

New Jersey amber mayflies: the first North American Mesozoic members of the order (Insecta; Ephemeroptera)

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Abstract

The following new genera and species of mayflies are described from Upper Cretaceous (Turonian) amber from Sayreville, New Jersey, U.S.A: *Cretomitarcys luzzii* (imago male), (Polymitarciidae: Cretomitarcyinae, new subfamily), *Borephemera goldmani* (imago male, Australiphemeridae), *Amerogenia macrops* (imago female) (Heptageniidae) and *Palaeometropus cassus* (subadult male) (Ametropodidae). Previously no mayflies were described from the Mesozoic of North America. Ametropodidae and Heptageniidae are newly recorded for the Mesozoic, and Australiphemeridae for the Upper Cretaceous. The mayflies in this amber probably inhabited a medium-sized or large river. Zoogeography of Upper Cretaceous mayflies is briefly discussed; with particular emphasis on significant faunistic differences between the temperate and subtropical areas.

Introduction

Through the kindness of Dr. D. Grimaldi (Department of Entomology, American Museum of Natural History, New York) I have had an opportunity to examine five mayfly specimens found among a large collection of fossil insects enclosed in Late Cretaceous amber of New Jersey. This material is interesting and important in several respects.

The fossil record of mayflies is rather good in comparison to many other insect orders, and many extinct taxa have been named (Hubbard, 1987). The mode of mayfly burial and preservation as fossils has never been a subject of special study but undoubtedly the remains of nymphs and nymphal exuvia of lentic species constitute the bulk of the material. It is not surprising because ancient lake sediments provide the main source of information on fossil insects in general. However, the lacustrine assemblages of mayflies are usually poor in species, and many families seem to be unrepresented or at least strongly underrepresented. Though mayfly nymphs are

often abundant in drift of modern rivers, lotic nymphs seem to be very rare in the fossil record like other insects inhabiting running waters (Zherikhin, 1980; Sinitshenkova, 1987). The alate mayflies are extremely short-lived, and the probability is quite low of an occasional burial for the flying stages of a lotic species in lake sediments. Thus, probably the largest part of past mayfly diversity became lost as a result of taphonomy. In contrast, the winged stages of mayflies are not rare in fossilized resins, and in this case lotic species seem to be represented much better. Both subadult and adult mayflies often rest at tree trunks, where they can be easily trapped by and entirely engulfed by liquid resin. Taphonomy of the Sayreville, New Jersey amber deposit indicates that the amber was deposited very close to the source and in a deltaic environment with deep sands, clays, and organic debris, including wood. Resin is easily transported by flowing rivers along with drift wood and bark. Also, lotic insects are rather common among amber inclusions (Ulmer, 1912; Wichard and Weitschat, 1996). Thus mayflies enclosed in

amber may compensate for the most significant bias in the rock fossil record of the order.

Up to now mayflies inclusions in amber have been recorded from the Upper Cretaceous of Taymyr Peninsula, North Siberia (Tshernova, 1971; Kluge, 1993, 1997); from the Eocene Baltic amber, Europe (Larsson, 1978; Kluge, 1993; Wichard and Weitschat, 1996); Fushun amber, China (Hong, 1979); from the Oligocene and Miocene ambers of the Dominican Republic (Poinar, 1992) and Chiapas, Mexico (Wichard and Weitschat, 1996), as well as from the Saxonian amber (Wichard and Weitschat, 1996), but they have been only partially described and a few are named. A single mayfly inclusion is discovered in the collection of apparently Cretaceous Burmese amber in the Natural History Museum, London (Sinitshenkova, 2000). A mayfly from the New Jersey Late Cretaceous amber, from the same deposit as the material described here, has been mentioned by Gelhaus and Johnson (1996).

