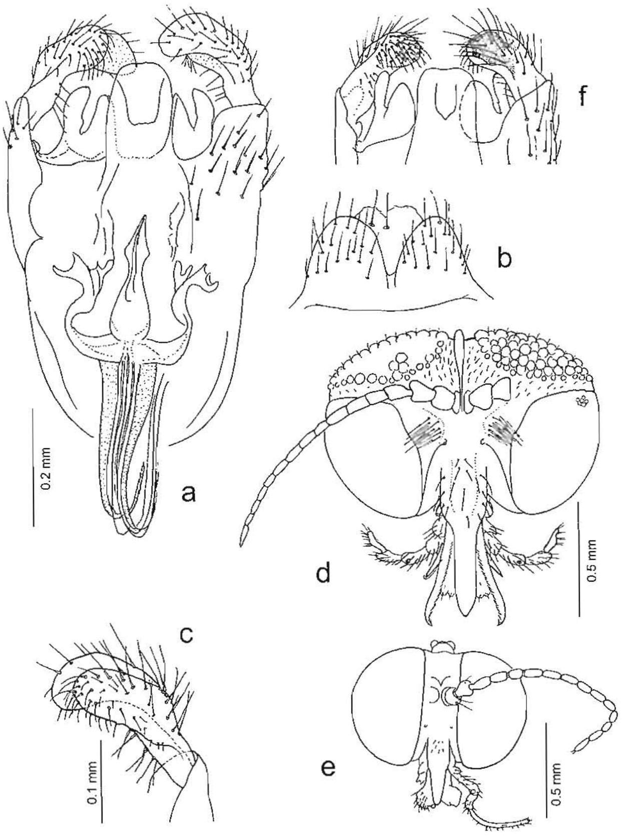

Fig. 15: *Blepharicera parva* sp. n., adults. a, b, male genitalia, dorsal view, tergite and cerci shown separately; c, left dististyle, dorsal; d, head of female; e, head of male; f, *Blepharicera japonica*, part of male genitalia, dorsal (from ZWICK 1990).

Adult. Male. Widely separate almost simple eyes, reduced upper portion forms narrow section at mesal rear margin of eye, behind ocelli. Rostrum shorter than head height, labella projecting slightly beyond labrum. No mandibles, hypopharynx, lacinia; palpal segments short except whip-like 5th segment. No facial pilosity. Antenna slender, most segments more than twice as long as wide. Coxae normal, simple. No tibial spurs. Tarsal claw falcate, with some hairs on sides near base.

Hypopygium slender, inner sclerites inverted as typical of *B. fasciata*-group. Tegmen lightly sclerotized, apex of common spade-shape. Inner dististyle divided into blade-like median and short finger-shaped lateral portions. Inner edge of outer dististyle with some basal setae, distally angularly bent mediad. Dorsal and ventral distal lobes deeply divided, dorsal lobe a bit angled and much shorter than the more regularly curved soft ventral lobe with medially projecting apex. Cercus narrowly rounded, no angles in contour.

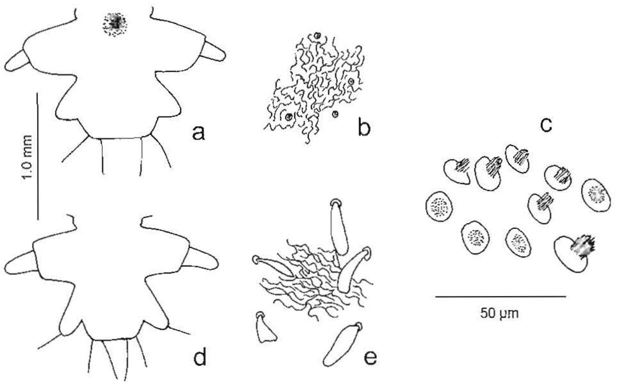

Fig. 16: *Blepharicera parva* sp. n. (a-c) and *B. japonica* (d, e). a, d, terminal body division of last instar larva, dorsal; b, e, details of integument on some middle abdominal segment; c, granula on abdominal segment of pupa. Figures a and d and c-e are to the same scales, respectively.

