

NEW DATA ON MAYFLIES (EPHEMEROPTERA) FROM MESOZOIC AND CENOZOIC RESINS

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Abstract: The Upper Cretaceous Siberian genus *Cretoneta* Chernova is transferred from the family Leptophlebiidae (infraorder Furcatergalia) to the family Siphonuridae *s. l.* (infraorder Pisciforma). Its type species, *C. zherichini* Chernova, is redescribed (based on male and female imagos and male subimago), and *C. acmoptera* sp. nov., based on male imago, is described. From the same locality, Palaeoanthidae fam. nov., of the superfamily Ephemeroidea (infraorder Furcatergalia), is described, with a single genus *Palaeoanthus* gen. nov. and two species — *P. orthostylus* sp. nov. (based on male and female subimagos and male imagos), and *P. minutus* sp. nov. (based on female imagos and subimagos). The new species of the family Leptophlebiidae — *Leptophlebia (Paraleptophlebia) electra* sp. nov. — is described from Baltic amber based on a male imago. Comparable diagnoses are given for the winged stages of the family Siphonuridae *s. l.*, superfamily Ephemeroidea, and family Leptophlebiidae. Age of the family Leptophlebiidae is discussed.

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Four of the mayfly species described were collected by staff from the Paleontological Institute, Russian Academy of Sciences, from Upper Cretaceous Taymyr retinite. Altogether, in this retinite six mayfly species have been found, two of which will be described later. The new species from Baltic amber is described here; more than 20 species have been described from the Baltic amber, including extant genera and even extant species.

Until recently, no definitive diagnoses of mayfly families based on characters of winged stages have been published. Therefore, some species described from fossil resins have incorrect family determinations. Here, I attempt to diagnose families and higher taxa properly.

ORDER EPHEMEROPTERA

SUBORDER ANTERITORNA KLUGE, 1992

Diagnosis. Fore wing tornus between CuA and CuP (or tornus possibly secondarily reduced) [6].

Composition. Three large infraorders — Pisciforma, Setisura and Furcatergalia — and probably one or several smaller infraorders.

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Diagnosis. Imagos and subimagos. (1) First tarsal segment (fused with tibia) usually not shortened. (2) If hind wings present, their MA bifurcate or unforked.

Composition. Superfamily Baetoidea.

SUPERFAMILY BAETOIDEA LEACH, 1815

FAMILY SIPHLONURIDAE BANKS, 1900 (*s. l.*)

Diagnosis. Imagos and subimagos. (1) Mesonotal suture distinct, transverse, usually more-or-less curved backward medially, forming angle (fig. 3a). (2) Furcasternal protuberances of mesothorax (containing bases of subalar-sternal muscles) contiguous, making median furcasternal impression absent (figs. 1a; 3b). (3) Paracoxa distinct not only on lateral side of episternum, but also on ventral side, completely separating katapisternum and anepisternum, both well developed (figs. 1a; 3a). (4) Tarsi five-segmented, with first segment fused with tibia and not greatly shortened (fig. 1c, h). (5) On fore wing CuA and CuP connecting basally forming acute angle (fig. 1i, j). (6) Cubital area of fore wing relatively narrow, usually with series of curved veins arising from CuA toward posterior margin of wing, but sometimes (in Recent genus *Metreletus* and the Cretaceous genus *Cretoneta* described below) with several intercalaries instead (figs. 1e, i, j; 3g, i).

Composition. *Cretoneta* Chernova from the Upper Cretaceous of Taymyr, a number of extant genera (Holarctic genera *Siphonurus*, *Parameletus*, *Ameletus*, *Metreletus*, et al.), and some extinct genera whose features have not been examined completely enough.

Remarks. In the last publications on Recent mayflies [6, 8, 10] the family Siphonuridae *s. l.* is divided into several smaller families, so that the Recent Holarctic genera *Siphonurus* and *Ameletus* are placed in different families. However, the composition and diagnoses of these small families are not yet clear; thus, it is expedient to accept the old broad definition of the family Siphonuridae, at least for the extinct groups, until their new systematics will be resolved.

Genus *Cretoneta*^{Tsl} Chernova, 1971

Cretoneta: Chernova, 1971: p. 614.

Type species. *C. zherichini*^{Tsl} Chernova, 1971.

Diagnosis. Imago and subimago. Anepisternum and katapisternum of mesothorax subequal (figs. 1a; 3a: AES, KES). First segment of middle and hind tarsi of male and female much (about 3 times) shorter than tibia, subequal to second segment (figs. 1c; 3j). First segment of fore tarsus of male long, not shorter than second segment (figs. 1h; 3d). Claws, at least on middle and hind legs of male and all legs of female, dissimilar: one blunt, another pointed (figs. 1c; 2a; 3j). Fore wing nearly oval, with tornus indistinct and hind margin short. Cubital area relatively short and wide, strongly narrowed apically, with few veins arising from CuA; sometimes only one of these

veins connected with CuA, while others intercalary (figs. 1e, i, j; 3g, i). Hind wings small, MA unforked (fig. 1j). Paracercus shortened (fig. 3c).

Composition. Type species, and *C. acmoptera* sp. nov.

Comparison. In form and venation of cubital area of fore wings *Cretoneta* differs from majority of Siphonuridae, and is similar only to the Recent west European *Metreletus* Demoulin, 1951; *Cretoneta* differs from *Metreletus* in longer first segment of fore tarsus of male, small size, oval wing, and diminished hind wing with unforked MA.