The taxa described below are the first North American Mesozoic mayflies known. Moreover, up to now the mayflies from the Taymyr amber were the only named Late Cretaceous mayflies. Few mayfly fossils have been discovered in Cenomanian tuffaceous mudstones at Obeshchayushchy Creek in the Magadan Region and in Cenomanian or Turonian clays at Timmerdyakh-Khaya in Yakutia, Russia as well as in Turonian clays at Kzyl-Dzhar, Kazakhstan (Zherikhin, 1978) but the nymphal remains from these sites are poorly preserved and undescribed. A mayfly from Arkhara in the Amur Region, Russia, also mentioned by Zherikhin (1978), is probably Danian, and not Cretaceous, in age (Krassilov, 1976). The traces of activity of burrowing mayfly nymphs in fossilized wood have been figured by Nessov (1988) from Cenomanian deposits at Khodzhakul in Karakalpakia, Northern Uzbekistan; similar ichnofossils have been discovered also in the Amur Region, Russia, together with Maastrichtian dinosaur bones (see below). This scarcity of the Upper Cretaceous record of mayflies is in strong contrast to their common occurrence in Lower

Cretaceous deposits, mainly lacustrine, of Asia (Zherikhin, 1978), Europe (Martinez-Delclos, 1991), Australia (Jell and Duncan, 1986), and South America (McCafferty, 1990). It can probably be explained as a result of the large-scale extinction of typical Mesozoic lacustrine biota near the Early/Late Cretaceous boundary (Zherikhin, 1978; Sinitshenkova, 1987).

A comparison between mayfly faunas of the Taymyr and New Jersey ambers is especially interesting because both assemblages, probably very comparable in taphonomic respect, originate from very different climatic regions of the Late Cretaceous. Paleobotanically, it is well demonstrated that at this time the Taymyr area was situated within the East Siberian paleofloristic province of the temperate Siberian-Canadian realm, possibly even northwards of the polar circle, while New Jersey lay within the Potomac province of the subtropical Euro-Chinese realm (Vakhrameev, 1988). Thus the discovery of mayflies in the New Jersey amber opens the door to studies in Late Cretaceous mayfly paleogeography.

All five specimens in hand are enclosed in the transparent yellow substance described by Grimaldi *et al.* (1989) as the second type of the New Jersey amber. They are rather well preserved and identifiable. The specimen mentioned by Gelhaus and Johnson (1996) was not available for study.

The mayfly classification system below is in accordance with McCafferty (1991), and Wang and McCafferty (1995).

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Systematics

Family Polymitarcyidae Banks, 1900
CRETOMITARCYNINAE Sinitshenkova,
NEW SUBFAMILY

Diagnosis: Imago, male. Antennae situated close to each other, short and strongly thickened; segmentation not observable but tumourous subglobose apical part seems to represent pedicel; flagellum perhaps reduced to small apical tubercle on pedicel. Middle and hind legs well developed, more so than the fore ones, fore tarsi clearly five-segmented. Vein MA of forewings forked more distally than the last fork of RS; two long and straight cubital intercalaries originating from wing base. Intercalaries near outer margin wing long, with additional shorter ones mostly on both sides of the main one; crossveins at the margin absent. Anal veins almost straight, not less than three. Crossvenation well developed. Hind wing with numerous longitudinal intercalaries, crossveins few and restricted to wing base. Forceps long, four-segmented. Two caudal filaments, rudiment of paracercus very short.

Genus monotypic. Based on the presence of two long, straight cubital intercalaries *Cretomitarcyinae* resembles *Asthenopodinae* (Hubbard, 1984; Hubbard and Dominguez, 1988) being distinguished from the latter by the distal forking of MA in the forewing and by the absence of crossveins along its outer margin. The new subfamily is sharply distinguished from *Campsurinae* by the genitalia and forceps structure, and also by the longer cubital intercalaries and distal forking of MA. *Cretomitarcyinae* is more similar to *Polymitarcyinae* by the MA forking more distally than the first RS fork, by the straight anal veins and numerous longitudinal veins in the hind wing being distinguished well by even the more distal MA fork, presence of the two long cubital intercalaries, by the long intercalaries at the wing margin, and the absence of crossveins at the forewing outer margin and on the hind wing.

Discussion: The absence of the antennal flagellum is unusual and somewhat confusing. The possibility that it has been lost in this instance on

both antennae can not be excluded with absolute certainty. However, the structure of the antennae is in any case peculiar, with a pedicel which is distinctly wider than the scape and possesses a small apical tubercle that may represent the rudiment of the flagellum.