Female. A very narrow crest between eyes runs to ocellar triangle which is not raised. Bare strip separates unequal portions of widely separate eyes. Upper portion in frontal view slightly smaller than lower, convex, very large bulging ommatidia in centre, lateral ones much smaller. Antenna short, of 15 segments, acutely pointed, setiform, each flagellar segment with single longer seta on outside, resulting in sparse setal fringe. Distinct facial hair patch between base of antenna and base of rostrum. Rostrum about as high as head. Mandibles serrate, long, apex curved mediad. Hypopharynx serrate, hidden behind labrum which is little longer than labella. Lacinia distinct. Palpus segments short, especially 5th. Mesocoxa with usual hairy appendage. Hind tibia with two small unequal spurs, base of hind tarsus with some procumbent long black setae. Tarsal claws as in male. Genitalia not distinctive, three spherical receptacles with sclerotized duct whose diameter widens abruptly short distance from receptacle.

Pupa. Shape and respiratory organs typical of genus, 3.8-4.8 mm long, 2.0-2.5 mm wide. Integument glossy, dorsal granules on metathorax and abdomen tiny, each with central dome of closely packed hair-like pegs (Fig. 16c). Anterodorsally on abdominal tergites granules aggregate and form slightly raised warts. Anterior and posterior lamellae of gills of same width and almost twice as wide as lamellae 2 and 3 between them. Brown, also all four gill lamellae of same colour.

Larva. Last instar larvae up to 6.5 mm long, typical of subgroup. Cephalic sclerites with usual mottling but each dark spot on raised area of integument, which is hemispherical on medial frontal sclerite, but flat and obliquely rising from low front to high posterior edge on lateral frontal sclerites. Antenna two–segmented, segments separated by pale section of same length as basal segment, latter distinctly shorter than apical segment. Each abdominal tergite may have anteromedian wart, surrounding integument and intercalary segments darker than rest of surface; although some specimens lacking warts altogether. Surface finely microreticulate, with numerous tiny insertion points; setae reduced to tiny acutely conical pegs and not easily visible. Soft pale hairs on sides of body. Ventral face of body with distinct but pale asperities between sucker and base of pseudopods. Seven gill filaments in each tuft. Body divisions medially brownish, anterior part of each division darker than posterior, pale mark at paramedian muscle attachments; neck–pieces and lateral portions of divisions pale.

Last body division with truncate sclerotized blackish distal edge. Lateral lobes of segment bluntly triangular, their posterior contour meeting body contour at right angles. Last pseudopod reduced to sclerotized area around setal insertion, medial edge of sclerite often downcurved to form small grapple.

Larval instars 3, 2 and 1, respectively, with five, three and no gill filaments, less distinctly patterned, dull grey, lobes of last body division less distinct. Antenna one–segmented in instars 1 and 2, with very short dark ring representing basal segment only in instar 3. Cuticular ornaments of first instar larva as described for *B. fasciata* (ZWICK 1980), that is, only single prothoracic transverse cuticular crest present on thorax.

Variation. The only variation concerns the expression of tergal warts and dorsal pilosity in larvae. In some populations, especially at the type locality, warts are shallow and inconspicuous; in most others, particularly in the Kievka river, warts are steeply rising and high. Similar variation is known in other species, for example *B. fasciata*. While some specimens appear almost bare, others are fairly pilose. However, this may depend less on absence or presence of hairs than on extent of bacterial and detrital coating which greatly affects visibility of hairs.

Distinction from related species. On the Asian mainland occur only species of the *fasciata*-subgroup, which were all redescribed by ZWICK (1990). However, *B. japonica* Kitakami, 1931 is the only species of which all stages and both sexes are known (KITAKAMI 1931, 1950).

B. yamasakii (Kitakami, 1950), from Manchuria: Adults are very similar to *B. parva*, but both sexes bear a hairy appendage on mesocoxa (in all other species, present only in females). The upper portion of the female eyes are "nearly flat", and the sides of the lower division are "nearly vertical" whereas in *B. parva* both divisions are distinctly convex. The pupa is not recognizably different. The larva differs by the dense pale pilosity and lack of integumental warts although the shape of the caudal body division is similar to *B. parva*.

