

Habrophlebiinae subfam. n. with description of a new species of *Habroleptoides* from the Caucasus (Ephemeroptera: Leptophlebiidae)

N.Ju. Kluge

Kluge, N.Ju. 1994. Habrophlebiinae subfam. n. with description of a new species of *Habroleptoides* from the Caucasus (Ephemeroptera: Leptophlebiidae). *Zoosystematica Rossica* 3(1): 35-43.

The phylogeny of the Leptophlebiidae is discussed. The paraphyletic subfamily Leptophlebiinae is divided into Leptophlebiinae s. str. (which is also probably paraphyletic) and the holophyletic subfamily Habrophlebiinae subfam. n. Nymphs and imagos of the Caucasian species *Habroleptoides pontica* sp. n. and *H. caucasica* Tshernova are described.

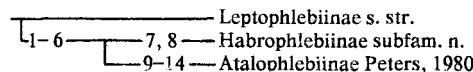
N.Ju. Kluge. Department of Entomology, Biological Faculty, St. Petersburg State University, Universitetskaya nab. 7, St.Petersburg 199034, Russia.

Phylogeny of the Leptophlebiidae

Peters (1980) has discussed the phylogeny of Leptophlebiidae, where two sister groups – subfamilies Leptophlebiinae and Atalophlebiinae have been established, both regarded as holophyletic taxa. The holophyly of Leptophlebiinae has been supported by only two apomorphies: “submedian, subapical patches of hair” on venter of lingua of hypopharynx and “heavy, thickened, pointed to blade-like setae or spines” on anterolateral margin of labrum. As for the first character, it is noted as present in Leptophlebiinae except for *Paraleptophlebia*, while in Atalophlebiinae hairs may be present on the apical margin or dorsum of the lingua. So this character is not distinct and reliable. The second character (regular row of stout bristles on anterior margin of labium) is also present in the outgroup (Ephemeridae), and also in some other Ephemeroidea, so it may be not an apomorphy, but a plesiomorphy of Leptophlebiinae.

It is most probable that Leptophlebiinae as treated by Peters are a paraphyletic group. At the same time the genera *Habrophlebia* and *Habroleptoides* (included by Peters in Leptophlebiinae) have synapomorphies with Atalophlebiinae and could be their sister group. So a new classification is suggested, whereby the former subfamily Leptophlebiinae s. l. is divid-

ed into the subfamilies Leptophlebiinae s. str. and Habrophlebiinae; the relationships of the three subfamilies are shown in the scheme.



The subfamilies Habrophlebiinae and Atalophlebiinae have the following synapomorphies. (1) Maxillary canines missing (Figs 8, 9); in Leptophlebiinae s. str. slender rudiments of three maxillary canines are present (Fig. 7); presence of three maxillary canines is a primitive state for Ephemeroptera (Kluge, in press). (2) Proximal dentiseta of maxilla is comb-like (Figs 8, 9); its form in Habrophlebiinae (Fig. 8) is intermediate between that in Leptophlebiinae s. str. (Fig. 7) and Atalophlebiinae (Fig. 9). (3) Dorsal surface of labrum with distal row of bristles. In the examined species of *Habroleptoides* (see below) this row is regular overall its length (Fig. 23), but in the examined *Habrophlebia* (*H. fusca* and *H. lauta*) it is regular only in its median part, turning into fields of irregularly arranged bristles in its lateral parts. In Atalophlebiinae the distal row is usually regular, being secondarily irregular in some genera (for example in *Hagenulus*). In contrast to Habrophlebiinae and Atalophlebiinae, in Leptophlebiinae all bristles on dorsal

surface of labrum are arranged irregularly, forming no rows. (4) Hypopharynx with lobes of superlingua curved and expanded laterally (Fig. 24). (5) Tibio-patellar suture of nymph reduced on middle legs (Fig. 28). As in the majority of Ephemeroptera, in Leptophlebiinae s. str. this suture is retained on middle and hind legs, being reduced on fore legs (among Ephemeroptera only in Baetidae and *Rhithrogena* the tibio-patellar suture is secondarily restored on fore legs). In Habrophlebiinae, tibio-patellar suture is developed only on hind legs (Fig. 29); in Atalophlebiinae, it can also be developed only on hind legs (in *Zephlebia*), or is reduced on all legs (in *Choroterpes*, Hagenulini). (6) Styliger of male imago with prominent dorsal plate (Figs 10, 39). Besides, prominent ventral plate can be developed or not developed (large prominent ventral plate is especially prominent in *Habrophlebia*). In Leptophlebiinae, large prominent ventral plate is present but dorsal plate is absent.

The subfamily Habrophlebiinae has the following autapomorphies: (7) Superlingua of nymphal hypopharynx with its lateral ends pointed (Fig. 24). (8) Structure of male imago genitalia similar in all representatives.