Discussion. Initially *Cretoneta* was placed in the family Leptophlebiidae [11]. It is similar to majority of Leptophlebiidae in small size and the characters connected with it: form of wings, and relatively large eyes of male. In the original description of *Cretoneta* the tarsal segments are figured incorrectly — they are shown as similar to those of Leptophlebiidae. But in the text of the original description no definitive characters have been mentioned as the basis on which *Cretoneta* was placed in the family Leptophlebiidae. Actually, *Cretoneta* has all characters of the family Siphonuridae as listed above (compare with the characters of Leptophlebiidae, listed below).

On the basis of the genital structure of *Cretoneta*, Chernova [11] regarded this genus to be related to the Jurassic genus *Mesoneta* (known from nymphs). Actually, similarity of the genital structures of *Cretoneta* and *Mesoneta* in only symplesiomorphic (styli^{clef}ger plate, forceps with two apical segments, penis bifurcate in its apical part - fig. 1d). Such genital structure is primitive for mayflies and is found in different, unrelated families. At the same time *Cretoneta* has a diverse genital structure and styli^{clef}ger plate, and penis may be more integral (fig. 3c). *Mesoneta* has plesiomorphic nymphal features of the paraphyletic group of infraorders Costatargalia (= Pisciforma + Setisura) [5] and probably belongs to Siphonuridae s. l., but there is no reason to regard *Cretoneta* and *Mesoneta* as more closely related.

Cretoneta zherichini ^{Tsh} Chernova, 1971

Cretoneta zherichini: Chernova, 1971: p. 614, figs. 1-4.

Holotype. PIN, No. 3130/4, inclusion in retinite, nearly complete specimen of male imago, without apex of the fore tarsi and without apex of the left fore wing; Taymyr, Maymecha River, basin of Khatanga River, Yantardakh; Upper Cretaceous, Upper Santonian, upper part of Kheta Formation.

Description. Male imago (fig. 1a-j). On all legs, including the fore ones, one claw is pointed, another blunt. Pterostigma has oblique anastomosing veins. Hind wing has slightly developed rounded costal projection. Styli^{clef}ger plate has very deep V-shaped incisor between forceps bases. Second segment of forceps is slightly curved. Penis is long, deeply V-shaped bifurcate, each bulb^{lobe} somewhat widened near its base. Rudiment of paracercus is long, and consists of several segments.

Female imago (fig. 2a, b). Postgenital plate is pointed. Wings and rudiment of paracercus are as in male.

Exuvia of male subimago (presumably assigned to this species) (fig. 2c). Abdomen, wings,

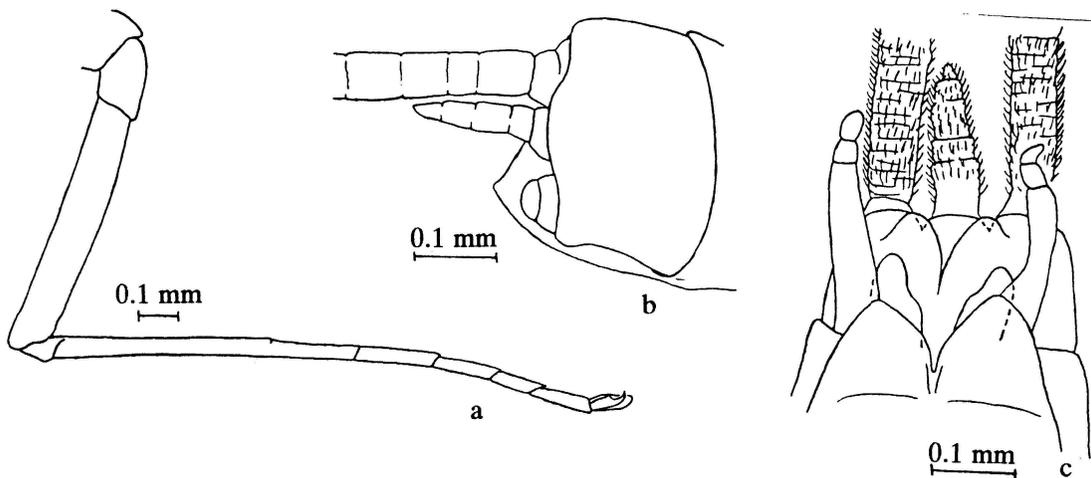


Fig. 2. *Cretoneta zherichini* Chern. *a, b* - female imago: *a* - Spec. No. 3311/598, fore leg; *b* - Spec. No. 3311/594 - apex of abdomen, dorsal view; *c* - exuvia of male subimago, Spec. No. 3311/595, apex of abdomen, ventral view.

legs, and part of thoracic sterna and pleura are covered by microtrichia; mesonotum is without microtrichia. All cuticle is colorless, without pigmented patterns on mesonotum. Divided penis bulbs have obtuse-angled projections on the inner side. Rudiment of paracercus is as in imago.

Dimensions. Length of fore wing - 4-5 mm.

Material. Holotypes, and from the same locality: No. 3130/9, paratype (fragment of male imago - head, thorax, right fore leg, left hind wing); No. 3311/593A (separate well-preserved fore wing; together with fragments of other specimens); No. 3311/593B (fragment of male imago - ventral side of thorax and abdomen, hind wing and intact genitalia; together with fragments of other specimens); No. 3311/594 (fragment of female imago - ventral side of the body, legs, wings, apex of abdomen; together with fragments of two other female imagos); No. 3311/595 (fragment of male imago - ventral part of head and thorax, left fore leg, and nearly intact left wings; together with exuvia of male subimago without head, prothorax and fore legs); No. 3311/598 (nearly intact female imago without abdominal segment X); No. 3311/599 (male imago - left half of head and thorax, right fore, left middle, and both hind legs, abdomen, and genitalia); No. 3311/600 (male imago - thorax, wing bases, middle and hind legs, abdomen genitalia); Nos. 3311/611, 3311/613-3311/634 (many specimens and fragments of male and female imagos and subimagos).