B. japonica: Adults resemble *B. parva*, but the male cerci are slightly pointed, the upper lobe of the outer dististyle is smaller than the lower (opposite in *B. parva*), and the lobes are shallowly separate. Females lack a hairy mesocoxal appendage but the trochanter is covered in dense black hairs. Eyes are simple, with no facial hair patches, and the rostrum lacks mandibles and hypopharynx. The width of the sclerotized receptacular duct changes gradually, not abruptly. *Blepharicera japonica* females have very slender, thin, skinny tarsi with strongly oblique articulations and heavy strongly curved claws; these details were previously overlooked. A similar character syndrome was recently noticed to be common in another tribe, Apistomyiini (ZWICK 1998). Pupae of *B. parva* and *B. japonica* can presently not be distinguished. Long lateral lobes of segment seven of *B. japonica* larva are directed obliquely backward (Fig. 16d). The surface bears pale, club-shaped flattened hairs among microreticulation (Fig. 16e) and no integumental warts. Three dark bands run over entire length of body. Cephalic sclerites are smooth, not sculptured as in *B. parva*. Instar 3 of *B. japonica* has already two distinct antennal segments, instar 2 possesses a small dark basal ring; otherwise not distinct from *B. parva*.

B. yankovskyi (Alexander, 1953): The single male from North Korea has very large eyes; the upper section is small but much less reduced than in *B. japonica*, and hence also different from *B. parva*.

B. dimorphops (Alexander, 1953) (from China, Fukien): Outer male gonostyle is very deeply divided, with both lobes slender, and this form is distinctly different from *B. parva* (figs. 8a-c of ZWICK 1990).

4.4.2. *Blepharicera* sp.

Material. Mongolia, Selenge, Mandal, Khonin Nuga [49°05'260N, 107°17'440E], Eroo River, 21.VI.2003, 1L3, 2L2, leg. P. Surenkhorloo (PZ).

The larvae resemble *B. parva*, but we are not certain of their conspecificity.

4.5. Genus *Neohapalothrix* Kitakami, 1938

Neohapalothrix Kitakami, 1938. Type species: *Neohapalothrix kanii* Kitakami, 1938, by original designation (KITAKAMI 1938: 341).

Asiobia Brodsky, 1954. Type species: *Asiobia acanthonympha* Brodsky, 1954, by original designation (BRODSKY 1954: 245). Synonymy of ZWICK, 1990: 253.

The phylogenetic status of the closely related genera *Neohapalothrix* and *Hapalothrix* (Europe; ZWICK, 1997b) is not firmly established because of conflicting characters. A dorsal larval feeler with geminate setae occurs only in Blepharicerini. ZWICK (1992) therefore included both genera in this tribe, assuming convergence for reduced wing veins and habitus characters. Most authors, however, regarded both genera as Paltostomatini because of reduced wing venation, curved front femora, short front and middle and very long hind legs. The labial brush here described for *Neohapalothrix* has so far only been observed in Paltostomatini (ZWICK 1998). In view of this last character we now assume that the genus actually belongs in that tribe. If so, the dorsal feeler must have evolved independently from Blepharicerini. Indeed, the feeler originates through splitting of the pseudopod, and is positioned in front of the pseudopod, not above it as is typical of Blepharicerini. Both traits are unique.

Neohapalothrix is endemic to Asia. The genus includes the type-species from Honshu and the widespread *N. manschukuensis* (Mannheims).

4.5.1. *Neohapalothrix manschukuensis* (Mannheims), 1938 (Figs. 17-20)

Curupira manschukuensis Mannheims, 1938. – Type-locality: Weischache, Manschukuo [China, Manchuria] (MANNHEIMS 1938: 329).

Asiobia acanthonympha Brodsky, 1954. – Type-localities: Russia: r. Angara, Padun; S-Primorje: r. Bikin; Kazakhstan: Altai, r. Bija (BRODSKY 1954: 250). – Synonymy of Zwick, 1990: 253.