Phylogenetic position. *Cretomitarcyis* is based on a single male specimen; thus its phylogenetic affinities may be discussed only on the basis of a reduced set of features that do not include phylogenetically important female (presence/absence of the imaginal stage) and nymphal characters. The phylogeny of ephemeroid taxa in general is still controversial and not well-grounded on many points (McCafferty, 1991). Not surprisingly for an ancient lineage, *Cretomitarcyis* retains many primitive character states. Especially the middle and hind legs are unusually well developed, showing no tendency to the reduction in all living polymitarcyid genera (the leg structure is not known for the Early Cretaceous genus *Pristiplocia* McCaff., constituting an extinct subfamily of its own). This character may indicate that *Cretomitarcyis* forms a sister group to all other Polymitarcyidae, with the possible exception of the Pristiplociinae; however, a reduction of the two hind leg pairs in other polymitarcyid lineages may well be independent, particularly since the pattern of reduction is different. No other characters support the separation of *Cretomitarcyinae* from other Polymitarcyidae. *Cretomitarcyis* shares the plesiomorphic four-segmented forceps with Polymitarcyinae, the five-segmented fore tarsi with Campsurinae, Asthenopodinae and some Euthyplociinae, the numerous and nearly straight anal veins in the forewings with Polymitarcyinae and some Euthyplociinae; unfortunately, all these characters are unknown in Pristiplociinae.

On the other hand, *Cretomitarcyis* demonstrates several apomorphies unique within the family, such as the highly modified antennae placed strikingly close to each other and the hind wings with unusually numerous intercalaries and very few crossveins. Here, again, nothing is known about these characters in *Pristiplocia*. The branching of MA in the *Cretomitarcyis* forewing is of a peculiar and probably autapomorphic type. In the primitive state, the MA branching point in

Polymitarciidae is located a little distad from the level of the first RS branch as in *Pristiplociinae*, *Euthyplociinae* and *Polymitarciinae*. In *Campsurinae* and *Asthenopodinae* an apomorphic displacement of this point occurs towards the wing base; in *Cretomitarciys* it is displaced in the opposite direction and much more distally than in the primitive state, being located somewhat distad from the level of the last branch of RS. Thus the unique apomorphic MA branching of *Cretomitarciys* probably originated separately from the primitive state. *Cretomitarciys* lacks crossveins near the outer margin of the forewing. This state is also unique in the *Polymitarciidae*: though a reduction of the crossveins occurs in *Euthyplociinae*, *Exeuthyplociinae*, *Campsurinae* and *Asthenopodinae*, in these subfamilies this process is less pronounced, with some crossveins still retained. The intercalary veins along the outer margin in *Cretomitarciys* are unusually long and mostly accompanied by two much shorter ones; a somewhat similar state occurs in *Pristiplocia*, where the intercalaries are also long and partially arranged in groups of three but in a very different manner. In all living subfamilies these intercalaries are short and mostly grouped in twos; this state is widespread within other *Ephemeroidea* and seems to be plesiomorphic. However, the long intercalaries can hardly be taken as a good synapomorphy between the *Pristiplociinae* and *Cretomitarciinae* in the absence of other characters supporting this clustering, especially because the arrangement of the intercalaries differs. Finally, the cubital venation of the forewing in *Cretomitarciys* is peculiar and probably combines apomorphic and plesiomorphic features. In general, the cubital venation of *Polymitarciidae* with several long intercalary veins behind CuA may be plesiomorphic for the *Ephemeroidea* (McCafferty, 1991) but shows many modifications in various ways. In *Cretomitarciys* these intercalaries are plesiomorphic both in length (originating from the wing base) and shape (nearly straight and subparallel to CuA as in *Polymitarciinae*, *Campsurinae* and *Asthenopodinae*), but apomorphic in their reduced number (as in *Exeuthyplociinae*, *Euthyplociinae*, *Polymitarciinae*, *Campsurinae* and

Asthenopodinae). In *Pristiplocia* they are rather long and numerous but distinctly arched.

An additional apomorphic feature of *Cretomitarciys* is the strong reduction of the paracercus in the male; this structure, unknown for *Pristiplocia*, is lost also (in male sex only) in the *Exeuthyplociinae*, *Euthyplociinae* and *Campsurinae*, strongly reduced in the *Asthenopodinae*, but well developed in the *Polymitarciinae*.