Cretoneta acmoptera Kluge, sp. nov.

Specific name. From Greek *acmo* (acute) and Greek *pteron* (wing).

Holotype. PIN, No. 3311/592, inclusion in retinite; nearly intact specimen of male imago without apex of left fore tarsus, without left middle leg, and without apex of left fore wing;

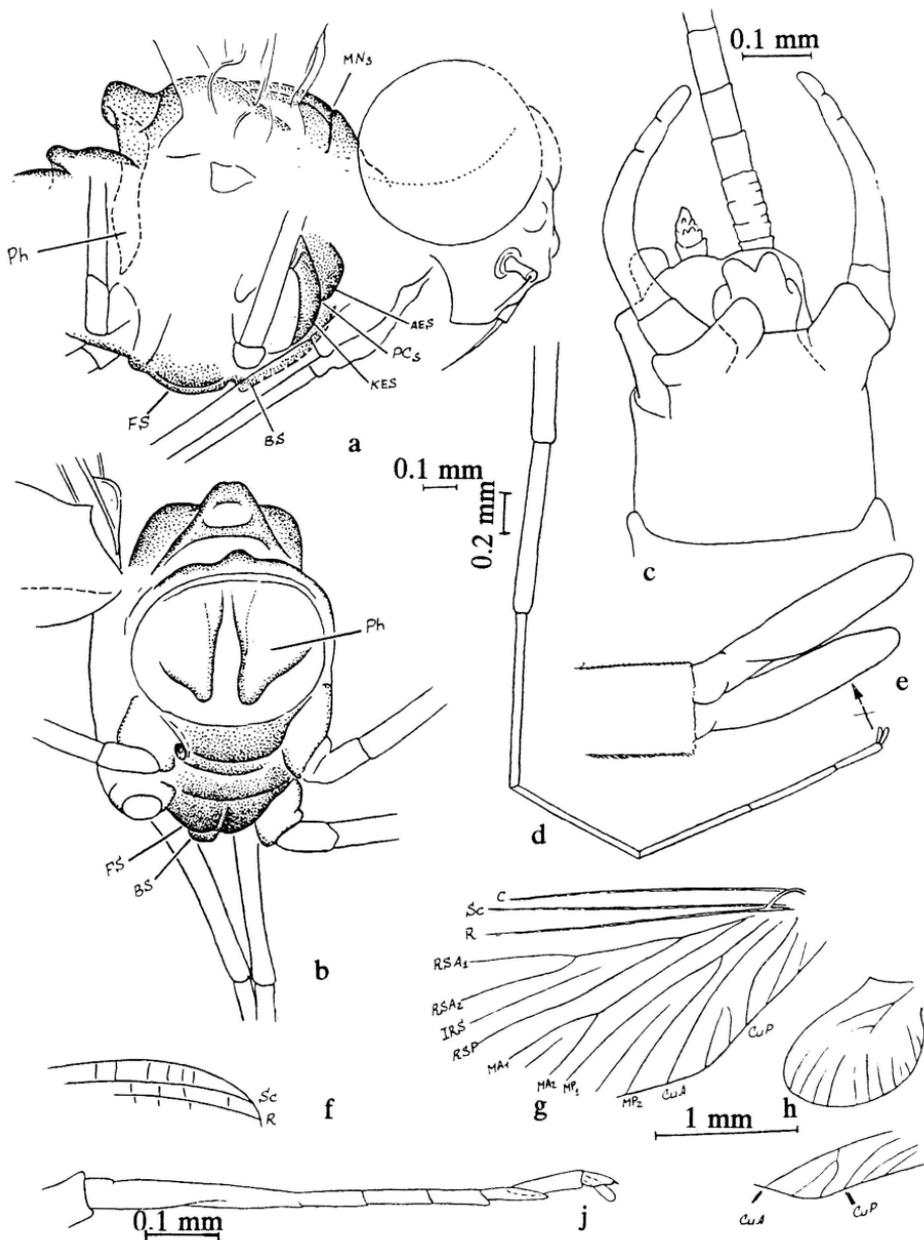


Fig. 3. *Cretoneta acmoptera*, sp. nov.; male imago, Holotype No. 3311/592: *a* - head and thorax, lateral view; *b* - thorax, caudal view; *c* - apex of abdomen, ventral view; *d* - fore leg; *e* - fore leg claws; *f-i* - fragments of wings; *j* - tibia and tarsus of hind leg. AES - anepisternum of mesothorax, RS - basisternum of mesothorax, FS - furcasternum of mesothorax, KES - karepisternum of mesothorax, MNs - mesonotal suture, PCxs - paracoxal suture, Ph — phragma.

Taymyr, Maymecha River, basin of Khatanga River, Yantardakh; Upper Cretaceous, Upper Santonian, upper part of Kheta Formation.

Description. Male imago (fig. 3*a-j*). Thorax and abdominal segments VII-X are pigmented, abdominal segments I-VI, legs, forceps, and caudal setae colorless. On fore legs both claws are blunt. Pterostigma has several simple unbranched veins perpendicular to Sc. Hind wing has acute costal projection. Styliger plate has trapeziform incisor between forceps bases. Second forceps segment strongly curves in middle, apical segments are slightly separated one from another. Penis is short, in most of its length fused with pair of round lateral protuberances, and pair of short rounded apices with V-shaped incisor between them. Rudiment of paracercus is short.