Neohapalothrix shirozui Saigusa, 1973: 226. – Type locality: Japan, Hokkaido, Teshio, Piuka (SAIGUSA 1973: 226). – Synonymy of ZWICK, 1997b.

Curupira manschukuensis was described from a single female and tentatively placed in the neotropical genus *Curupira*. In the same year, KITAKAMI erected the genus *Neohapalothrix* for his new species, *kanii*, from Japan. Subsequently, KITAKAMI anticipated and established, respectively, the correct generic combination of the mainland species (KITAKAMI 1941a, 1951). However, it was later described and named two more times. BRODSKY (1954) presented all life stages. The amazing male tarsal structures were again illustrated by SAIGUSA (1973) and ZWICK (1997b) who also described changes in pseudopod structure between larval instars, comparing them with *Hapalothrix*.

Neohapalothrix manschukuensis was known from the Altai (BRODSKY 1954) and the Russian Far East; the new Mongolian record is therefore not surprising. The new record from Sakhalin closes a gap in the distribution, because a single male was taken on Hokkaido (SAIGUSA 1973). *Neohapalothrix manschukuensis* is common in the Russian Far East, conspecificity of all stages is definitely established through the metamorphotype-approach. We describe previously unknown details and present some ecological observations.

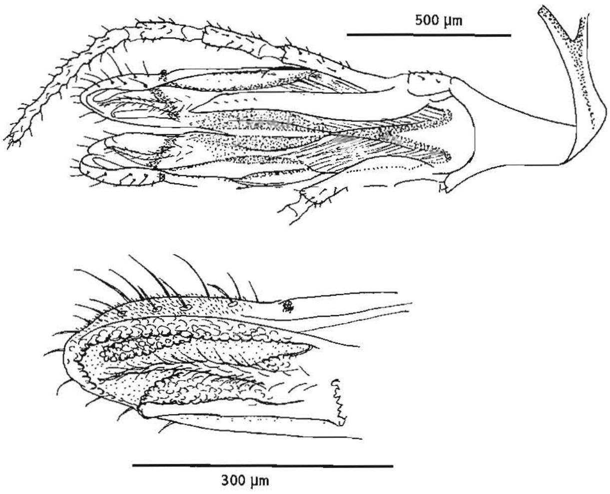

Fig. 17: *Neohapalothrix manschukuensis*. Female maxillolabium, dorsal view, and enlarged detail of left half of figure. Muscles diagrammatic.

Material (all in PZ). RFE09, 21P, 12L4; RFE14, 33L3, 64L2, 6L1; RFE15, 100L4, 36L3, 5L2, 3L1; RFE16, 4♂, 18♀, 20P, 5E, 18L4; RFE18, 43P, 8L4, 1L3; RFE19, 12L3; RFE21, 28L4, 84L3, 4l2; RFE23, 61P, 33L4, 3L3; RFE28, 24L4, 14L3, 1L2; RFE30, 88P, 13L4; RFE33, 341P, 19L4, 2L3; RFE35, 7P, 29L4, 1L2; RFE38, 23L4, 3L3; RFE39, 37P, 21L4; RFE47, 39L4, 2L3; RFE48, 3P, 50L4, 7L3, 1L1; RFE52, 1P; RFE53, 2♂; RFE56, 9P, 5L4, 1L3. Russian Far East, Sakhalin: Tym River at Ado-Tymovo Village, 10.07.1985, E. Makarchenko, 1 L4 (TA).

Additional material: Mongolia, Selenge: Mandal, Khonin Nuga [49°05'260N, 107°17'440E], Eroo River, 21.VI.2003, 28P, 43L4, 1L3; 25.VI.2003, 35♀; Eroo River [49°05'N, 107°17'E], 26.VI.2003, 2♀; 13.VII.2003, 2♀; Eroo hot spring, Irchleh River, [49°05'N, 107°17'E], 28.VI.2003, 16L4, 8P; Mandal, Ataa River, 18.VII.2003, 1L3; Mandal, Bar-Chuluut River [48°58'638N, 106°57'013E], 13.VII.2003, 2♀; Mandal, Bar-Chuluut River [49°02'784N, 106°58'669E], 09.VII.2003, 1L4 (all leg. P. Surenkhorloo; in PZ).