The subfamily Atalophlebiinae has the following autapomorphies. (9) In males, upper portion of eyes with square facets. (10) In nymph, lingua of hypopharynx with lateral projections (except for *Castanophlebia*, *Terpides*, *Fittkaulus*). (11) Maxilla with single dentiseta (the proximal one) (Fig. 9). Initially, all Furcatergalia have two dentisetae (Kluge, in press); in Leptophlebiinae s. str. and Habrophlebiinae, both dentisetae are retained (Figs 7, 8), but in Atalophlebiinae, the distal one is reduced. (12) Anteromedian emargination of labrum with flat denticles. In Leptophlebiinae and Habrophlebiinae, such denticles are absent (Fig. 23); in Atalophlebiinae, they are present or secondarily reduced. (13) Dorsal surface of labrum with the second transverse row of bristles proximad to the distal one. In some groups of Atalophlebiinae, this second row can be secondarily reduced. (14) Stout bristles on anterior margin of labrum reduced.

Discussion. In the phylogenetic tree of Eastern Hemisphere Leptophlebiidae figured by Peters & Edmunds (1970), *Habrophlebia* and *Habroleptoides* together with some genera of Leptophlebiinae s. str. are included into the "daughter line 1A". This line is shown as holophyletic, but characterized only by plesiomor-

phic characters. Its sister group – "line 1B" (which includes *Habrophlebiodes*, *Dipterophlebiodes*, and *Gilliesia*) – is characterized by reduction of cubital area of fore wing and by presence of distal row of bristles on dorsal surface of nymphal labrum. Actually the cubital area can be reduced independently also in some Habrophlebiinae (Figs 13, 42). The distal row of bristles on the labrum is regarded by me to be a synapomorphy of Habrophlebiinae and Atalophlebiinae (see above), but not a character of the "line 1B": nymphs of *Gilliesia* are still unknown, and the nymph of *Dipterophlebiodes* has no such row present (Peters, 1972), in *Habrophlebiodes* such row is shown only for *H. prominens* Ulmer, 1939 (only by Peters & Edmunds, 1970: Fig. 244, but not by Ulmer, 1939: Fig. 282). The nymph of *Habrophlebiodes americana* Banks, 1903 examined by me has no regular distal row on labrum. Probably *Habrophlebiodes* is an artificial group including non-related Leptophlebiidae which have symplesiomorphies with *Paraleptophlebia*, but differ from it in the presence of costal process of hind wing.

The following corrections should be made in the key to mature nymphs of the "daughter line 1" (= subfam. Leptophlebiinae sensu Peters, 1980) in the paper by Peters & Terra, 1974. (1) Posterolateral spines on abdominal segment VIII are absent not only in *Dipterophlebiodes*, but also in *Habroleptoides*. (2) Superlingua of hypopharynx of *Habroleptoides* has lateral areas not rounded; Fig. 198 in Peters & Edmunds, 1970, and Fig. 9 in Peters, 1979, are wrong (see Fig. 24; Schoenemund, 1929: Abb. 1d). (3) Dense long hairs on prothoracic legs are developed not only in *Calliarcys*, but also in some of *Habroleptoides* – specifically in *H. sp. (? confusa)*. (4) Even row of hairs on anterior margin of labrum is present in *Habroleptoides*. (5) *Habrophlebiodes* has mid-dorsal and inner rows of bristles ("spines") in labial segment 3 (Ulmer, 1939: Fig. 285), like other Leptophlebiinae and Habrophlebiinae. (6) Denticles on claws vary in different species of *Habroleptoides* and do not allow it to be distinguished from *Paraleptophlebia*. Taking these corrections into account, this key may be used with the exception for *Habrophlebiodes*: nymphs of this genus may be distinguished from nymphs of the genus *Paraleptophlebia* only by the form of hind wing pads.

Subfamily **Habrophlebiinae** subfam. n.

Description. This subfamily is characterized by the synapomorphies with Atalophlebiinae, the symplesiomorphies with Leptophlebiinae, and the unique autapomorphies of its own listed above. Besides, all Habrophlebiinae have the following common characters: (1) claws of imago and subimago dissimilar, one apically hooked, the other obtuse, pad-like (only in some species fore legs of male with both claws obtuse); (2) hind wing with distinct costal projection, with a cross-vein running from the base of costal projection and crossing the subcostal vein (Figs 14, 16, 43, 46); (3) subimaginal mesonotal exuvia with dark macula at hind lateral part of posterior scutal protuberance,* but with light anterior and medial areas of this protuberance (Fig. 47); (4) subanal plate of female imago and subimago deeply cleft.

Composition and distribution. The subfamily includes two genera – *Habrophlebia* Eaton, 1881 and *Habroleptoides* Schoenemund, 1929, both distributed mainly in the Western Palaearctic. The genus *Habrophlebia* includes two subgenera – *Hesperophlebia* Peters, 1979 and *Habrophlebia* s. str. The first consists of a single species *H. (Hesperophlebia) vibrans* Needham, 1908 (= *H. jocosa* Banks, 1914, = *H. pusilla* Traver, 1932) distributed in Eastern Nearctic. The subgenus *Habrophlebia* s. str. includes five West Palaearctic species. Two of them, *H. (H.) fusca* (Curtis, 1834) (= *H. konjarensis* Ikonomov, 1963) and *H. (H.) lauta* McLachlan, 1884, are widely distributed in Europe: besides Western Europe, both species are found in East European Plain and the Urals, *H. (H.) lauta* also in Western Caucasus; but they have not been found in Siberia or Middle Asia. Two species, *H. (H.) consigliani* Biancheri, 1959 and *H. (H.) eldae* Jacob & Sartori, 1984 are known only from Italy (Bellfiore & Gaino, 1985). One species, *H. (H.) vaillantorum* Thomas, 1986 is known only as nymphs from Morocco (Thomas & Bouzidi, 1986). The second genus, *Habroleptoides*, is known only from mountain regions of Western Europe, the Moroccan Atlas, and the Caucasus; 15 species have so far been described and one more is described below.