Dimensions. Length of fore wing - 3.5 mm.

Comparison. The new species differs from *C. zherichini* in the structure of genitalia, acute costal projection of hind wing, and blunt claws of fore legs of male imago.

Material. Holotype.

INFRAORDER FURCATERGALIA KLUGE, 1989, *s. str.*

Diagnosis. Imagos and subimagos. (1) First tarsal segment (fused with tibia) strongly shortened (figs. 4*e*; 5*h, i*) (with exception of weak or generally shortened tarsi). (2) If hind wings present, their MA unforked (fig. 4*b*).

Composition. Superfamilies Ephemeroidea *s. l.*, Caenoidea, Ephemerelloidea, Leptophlebioidea.

Remarks. This infraorder must be accepted in the narrow sense, without the superfamily Baetiscoidea (= Prosopistomatoidea) which was initially included in the suborder Furcatergalia [5], but actually is not related to it [6].

SUPERFAMILY ^EEPHEMEROIDA LATREILLE, 1870

Diagnosis. Imagos and subimagos. (1) Mesonotal suture more-or-less strongly curved backward in its lateral portions (sometimes disappearing). (2) Furcasternal protuberances of mesothorax contiguous, so median furcasternal impression absent (fig. 4*g*) (contra to other Furcatergalia). (3) Paracoxal suture on ventral side of episternum becoming shallow and indistinct (figs. 4*g*; 5*m*). (4) Legs developed or rudimentary; if well developed, tarsal structure typical for Furcatergalia. (5) On fore wing CuA and CuP connecting basally, forming acute angle; basal parts of CuA and MP₂ curved, strongly divergent with MP₁ (figs. 4*c, d, g*; 5*f, k*) (besides Ephemeroidea, such venation present only in Neoephemeridae).

Composition. Extant families Ephemeridae *s. l.* (incl. Palingeniidae), Potamanthidae, Euthyplociidae, Polymitarciidae, Behningiidae, and Cretaceous families Torephemeridae Sinitshenkova, 1989 (known only from nymphs), and Australiphemeridae McCafferty, 1991 (known from imagos).