Adults. Both sexes of similar habitus. Female front femur slightly less sinuous than male. Female holoptic, eye little smaller than in male but also sharply divided into upper and lower portions. Rostra differ little, except longer maxillo-labium with base bent back distinctly only in females. Labella alike in both sexes. Soft scaly inner face forms anterior finger-shaped fold and larger posterior lobe with flat smooth medial face. Delicate brush at base of posterior lobe formed by slender cone with hair-like outgrowths of cuticle.

Female genitalia remarkable for short palpus-like apex of cercus not extending backward beyond general contour line. Oviscapt with truncate deeply divided but narrowly adjacent lobes. Dorsal face of each lobe without cover, side forming lateral wall ending in small dorsal angle. Sclerotized base of oviscapt truncate with prominent corners, almost bifid. Median of three pear-shaped black receptacles slightly smaller, all with short straight stalks.

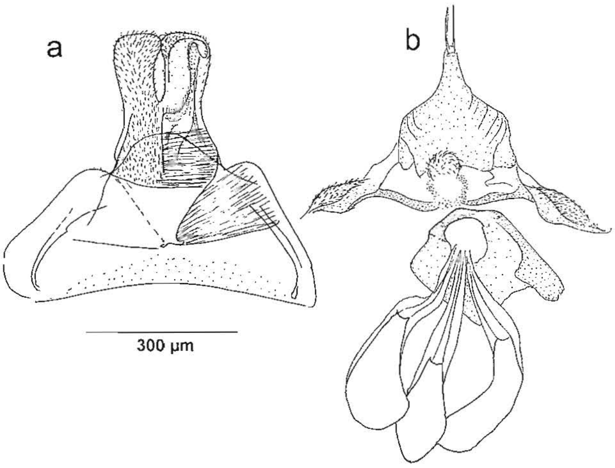

Fig. 18: *Neohapalothrix manschukuensis*, female genitalia. a, sternite 8 and oviscapt; muscles diagrammatic, as seen by transparency; left half of figure shows oviscapt in ventral, right half in dorsal view. b, sclerites from female genital cavity, with attached receptacles.

Larval instars. First instar larva (Figs. 19a-c) of normal habitus, dorsal side convex, rounded. Anal body division semicircular, no lobes; pseudopod seven represented only by tiny wart with long seta. Long, flattened cuticular structures resembling blunt hairs stand in transverse rows across body. One long row per thoracic segment. Each abdominal segment with short anterior plus long posterior row. Slender hair-like tergal and subtergal sensilla standing in posterior rows recognized by insertion points only at magnification over 200. Pseudopods in dorsal view largely hidden under body.

Base of each pseudopod with group of three spine-like cuticular outgrowths and a large seta (tergopleural and/or pre-dorsopseudopodal sensilla, HOGUE 1978), geminate setae (dorsopseudopodal setae of HOGUE 1978) typical of first instar pseudopods close to apex. Colourless delicate cuticular tube everted from tip of pseudopod with about 10 tiny sharp hooks at end. Antenna 1-segmented. No gills. Lateral rectal tubules very long, median ones minute.

Second instar larva with hard central cone on each abdominal segment. Integument with long curved hairs, some blunt, others apically thinned and finely pointed. On sides of body also short transparent spatulate and curved setae. Pseudopods forked (Fig. 19d), long posterior branch with rough ventral sole and three long dorsal setae. Short anterior branch with two or three long hairs in addition to geminate setae; ventrally smooth. Antenna 2-segmented. Single gill filaments, rectal tubules unchanged.