To summarize, *Cretomitarciys* shows a peculiar set of apomorphies which does not allow placing it into any previously known lineage and justifies the creation of a new subfamily. However, its phylogenetic affinities are ambiguous. The following possibilities exist, and only future finds of other *Pristiplociinae* and *Cretomitarciinae* can provide for a definitive choice among them:

- 1) *Cretomitarciys* may represent a sister group to other *Polymitarciidae*;
- 2) *Cretomitarciys* may represent a sister group to other *Polymitarciidae* except *Pristiplociinae*;
- 3) *Cretomitarciys* may represent a sister group to *Polymitarciinae* + *Campsurinae* + *Asthenopodinae*; this clustering is based on nymphal synapomorphies, so that it is impossible to determine whether *Cretomitarciys* can be placed here, if its nymph is ever discovered. *Exeuthyplociinae* + *Euthyplociinae*, forming the sister group to this cluster, lack these nymphal synapomorphies and are synapomorphic in having the 1-segmented forceps, which excludes any possibility of grouping *Cretomitarciys* with them.

CRETOMITARCIYS Sinitshenkova,
NEW GENUS

Diagnosis: As for subfamily. Monotypic

Type species: *C. luzzii* Sinitshenkova, sp.n. Late Cretaceous, Turonian; New Jersey, U.S.A.

Etymology: The generic name *Cretomitarciys* is from the Cretaceous period and the generic name *Polymitarciys*.

Cretomitarcys luzzii Sinitshenkova, new species
Figures 1-5

Description: Imago, male. General body color yellowish-white. Head with broad projection on occipital margin. Fore tibia slightly shorter than femur, tarsus longer than tibia; first tarsal segment the shortest, second and fourth ones shorter than third and fifth; claws blunt, about as wide as last tarsal segment. Mid- and hind femora evidently longer and stouter than fore femur. Forewing widely rounded at apex, 1.6 times as long as wide. Costal area is two times as wide as subcostal area. RS system with forebranch forked, hind branch simple. Four slightly curved veinlets attaching second ICuA to hind margin, CuP and four anal veins slightly curved.

Measurements (in mm): body length 2.8; foreleg length 0.6; forewing length 2.6, its maximum width 1.6; hindwing length 1.1, its maximum width 0.6.

Type: Holotype: AMNH NJ-257, the entirely preserved adult male in good condition in amber. U.S.A, New Jersey: Middlesex Co. Sayreville, White Oaks Pits 1995 coll. K.Luzzi (KL-200); Late Cretaceous, Turonian.

Etymology: The specific name *luzzii* in honor of the collector Keith Luzzi.

Family **Australiphemeridae** McCafferty, 1991
BOREPHEMERA Sinitshenkova,
NEW GENUS

Diagnosis: Imago, male. Relatively small mayflies with typical ephemeroid forewing: costal area wide up to wing apex, MA forked near midlength, MP₂ and CuA strongly arched near base, veinlets in cubital area simple, S-shaped, with short intercalaries near hind wing margin, A₁ simple, slightly curved, no veinlets in anal region; forceps four-segmented, with two apical segments short; two caudal filaments. Monotypic.

Type species: *B. goldmani* Sinitshenkova, new species. Late Cretaceous, Turonian; New Jersey, USA.

Etymology: The generic name *Borephemera* is from *borealis* (Latin) – northern, and the generic name *Ephemera*.

Differs from the previously known genera by the simple veinlets in the cubital area, by the presence of short intercalaries at the hind margin of the forewing, by the absence of veinlets attaching A to outer margin, and by the more arched bases of MP₂ and CuA.

Discussion: For Australiphemeridae, a weak basal arching of MP₂ is characteristic. In *Borephemera* this arch is more developed than in other genera (*Australiphemera* and *Microphemera*) but still much less than in other Ephemeroidea. It manifests a parallel development of the typical ephemeroid MP₂ seen in different lineages within the superfamily; in this respect *Borephemera* seems to be more advanced than the Early Cretaceous australiphemerid genera. The male genitalia, unknown for the previously described australiphemerids, are of a generalized ephemeroid type.

Borephemera goldmani Sinitshenkova, new species
Figures 6-8

Description: Imago, male. Body white, with indefinite brownish pattern on abdominal terga. Middle and hind legs well-developed. Forewing in cubital area with three long S-shaped curved intercalaries and four short veins between them on the hind margin; two veinlets between CuA and A₁, no veinlets between anal veins. Hind wing about half the forewing length, with numerous crossveins and short intercalaries near wing margin, crossveins near wing margin absent. Second joint of forceps is the longest; two terminal joints short, the apical one twice as long as penultimate and not much longer than wide.