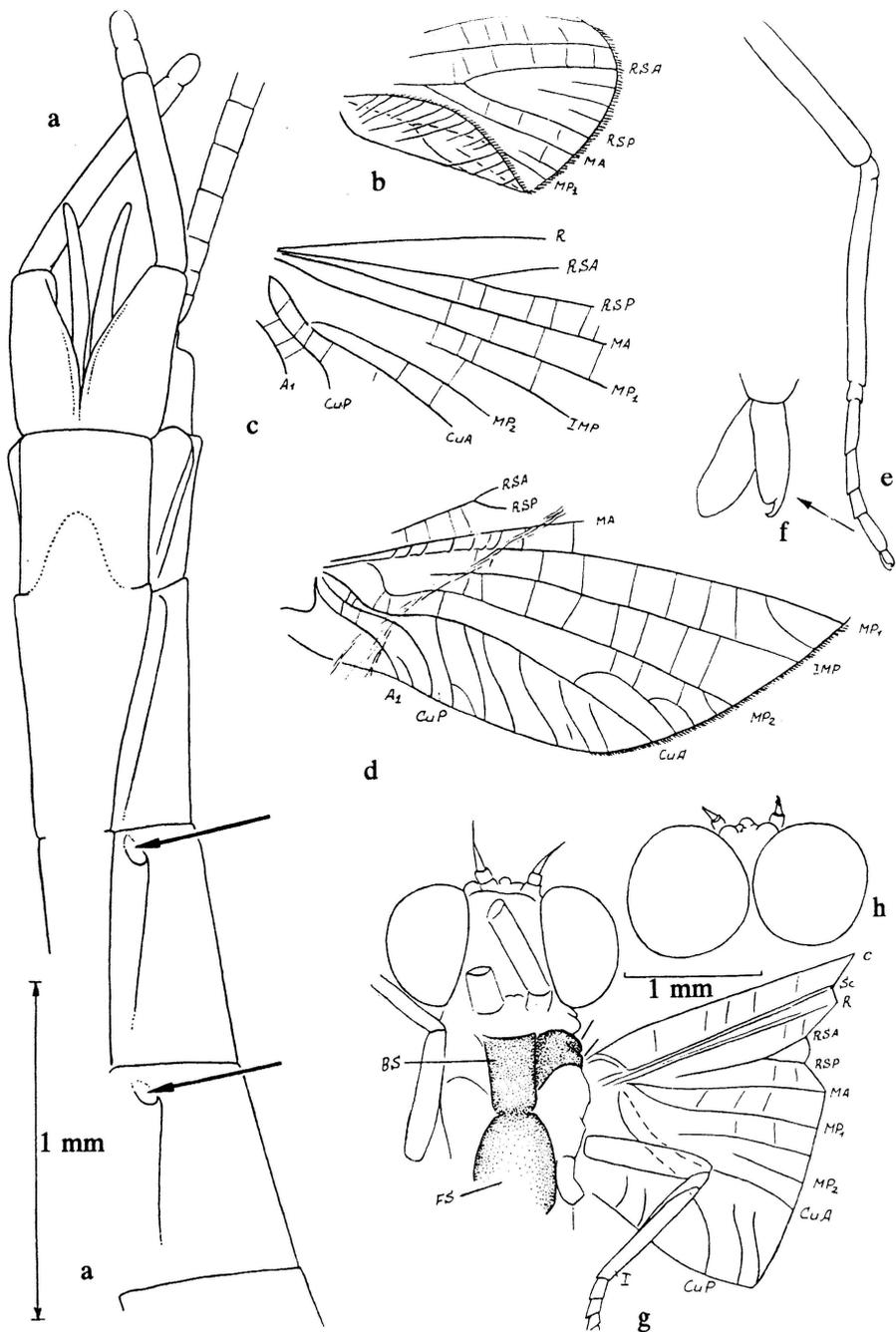


Fig. 4. *Palaeoanthus orthostylus* sp. nov.: a-d - Holotype No. 3311/601, male subimago; a - distal part of abdomen, ventral view (pointers show traces of tergal-bases); b - fragment of hind wing, c-d - fragments of fore wings; e, f - paratype No. 3311/611, female subimago; e - fore leg, f - claw; g, h - paratype No. 3311/610, male imago; g - head and thorax, ventral view, h - head, dorsal view. Designations as in Fig. 3b, c, d, e, g, h - all same scale.

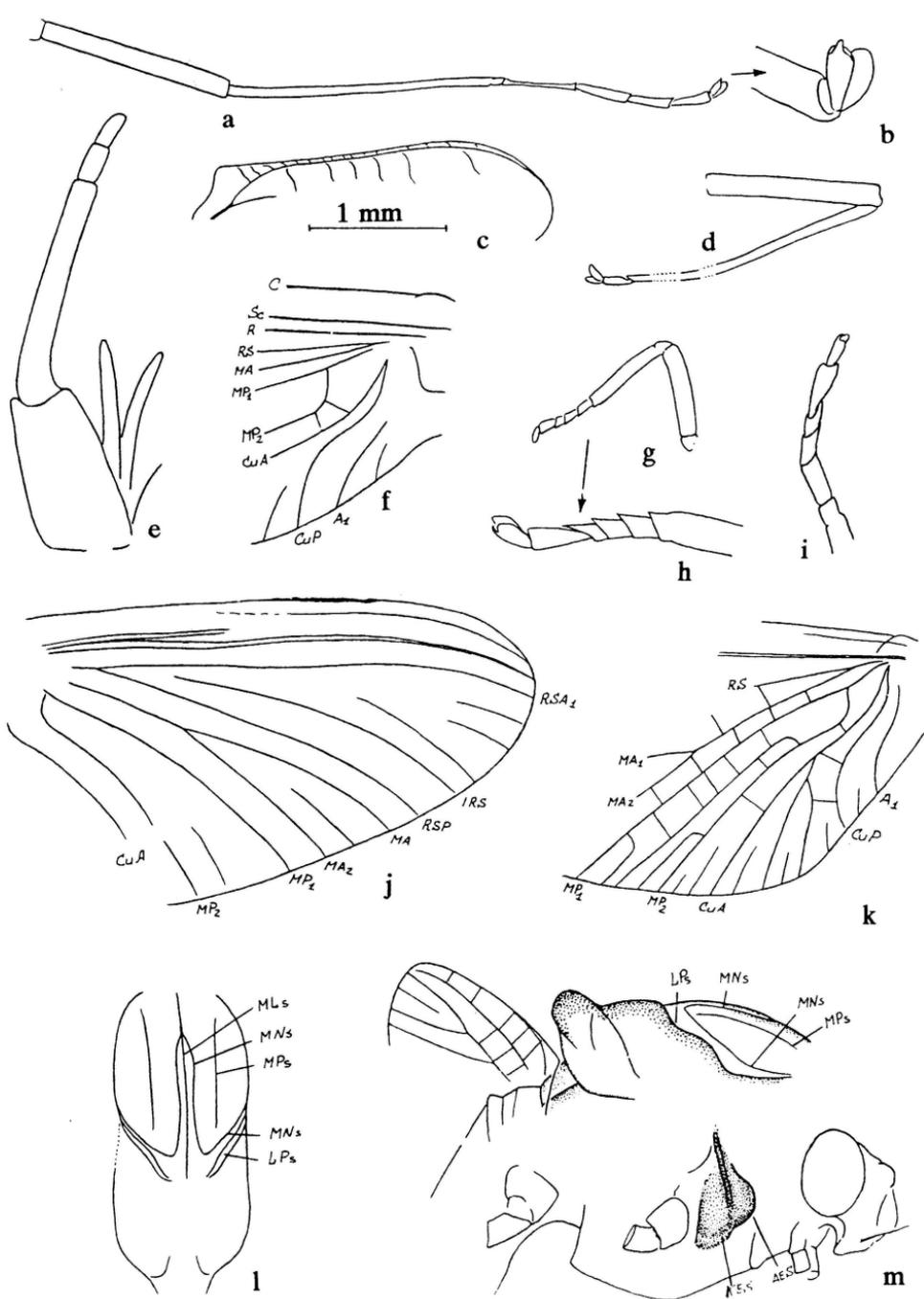


Fig. 5. *Palaeoanthus* spp. *a-f* - *P. orthostylus* sp. nov., paratype No. 3311/609, male imago: *a* - fore leg, *b* - claws, *c* - costal margin of hind wing, *d* - hind leg, *e* - genitalia, *f* - fragment of fore wing; *g-m* - *P. minutus* sp. nov., female imagos; *g-j* - paratype No. 3311/605: *g*, *h* - hind leg, *i* - tarsus of fore leg, *j* - fragment of fore wing; *k-m* — holotype No. 3311/604: *k* - fragment of fore wing, *l* - mesonotum from inside, *m* - head and thorax, lateral view (fore wing not shown). LPs - lateroparapsidal suture, MLs - median suture, MNs - mesonotal suture, MPs - medioparapsidal suture. *a*, *c*, *d*, *f*, *g*, *i*, *j*, *k* - all the same scale.