According to Peters (1979), the distribution

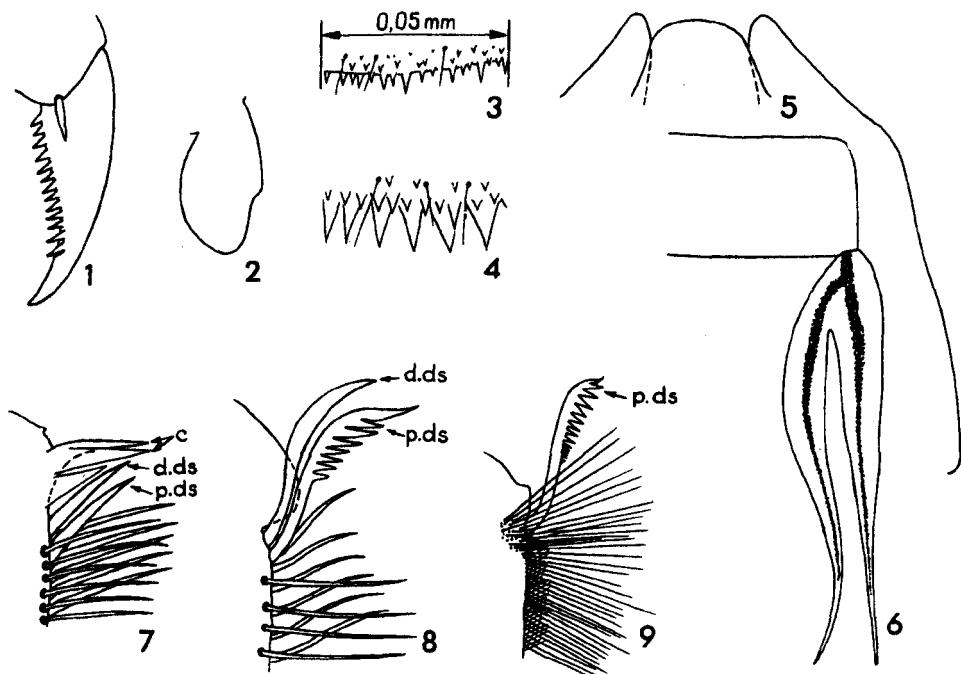
of the phylogenetic branch *Habroleptoides* – *Habrophlebia* – *Hesperophlebia* is connected with the Eastern North American – European landmass in the Late Cretaceous. But according to my data, the presence of Leptophlebiidae in Cretaceous is not confirmed by fossils and is doubtful (Kluge, 1993).

Genus **Habroleptoides** Schoenemund, 1929

Description. The genus can be distinguished from the genus *Habrophlebia* by presence of a projection on the inner margin of the first forceps segment of the male imago, and by the absence of a processes on the bifurcate tergaliae of the nymph; female imagos of *Habroleptoides* can be distinguished from those of the subgenus *Habrophlebia* s. str. by the absence of an ovipositor (in the subgenus *Hesperophlebia* the ovipositor is also absent). At least the examined species of *Habroleptoides* (*H. confusa*, *H. caucasica*, *H. pontica* sp. n.) have no longitudinal carina on the mesothoracic sternum (in contrast to the examined *Habrophlebia* – *H. fusca* and *H. lauta*, which have such a carina, as well as Leptophlebiinae – Tsui & Peters, 1972: Figs 50, 51); instead of the carina, *Habroleptoides* has only a dark longitudinal median line in the same place. At least the examined species of *Habroleptoides* have colour patterns of the mesonotal cuticle contrasting and distinct (Fig. 47) (unlike the examined *Habrophlebia*, which have a diffuse pattern on the posterior scutal protuberance).

Classification. Sartori (1986) classified all *Habroleptoides* in 7 groups which are characterized only by imaginal characters: structure of styliger and forceps of male and number of transverse and intercalary veins on wings. The new species *H. pontica* sp. n. has the structure of the genitalia strongly differing from that of *H. caucasica*. But the body proportions, form of fore and hind wings, and nymphal characters of both species are very similar, permitting me to suggest a close relationship of these species and to place them in the same species group. Thus the *caucasica* group is accepted here in different sense from the *caucasica* group of Sartori.

* For explanation of this term see Kluge, 1994.