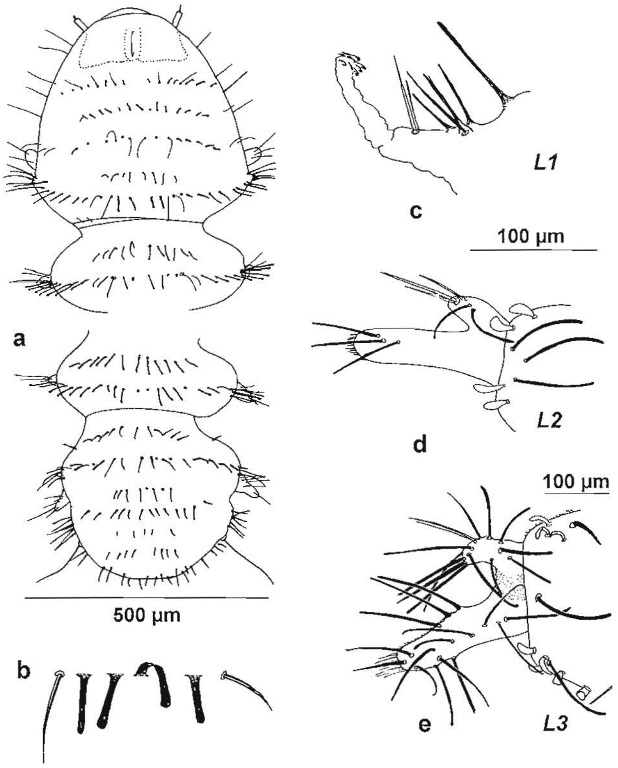

Fig. 19: *Neohapalothrix manschukuensis*. a, first instar larva (cephalic division plus abdominal segment 3; abdominal segments 5 and following); b, detail of dorsal armature, not to scale. Left side of abdominal segment three and pseudopod: c, first instar, posterior view (from a slide mount); d, e, 3rd and 4th instar, respectively, dorsal views. Same scale for c and d.

Branches of pseudopod deeply separate in 3rd (Fig. 19e) instar larva, completely divided in 4th instar. Hair cover denser, four and seven gill filaments, respectively. Abdominal segments 1-6 with strong dark dorsal spine on raised middle portion; body cross-section resembles equilateral triangle (lateral view in BRODSKY 1954 is far too flat!). Dorsal side sometimes (3rd instar) or normally (4th instar) patterned in dark brown and yellowish. Extent of pale pigment varies from only abdominal segments one and two and sides of five and six pale to mainly light specimens with dark cephalic sclerites, spines and pseudopods, and brown segments three and 4.

Ecological notes. Scientists of IBSSAN repeatedly picked numbers of adults from flowers of *Angelica saxatile* (Turcz.) (Daucaceae) and *Filipendula palmata* (Pall.) (Rosaceae). During our field work, adults were observed flying over the river banks, just before complete darkness. Dying and dead spent females were found between pebbles in stagnant water along the Khor River below Sukpai. Females seemed to have oviposited in areas where the river was receding. Individual last instar larvae and pupae observed on pebbles in the same area were alive but thickly covered with mud. Normally, larvae and pupae were found completely submerged, in strong current.

There is an obvious preference for large watercourses and potamal habitats. Population structure varied much between samples taken almost simultaneously. At several localities, water temperature was recorded at 20 min intervals (Gemini Tinytag datalogger ®) over night, between 19:00 and 8:00 hrs. The relationship between nocturnal minimum temperature and predominant developmental instar is shown in Figure 20; accelerated development in warm water is obvious. The sample from Komissarovka River is an exception but may be too small for safe judgement.

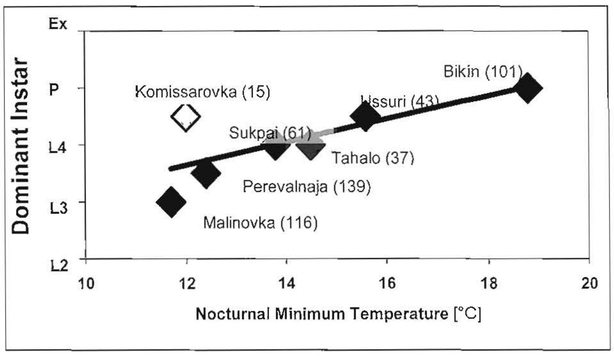

Fig. 20: *Neohapalothrix manschukuensis*, dominant instars (larval instars L2-L4, P = pupae, E = exuviae) in samples from rivers with different nocturnal minimum temperature, 11-24 June, 1998. Figures in parentheses are numbers of specimens in the sample.

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