Diagnosis. Imagos and subimagos. Prothorax short (figs. 4g; 5m) (contra Ephemeridae). On fore wing, furcation of MA far from wing base (fig. 5j) (contra Euthyplociidae, Polymitarciidae, Behningiidae, Palingeniidae); basal arch of MA₂ strongly developed (figs. 4d; 5f, k) (contra taxa above and Australiphemeridae); A₁ unforked (contra Potamanthidae), no veins arising from A₁ toward hind margin of wing (contra Ephemeridae). On hind wing, furcation of RSA and RSP not far from furcation of RS and MA (figs. 4b; 5m) (contra Potamanthidae); costal projection of hind wing obtuse (fig. 5c). Legs well developed, structure of tarsus typical for Furcatergalia; on each leg one claw blunt (figs. 4f; 5h). On abdomen, traces of nymphal tergalia on bases (visible in subimago) on all segments I-VII having primitive position on hind part of segment (fig. 4a) (contra Ephemerinae and Hexagenitinae in family Ephemeridae, with bases of tergalia VII strongly turned anteriorly). On forceps (figs. 4a; 5e) with two apical segments (contra Euthyplociidae), first segment not developed, being completely fused with second segment (as Potamanthidae and Euthyplociidae, but contra Ephemeridae and Polymitarciidae). In male and female, paracercus long, subequal to cerci. Females molting in winged stage (contra Polymitarciidae, Behningiidae and Palingeniidae).

Composition. *Palaeoanthus* gen. nov.

Distribution. Upper Cretaceous of Siberia.

Comparison. The family Palaeoanthidae is similar to Potamanthidae in the complex of symplesiomorphies and in reduction of first segment of forceps; but it differs from Potamanthidae by unforked A₁ of fore wing and short stem of RSA+RSP on hind wing [1]. The same features of wing venation are present in Cretaceous Neotropical family Australiphemeridae [8], but, in contrast to them, Palaeoanthidae have MP₂ curved as strongly, as in Potamanthidae and Ephemeridae.

Genus *Palaeoanthus* Kluge, gen. nov.

Generic name. Greek *palaios* (old), and Greek *anthus* (flower).

Type species. *P. orthostylus* sp. nov.

Diagnosis. Femora 6 times shorter than body length, tarsi shorter than tibia.

Composition. Type species, and *P. minutus* sp. nov.

Palaeoanthus orthostylus Kluge, sp. nov.

Specific name. From Greek *ortho* (straight) and Greek *stylus* (forceps).

Holotype. PIN, No. 3311/601, inclusion in retinite; hind part of body of male subimago: impression of mesothoracic scutellum, crumpled wings, most of abdomen with well-preserved genitalia and one caudal seta (right cercus); Taymyr, Maymecha River, basin of Khatanga River, Yantardakh; Upper Cretaceous, Upper Santonian, upper part of Kheta Formation.

Description. Male subimago (fig. 4a-d). Cubital area of fore wing is long and narrow, narrowing toward apex; veins arising from CuA are mostly unbranched. Styli-plate is long and narrow, medially deeply V-shaped cleft; forceps are cylindrical, long and straight; penis-bulbs are very long and slender, completely separated.

Male imago (figs. 4g, h; 5a-f). Eyes are large, contiguous dorsally. Femora of all legs are subequal, 6 times shorter than body length; tarsus is shorter than tibia. Genitalia are nearly the same as in subimago, only apical segments of forceps are a little longer.

Female subimago (fig. 4e, f). Wings are as in male. On fore leg, tarsus is slightly shorter than tibia.

Dimensions. Body length - 9 mm.

Material. Holotype and from same locality, paratype: male subimago No. 3130/13 (apex of abdomen with well-preserved genitalia); male imago No. 3311/609 (ventral and left side of thorax, left eye, base of left fore wing, crumpled hind wing, legs, genitalia; together with genitalia of another male imago); male imago No. 3311/610 (head, ventral part of thorax, base of fore wing, parts of legs); female subimago No. 3311/611 (proximal part of right fore wing, fore leg; together with male subimago of *Cretoneta zherichini* Chern.).

Palaeoanthus minutus Kluge, sp. nov.

Specific name. From Latin *minutus* (small).

Holotype. PIN, No. 3311/604, inclusion in retinite; female imago: head and thorax with crumpled sterna, without legs, with proximal part of right fore wing and crumpled hind wings, abdomen; Taymyr, Maymecha River, basin of Khatanga River, Yantardakh; Upper Cretaceous, Upper Santonian, upper part of Kheta Formation.

Description. (fig. 5g-m). Female imago. Mesonotal suture is very strongly curved backward in its lateral portions, running close to median suture and lateroparapsidal sutures. Cubital area of fore wing is short and wide, with single forked vein arising from CuA and several intercalaries. Femora are 6 times shorter than body length, tarsus shorter than tibia.

Exuviae of female subimagos. Structure of mesonotum and legs are the same as in imago.

Dimensions. Length of body and fore wing - 4 mm.

Comparison. *P. minutus* sp. nov. differs from *P. orthostylus* in smaller size and shorter cubital area of fore wing with fewer veins arising from CuA.