Figs 1-9. Leptophlebiidae, nymphs. 1-6, *Habroleptoides* sp. (? *confusa*) (1-5, Armenia, 6, the Czech Republik): 1, claw, 2, hind wing pad, 3, hind margin of abdominal tergum IX, 4, the same of tergum X, 5, outline of abdominal sternum IX of male, 6, right half of abdominal tergum IV (mounted on a slide) with tergalia. 7-9, inner-apical angle of left maxilla (dorsal view): 7, *Habrophlebiodes americana* Banks (subfam. Leptophlebiinae), 8, *Habrophlebia fusca* Curt. (subfam. Habrophlebiinae subfam. n.), 9, *Zephlebia borealis* Phillips (subfam. Atalophlebiinae). c, maxillary canines, d.ds, distal dentiseta, p.ds, proximal dentiseta.

***Habroleptoides* sp. (? *confusa* Sartori & Jacob, 1986)** (Figs 1-6)

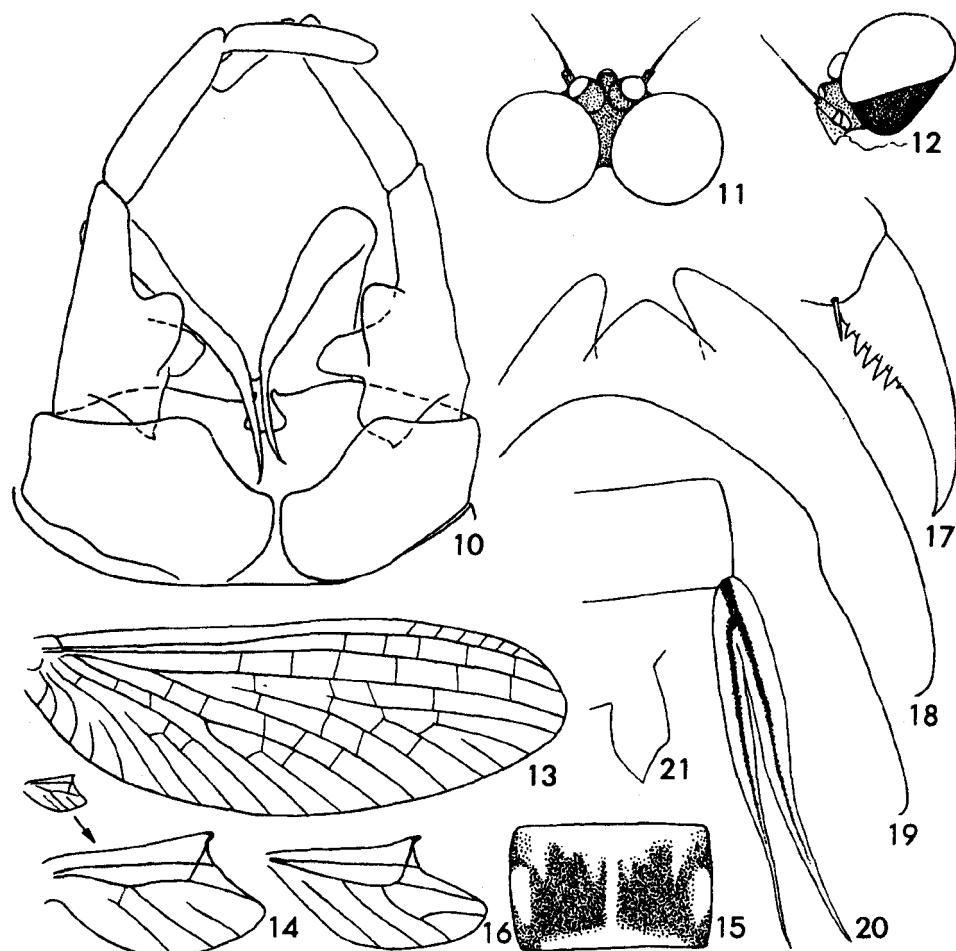
Material. Armenia: 1 nymph, stream near Ahpat (near Allaverdi), 2.V.1956 (L. Zhiltzova); 5 nymphs, stream in basin of Megrichet River (Megri distr.), 21.IV.1956 (L. Zhiltzova); 10 nymphs, stream – tributary Of Azat River near Garni, 8-13.VIII.1985 (N. Kluge); 4 nymphs, N of Vedi, 31.XI.1981 (A. Korolev). Czech Republic: nymphs, Závišinský potok, Bezdědovice (Blatná), 22.X.1956 (V. Landa).

Nymph. Body relatively robust, with widened abdomen: width of tergum VI about 3 times greater than its length. Distal row of bristles on dorsal surface of labrum in its lateral parts very dense. Tarsi with dense long bristles on inner margin; besides, in fore tarsi all surface covered by dense long hairs. Claws with long row of denticles on inner margin. Abdominal terga

I-VIII without denticles on hind margin, terga IX and X with small pointed denticles. Posterolateral spines developed only on segment IX.

Caucasica group (Figs 10-45)

Nymph. Body slender, with long narrow abdomen: width of tergum VI slightly more than twice its length. Distal row of bristles on dorsal surface of labrum sparse, including its lateral parts (Fig. 23). Tarsi with minute sparse bristles on inner margin; fore tarsi with sparse long hairs (Figs 27-29). Claws with very short row of denticles on inner margin (usually occupying no more than half of claw length (Figs 17, 35, 36). Hind wing pad pointed (Figs 21, 26). Abdominal terga I-IX without denticles on hind



Figs 10-21. *Habroleptoides caucasica* Tshernova. 10-15, male imago: 10, genitalia, 11-12, head (dorsal and ventral view), 13, fore and hind wings in the same scale, 14, hind wing, enlarged, 15, abdominal tergum VI (spread on slide); 16, female imago, hind wing; 17-21, mature nymph: 17, claw, 18, outline of abdominal sternum IX of male, 19, the same of female, 20, right half of abdominal tergum IV (mounted on a slide) with tergalia, 21, hind wing pad.

margin, only tergum X with small pointed denticles (Figs 37, 38). Posterolateral spines developed only on segment IX.

Imago. Thorax relatively small: length of mesonotum about 0.2 of fore wing length (in contrast to *H. confusa* which has mesonotum length about 0.3 of fore wing length, as in the bulk of Leptophlebiidae). Fore wings narrowed in proximal part; hind wings small, costal field distally to costal projection very short (Figs 13, 14, 42, 43) (in contrast to all other

Habrophlebiinae having long narrow costal field distally to costal projection).

This group includes *H. caucasica* Tshernova and *H. pontica* sp. n.

***Habroleptoides caucasica* Tshernova, 1931 (Figs 10-21)**

H. caucasica Tshernova, 1931: 216 (male and female imagos); Sartori, 1986: 921 (male and female imagos).

Material. Russia, Krasnodar Terr.: 24 ♂, 8 ♀ imagos (all reared from nymphs), 41 nymphs, Psekups River near railway st. Chinary, 5-6.VI.1988 (N. Kluge); Sochi, Lazarevskaya, Fokin gorge (= Rose gorge) near experimental station of the Russian Institute of Plant Protection: 1 ♂ imago, 2 ♂, 1 ♀ subimago (all reared from nymphs), 1 nymph, 8-12.VI.1988 (N. Kluge); 2 ♂, 1 ♀ imagos (all reared from nymphs), 1 nymph, 23-25.VIII.1991 (N. Kluge); 1 ♂ imago, 19.VIII.1985 (V. Ivanov); 11 ♂ imagos, Lazarevskaya, Tatyanskoje, left tributary of Psezuapse River, 28.VII.1988 (V. Ivanov); 1 nymph, Krasnaya Polyana, Paura River, 29.VI.1957 (L. Zhiltzova). Georgia, Abkhazia: 2 nymphs, Kodori River near Lata, 29.VIII.1982 (N. Kluge).

Nymph. Cuticle very light, unicolorous. Through the cuticle brown hypodermal patterns are visible: head with intensive dark patterns behind bases of antennae, with maculae on mandibles, transverse maculae on clypeus and labrum; thorax with intensive brown maculation; dorsal and ventral sides of fore femur largely brown, fore tibia with dark band at apex; middle and hind legs completely pale; abdomen with varying dark hypodermal patterns. Abdominal terga with varying coloration: it may be completely dark, with narrow light median line, with a pair of longitudinal submedian light stripes near anterior margin, or with more or less large light median macula at fore margin (as in Fig. 15, but not as in Fig. 44). Each abdominal sternum with a pair of more or less large dark lateral maculae; sterna can be largely light or largely dark. Tergaliae colourless with dark brown tracheae. Claws with 5-8 denticles somewhat larger than in *H. pontica*.

Subimago (pigmentation of the cuticle is described below). Thorax with contrasting dark brown patterns; wings light brownish; legs light with brown apex of femur and brown base of tibia; abdomen brown, caudal filaments colourless.

Eggs. Oval, about 0.16x0.07 mm. Surface with numerous narrow longitudinal irregular costae visible in light microscope (similar to that of *H. modesta* and *H. umbratilis* – see Gaino & Mazzini, 1984: Figs 2a-f).

***Habroleptoides pontica* sp. n.**

(Figs 22-47)

Holotype. ♂ imago (reared from nymph), Russia, Krasnodar Terr., Sochi, Lazarevskaya, Fokin gorge (=