Material. Holotype, and from same locality: female imago No. 3311/605 (ventral side of head and thorax, left fore wing, legs); imago No. 3311/606 (proximal parts of wings, fragments of legs); exuviae of two female subimagos Nos. 3311/607 and No. 3311/608.

SUPERFAMILY LEPTOPHLEBIOIDEA BANKS, 1990

Includes the single family - LEPTOPHLEBIIDAE.

FAMILY LEPTOPHLEBIIDAE BANKS, 1900

Diagnosis. Imagos and subimagos. (1) Mesonotal suture poorly visible, being strongly elongate and curved backward in its lateral portions, running close to median suture and lateroparapsidal sutures (as in fig. 5*l, m*) (sometimes disappearing). (2) Furcasternal protuberances of mesothorax distinctly separated by median furcasternal impression [12: figs. 49-51]. (3) Paracoxal suture on ventral side of episternum becoming shallow and indistinct [12: figs. 49-51]. (4) Legs well developed, with tarsi 5-segmented, tarsal structure typical for Furcatergalia: first segment fused with tibia and greatly shortened. (5) On fore wings, base of CuP strongly curved, turning from base of CuA toward base of PCu (fig. 6*b*). (6) Cubital area of fore wing with intercalaries.

Composition. Two subfamilies — Leptophlebiinae and Atalophlebiinae Peters, 1980.

SUBFAMILY LEPTOPHLEBIINAE BANKS, 1900

Diagnosis. Male imagos. (1) Styliger plate deeply cleft. (2) Upper part of eyes with usual hexagonal facets (in Atalophlebiinae facets of upper eye square).

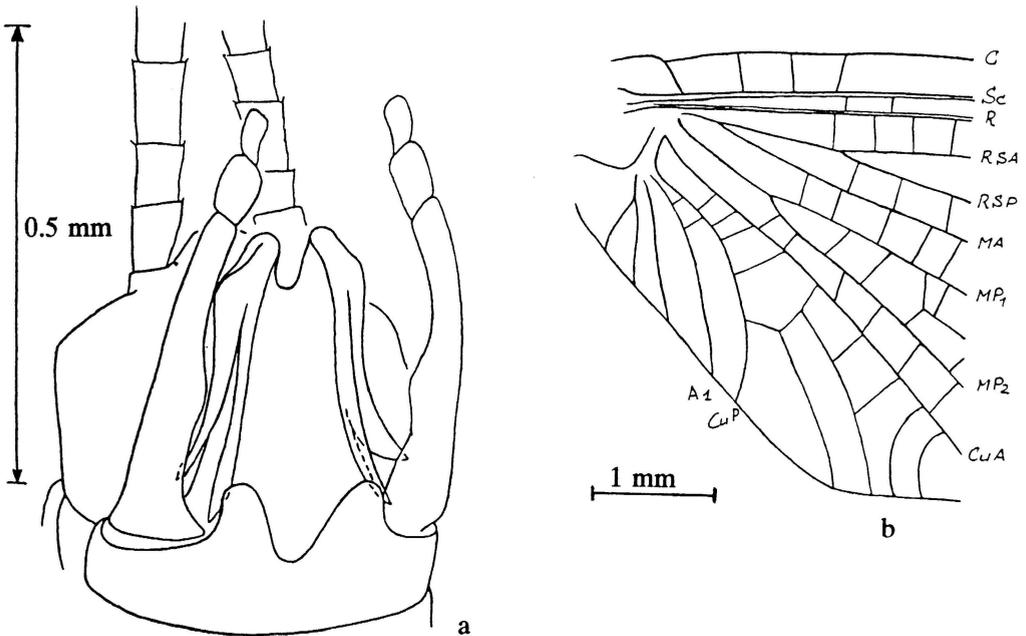


Fig. 6. *Leptophlebia (Paraleptophlebia)* spp. *a* - *L. (P.) electra* sp. nov., holotype No. 363/90, male imago: genitalia; *b* - *L. (P.) cincta* (Retzius, 1783) (Recent, Europe): proximal part of fore wing.

Composition. About 6 Recent genera, one of which, *Leptophlebia* s. l., is also known from Baltic amber.

Genus *Leptophlebia* Westwood, 1840, s. l.

Type species. *L. vespertina* (Linnaeus, 1758) (originally *Ephemera*; Recent, west Palaearctic).

Diagnosis. (1) Basisternum of mesothorax with longitudinal carina [12: figs. 49-51]. (2) Longitudinal furcasternal impression of mesothorax [12: figs. 49-51]. (3) Claws on all legs (including fore legs of male) dissimilar: one blunt, another pointed. (4) On fore wings, furcation of MA asymmetrical, and (5) furcation of MP close to wing base [3: fig. 33a, c; 4: figs. 7; 8a; 9]. (6) Hind wings well developed, without costal projection, with Sc terminating near wing apex, and with costal field narrow over all its length [4: fig. 8c].

Composition. About 70 Recent Holarctic species, and probably three species from Baltic amber (see below).

Remarks. Here this genus is accepted in the wide sense, including the subgenus *Paraleptophlebia* Lestage, 1917, which some authors regard as a separate genus.

Subgenus *Paraleptophlebia* Lestage, 1917

Leptophlebia (*Paraleptophlebia*) *electra* Kluge, sp. nov.

Specific name. From Greek *electron* (amber).

Holotype. PIN, No. 363/90, inclusion in amber; nearly intact specimen of male imago with broken paracercus; Baltic, Upper Eocene.