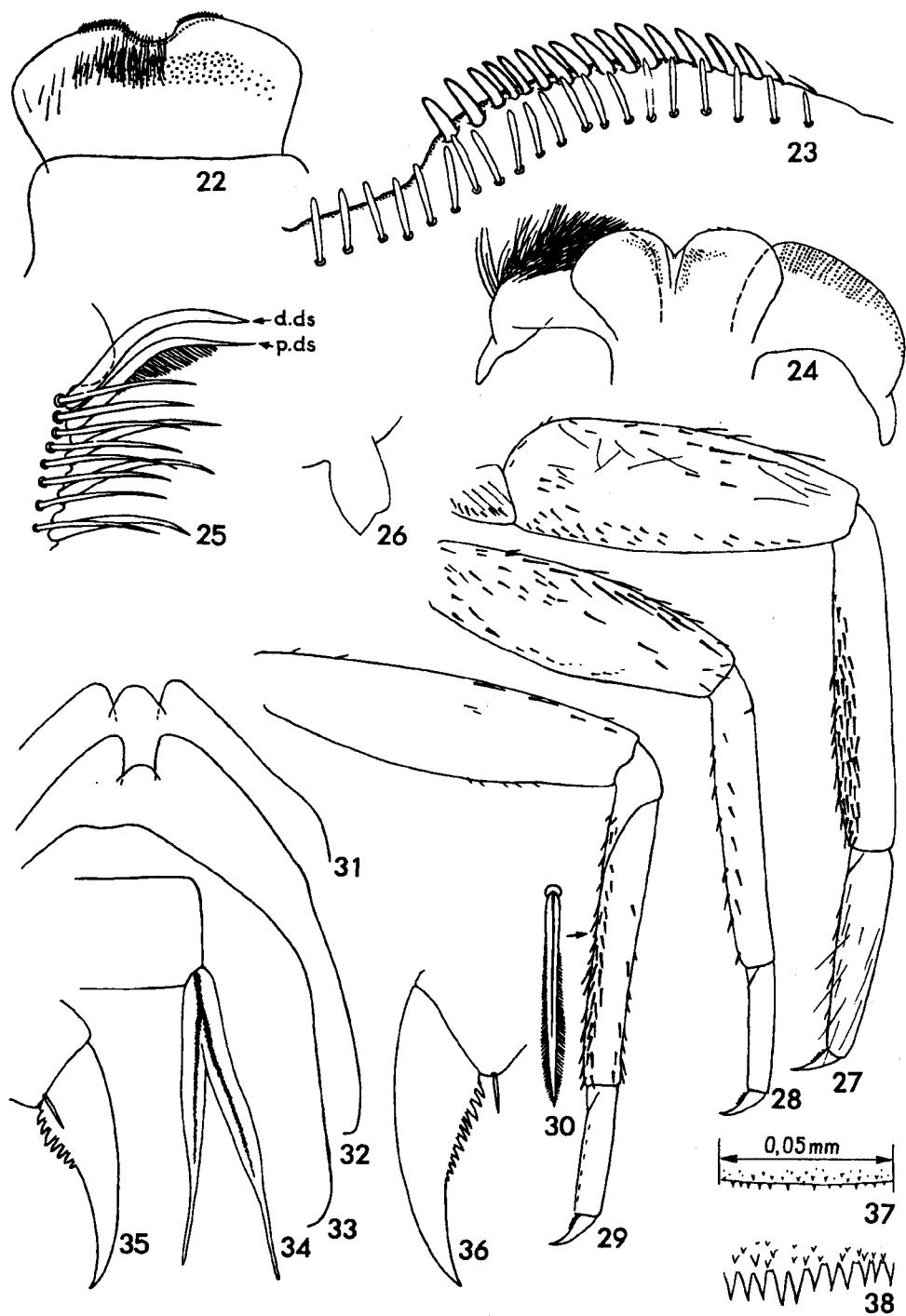
Rose gorge) near experimental station of Russian Institute of Plant Protection, 24.VIII.1991 (N. Kluge) (deposited in the Zoological Institute, Russian Acad. Sci., St.Petersburg).

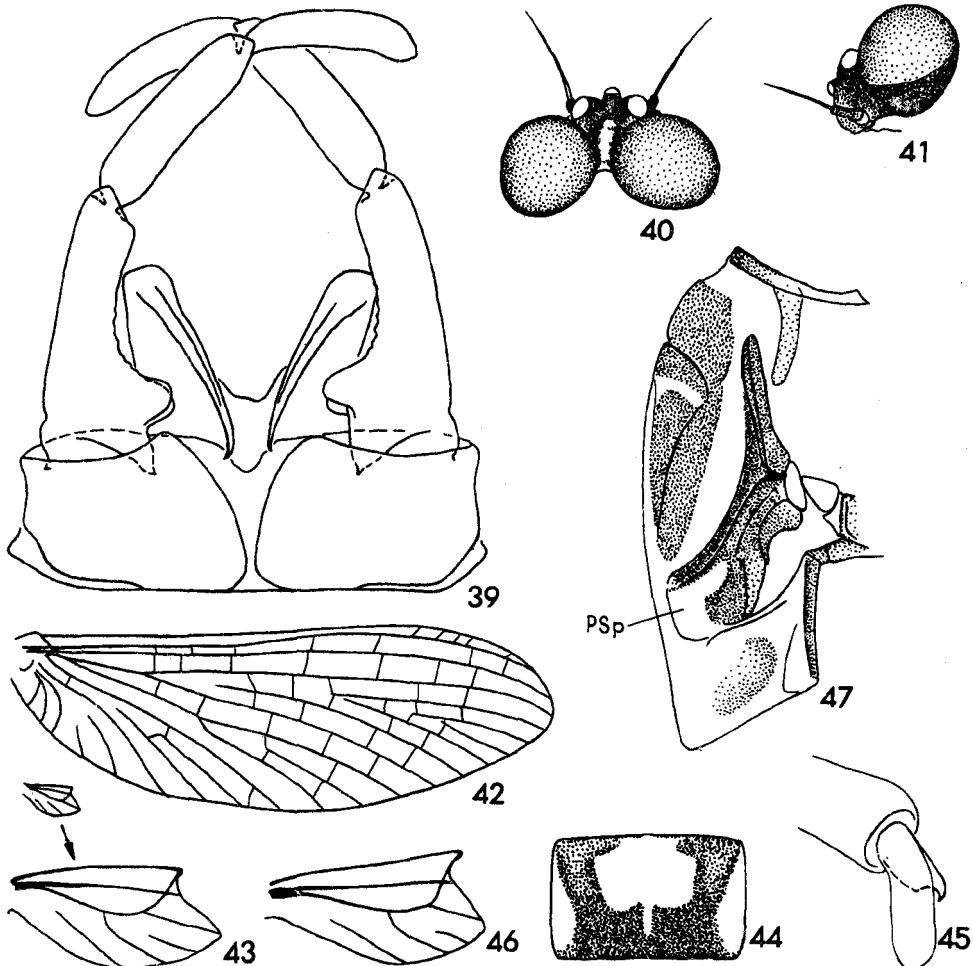
Paratypes. 9 ♂, 7 ♀ imagos, 2 ♂ subimagos (all reared from nymphs), 36 nymphs, the same locality as holotype, 20-27.VIII.1991 (N. Kluge); 4 ♂, 1 ♀ imagos, the same locality, 19.VIII.1985 (V. Ivanov); Lazarevskaya, Mamed gorge: 2 ♂ subimagos, 17.VIII.1985 (V. Ivanov); 1 ♂ subimago, 1 ♀ subimago, 19.VII.1988 (V. Ivanov); 1 nymph, Psekups River near railway st. Fanagoriyskoye, 25-27.VIII.1991 (N. Kluge).

Nymph. Cuticle very light, unicolorous. Through cuticle brown hypodermal patterns are visible: dark transverse band connecting oculi and ocelli (corresponds to head nerve ganglion); maculation on pro- and mesonotum; dark maculae on dorsal and ventral surfaces at middle and at apex of fore femur and at apex of fore tibia; indistinct dark macula on dorsal surface at apex of hind femur; contrasting dark brown patterns on each abdominal terga as in Fig. 44 (the same in both sexes and all ages); paired transverse brown maculae with dark brown tracheae. Claws with 7-12 small denticles.

Male imago. Body slender, with small thorax and head. Head dark brown with white longitudinal median stripe. Eyes separated mesally by distance equal to diameter of lateral ocellus. Upper portion of eyes dark grey, lower portion black. Pronotum yellowish with brown maculation. Meso- and metathorax light brown, pleura yellowish with dark brown maculation. Fore legs brown, with apex of femur and tibia darkened and tarsus becoming lighter toward apex. Middle and hind legs dull yellowish, with brownish band on femur apex. Claws of fore leg dissimilar, the hooked one very small. Wings hyaline with brown longitudinal and cross-veins. Fore wing narrowed proximally, hind wing small. Abdomen yellowish, terga II-IX with distinct contrasting brown patterns as in Fig. 44. Abdominal sterna II-VIII with indistinct brown stripe parallel to hind margin. Sternum IX brown, styliger dull yellowish, forceps brownish with distal segments paler. Dorsal plate of styliger without processes on sides of its median incisor. First segment of forceps with dorsal projection besides the inner one;

Figs 22-38. *Habroleptoides pontica* sp. n., nymph. 22, labrum, 23, left half of anterior margin of labrum (dorsal view), 24, hypopharynx, 25, inner-apical angle of left maxilla (dorsal view) (d.ds, dorsal dentiseta, p.ds, proximal dentiseta), 26, hind wing pad; 27-29, fore, middle, and hind legs; 30, bristle on inner margin of tibia; 31-32, outline of abdominal sternum IX of male; 33, the same of female, 34, right half of abdominal tergum IV (mounted on a slide) with tergalia, 35-36, claw, 37, hind margin of abdominal tergum IX, 38, the same of tergum X (26-29, 32, 35, holotype).





Figs 39-47. *Habroleptoides pontica* sp. n., imago and subimago. 39-45, male imago: 39, genitalia, 40-41, head (dorsal and ventral view), 42, fore and hind wings in the same scale, 43, hind wing enlarged, 44, abdominal tergum VI (mounted on a slide), 45, fore leg claw; 46, female, hind wings; 47, subimago: right half of mesonotal exuvia (PSp, posterior scutal protuberance). (39, 45, 47, holotype).

inner margin concave between appendages and apex of segment. Caudal filaments brownish yellow, with dark brown articulations.

Body proportions (dimensions divided by fore wing length) of holotype are as follows: mesonotum length - 0.19; maximum head width with eyes - 0.175; fore leg: femur - 0.31, tibia - 0.52, tarsus - 0.55; middle leg: femur - 0.17, tibia - 0.26, tarsus - 0.06; hind leg: femur - 0.19, tibia - 0.29, tarsus - 0.06.