Description. Male imago (fig. 6a). Thorax and abdomen are brown, foreceps and caudal setae are light, penis brown with light ventral appendages. Eyes are large and contiguous. Penis ^{lobes}bulbs fuse for large distance, divided only on apex by roundish incisor; from its apices toward base runs two pairs of long, flat, slightly curved processes. Structures of eyes, thorax, legs, and wings, have features of the infraorder, family, subfamily, and genus listed above.

Dimensions. Length of fore wing - about 6 mm.

Comparison. New species distinctly differs from *L. (P.) prisca* (see below) in less deep incisor between penis ^{lobes}bulbs; it differs also from the majority of Recent species of genus in same feature.

Discussion. On the basis of the penis structure, which is similar to that of the type species of *Paraleptophlebia* - Recent *L. (P.) cincta* (Retzius, 1783) — this species is placed in the subgenus *Paraleptophlebia*. In both species penis ^{lobes}bulbs are divided by a wide roundish incisor and have ventral processes which run from the penis apices toward its base, but at the same time these appendages are not contiguous medially (contra *Leptophlebia* s. str.).

Until now, only one species of *Leptophlebia* — *L. (Paraleptophlebia) prisca* (Pictet, 1856)

(originally placed in *Potamanthus*) (from the Baltic amber) — has been described. Lectotype of this species (designated by Demoulin, 1968) is male imago without apex of abdomen and genitalia [3]. As determination of species of *Leptophlebia* is impossible without male genitalia, it is unclear which species should carry the name *L. (P.) prisca*. Demoulin placed in *L. (P.) prisca* the male subimago, which has deeply separated penis ^{lobes} ~~bulbs~~, and with apices curved laterally [3: fig. 32b], and also the male imago, with penis ^{lobes} ~~bulbs~~ deeply separated, but whose apices are not curved laterally [3: fig. 33d]. Judging by the figures, these specimens probably belong to different species. Demoulin also placed in *L. (P.) prisca* the male imago with poorly preserved genitalia [3: fig. 31], and the paralectotypes: female subimago, male subimago, and fragment of male imago [3: fig. 30]. His illustrations do not allow determination of these specimens. In his later paper Demoulin [4] placed in *L. (P.) prisca* also the specimens (male imagos) described by him earlier as *Oligophlebia calliarcys* Demoulin, 1965, and *Oligophlebia ? longiceps* Demoulin, 1965 [2]. For the first, genitalia are figured [2: fig. 2]. Thus, the difference described above in genital structure between *L. (P.) prisca* and the new species is attributed not to the lectotype of *L. (P.) prisca*, but to the three male specimens with preserved penes that have been assigned to this species.

Material. Holotype.

REMARKS ON THE AGE OF CERTAIN FAMILIES OF MAYFLIES

Siphonuridae *s. l.* is a very old and primitive family, known from the Jurassic until the Recent. *Cretoneta* was regarded as one of the oldest representatives of the family Leptophlebiidae, proving the presence of Leptophlebiidae in the Mesozoic. Since the genus *Cretoneta* has now been transferred to the family Siphonuridae, such an old age of the family Leptophlebiidae becomes doubtful.

Formerly, the family Leptophlebiidae was regarded as primitive, paraphyletic, and ancestral to Ephemeroidea and other Furcatergalia [5], but now it becomes clear that it is a holophyletic taxon [6, 7, 8]. This is proven by the apomorphies in the structure of nymphal maxillae. The structure of the imaginal furcasternum of Leptophlebiidae is more progressive than that of Ephemeroidea: the appearance of median impression between the furcasternal protuberances in Leptophlebiidae is connected with displacement of the metathoracic nerve ganglion anteriorly, into the mesothorax, between the bases of the subalar-sternal muscles (in Ephemeroidea and other mayflies with primitive furcasternal structure, the metathoracic nerve ganglion is situated in the metathorax, behind these muscle bases, which are close together). Therefore, Leptophlebiidae cannot be ancestral to Ephemeroidea, and can be much younger.

As was shown earlier [5], the Mesozoic genera *Mesoneta* and *Mesobaetis*, which are known from nymphs and were placed by some authors in the family Leptophlebiidae, cannot belong to this family, because they have the structure of caudal setae and tergalia typical for the paraphyletic group of infraorders Costatergalia (= Pisciforma + Setisura), but not for the infraorder Furcatergalia. Some other Mesozoic species have also been placed in the family Leptophlebiidae — *Leptoneta calyprata* Sinitshenkova, 1989, from the Upper Cretaceous of Mongolia [9], and "*Leptophlebiidae* (?) sp. 1, sp. 2, sp. 3," from the Lower Cretaceous of Brazil [7]. The systematic position of these species is not quite clear, as no apomorphies of Leptophlebiidae are mentioned in their descriptions.

Demoulin [3] placed in the family Leptophlebiidae two monotypic genera — *Xenophlebia*

Demoulin, 1968, and *Blasturophlebia* Demoulin, 1968, from Baltic amber. *Blasturophlebia hirsuta* Demoulin, 1968 (based only on subimaginal exuvia), may belong in Leptophlebiidae or in Ephemeroidea. But *Xenophlebia aenigmatica* Demoulin, 1968 (based on well-preserved male imago), is similar to *Cretoneta* and may belong in Siphonuridae. *l.*: contra true Leptophlebiidae, CuA and CuP of fore wings arise from the same point, distinct mesonotal suture is siphonurid type, first tarsal segments are not much shortened and paracercus is very strongly reduced [3: fig. 35a, e]. Therefore, the oldest mayflies, which undoubtedly belong to Leptophlebiidae, are species of the subgenus *Paraleptophlebia* from Baltic amber.

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