Female imago. Head with frons dark brown, face anteriad antennae yellowish with white,

occiput posteriad lateral ocelli white. Colour of thorax, legs, wings, abdomen, and caudal filaments as in male.

Subimago (pigmentation of the cuticle is described). Thorax with contrasting dark brown patterns; wings and abdomen light brownish; legs light with brown apex of femur and base of tibia; caudal filaments colourless.

Eggs. Oval, about 0.15x0.07 mm. Surface without longitudinal costae (at least no costae visible in light microscope).

Dimensions. Length of fore wing of male and

female 5-6 mm.

Comparison. The new species clearly differs from all others in its hypodermal brown patterns on the abdominal terga, which are well developed in all stages and both sexes. In form of hind wing with short subcostal vein the new species differs from all *Habrophlebiinae* except for *Habroleptoides caucasica*; it differs from *H. caucasica* in the form of styliger and first segment of forceps. In the absence of submedian processes on dorsal plate of styliger ("processus d'accrochage du penis" according to Sartori, 1986), the new species differs from all *Habroleptoides* except for *H. assefae* Sartori & Thomas, 1986 and *H. malickyi* Gaino & Sowa, 1983; it differs from these species in the presence of dorsal projection on first segment of forceps.

Biology. In contrast to *H. caucasica*, whose imagos fly throughout the summer, *H. pontica* is probably a late summer species: all the material was collected in the end of summer, while in June 5-12 (1988), despite a careful search, neither imagos nor nymphs were found in the same locality.

References

- Belfiore, C. & Gaino, E. 1985. Le specie italiane del genere *Habrophlebia* Eaton, 1881 (Ephemeroptera, Leptophlebiidae). *Boll. Assoc. rom. entomol.*, 39(1-4): 11-18.
- Gaino, E. & Mazzini, M. 1984. Scanning microscope study of the eggs of some *Habrophlebia* and *Habroleptoides* species (Ephemeroptera, Leptophlebiidae). *Proc. IV Int. Conf. on Ephemeroptera, Czechoslovak Acad. Sci., Inst. of Entomol.*: 193-202.
- Kluge, N.Ju. 1993. New data on mayflies (Ephemeroptera) from fossil Mesozoic and Cainozoic resins. *Palaeontological Journ.*, 27(1A): 35-49.
- Kluge, N.Ju. 1994. Pterothorax structure of mayflies (Ephemeroptera) and its use in systematics. *Bull. Soc. ent. France*, 99(1): 41-61.
- Kluge, N.Ju. (in press). Phylogeny and higher classification of Ephemeroptera. *Proc. VII Int. Conf. on Ephemeroptera*.
- Peters, W.L. 1979. Taxonomic status and phylogeny of *Habrophlebia* and *Habroleptoides* (Leptophlebiidae: Ephemeroptera). *Proc. II Int. Conf. on Ephemeroptera, Pol. Acad. Sci., Lab. of Water Biol.*: 51-56.
- Peters, W.L. 1980. Phylogeny of the Leptophlebiidae (Ephemeroptera): an introduction. *Advances in Ephemeroptera Biology*, Plenum Publishing Corporation: 33-41.
- Peters, W.L. & Edmunds, G.F., Jr. 1970 Revision of the generic classification of the Eastern Hemisphere Leptophlebiidae (Ephemeroptera). *Pacific Insects*, 12: 157-240.
- Peters, W.L. & Da Terra, L.S.W. 1974. Description of the nymph and the phylogenetic relationships of *Calliarcys* Eaton from Portugal (Ephemeroptera, Leptophlebiidae). *Ciência Biol.* (Portugal), 1(3): 61-69.
- Sartori, M. 1986. Revision taxonomique du genre *Habroleptoides* Schönenmund, 1929 (Ephemeroptera, Leptophlebiidae) III. — Description de *H. annae* nov. sp. et de *H. thomasi* nov. sp. et synthèse finale des stades ailés. *Rev. suisse Zool.*, 93(4): 919-949.
- Schoenmund, E. 1929. *Habroleptoides*, eine neue Ephemeropterengattung. *Zool. Anz.*, 80(5/6): 222-232.
- Thomas, A.G.B. & Bouzidi, A. 1986. Trois Ephéméroptères nouveaux du Haut Atlas marocain (Héptageniidae, Baetidae, Leptophlebiidae). *Bull. Soc. Hist. Nat.*, Toulouse, 122: 7-10.
- Tshernova, O.A. 1930. Beiträge zur Kenntnis der paläarktischen Ephemeropteren. I. *Zool. Anz.*, 92(7/8): 214-218.
- Tsui, P.T.P. & Peters, W.L. 1972. The comparative morphology of the thorax of selected genera of the Leptophlebiidae (Ephemeroptera). *J. Zool.*, London, 168(3): 309-367, 55 figs.
- Ulmer, G. 1939. Eintagsfliegen (Ephemeropteren) von den Sunda-Inseln. *Arch. Hydrobiol.*, Suppl. 16: 443-692.

Received 11 January 1993.