Measurements (in mm): body length (without head) 5.0; forewing length 4.9, its maximum width 2.6; middle femur length 1.1, middle tibia with tarsus and claw length 1.3.

Type: Holotype: AMNH no. NJ-116C. The original amber piece was broken into three fragments accidentally during examination: the first contains the mayfly body (without the head) split

roughly along its midline, the complete left forewing, and middle and hind legs; the second contains the right side of the mayfly abdomen, with an incomplete impression of the right forewing and the left fore- and hindwing, together with a small parasitic wasp; the third piece contains fragments of the thorax and the head of the mayfly with an incomplete right foreleg and the impression of wing bases. U.S.A., New Jersey: Middlesex Co. Sayreville, White Oaks Pit. 1996, coll. Yale Goldman. Late Cretaceous, Turonian.

Etymology: The species is named after the collector, Yale Goldman.

Discussion: A round body at the base of the cerci likely does not represent neither styliger nor penis lobes; it probably is a bubble inside the piece of amber.

Family Heptageniidae Needham, 1901

AMEROGENIA Sinitshenkova, NEW GENUS

Diagnosis: Imago, female. Head with very large lateral eyes. Forewing venation typical for Heptageniidae, hind wing venation reduced. Hind tarsi clearly 5-segmented. Two caudal filaments. *Amerogenia* differs from other known genera by the large eyes of the adult female. Monotypic.

Type species: *A. macrops* Sinitshenkova, sp. nov.; Late Cretaceous, Turonian; New Jersey, USA.

Etymology: The generic name *Amerogenia* is from America and the generic name *Heptagenia*.

Discussion: The living genera of Heptageniidae are rather uniform in adult morphology and in many cases their alate females can not be identified with certainty. *Amerogenia* possesses unusually large eyes and a reduced hindwing venation, which allows formal separation of it from all other known genera. Its position within the family is unclear, however. The suprageneric taxa established by Kluge (1988) are based on nymphal characters and partly on the morphology of the tergal region of the adult thorax, which

can not be seen on the type specimen of *A. macrops*. The wing venation as well as the structure of the tarsi is typical for the family; a reduced hindwing venation is probably a consequence of the small body size and, thus, probably has little phylogenetic value.

The living Heptageniidae are rheophilous, and this is the most likely reason for the rarity of fossil heptageniids. Besides the Late Eocene Baltic amber, only two fossils are known, both represented by nymphs: *Stenonema* sp. from the Eocene of Republic, Washington, USA (Lewis and Wehr, 1993), and *Miocenogenia gorbunovi* Tshernova. from the Miocene of West Siberia, Russia (Tshernova, 1962). From the Baltic amber 10 species belonging to three living genera and two monobasic extinct genera are described (Demoulin, 1956, 1968; Kluge, 1986). *Amerogenia* is the first heptageniid found in the Cretaceous.

Amerogenia macrops Sinitshenkova, new species Figs. 9-13

Description: Imago, female. Body 1.6 times as long as mid or hind leg. On hindwing four longitudinal veins in RS system, two distal ones are connected. M forking near wing base; crossveins few. On hind tarsus first segment is shortest; apical one longest; second, third and fourth almost equal in length, each of them twice as long as first segment. Ninth abdominal sternite deeply cleft apically.

Measurements (in mm). Body length 3.8; hind leg length 2.3; forewing length 4.1, its maximum width 1.6; hind wing length 1.0, its maximum width 0.6; fragment of cerci length 3.9.

Types: Holotype: AMNH NJ-15. Adult female in amber, with well preserved body, wings, legs and caudal filaments, seen from the ventral side. U.S.A., New Jersey: Middlesex Co. Sayreville, White Oaks Pit. 1996, coll. J.J. Leggett. Late Cretaceous, Turonian. Paratype: AMNH NJ-718. Adult female in amber, with clear venation of the right forewing, visible right hind wing, left middle and hind legs, without caudal filaments. The same site as holotype, 1996, coll. AMNH exped.

Etymology: The specific name *macrops* (Greek) - with large eyes.

Family **Ametropodidae** Bengtsson, 1913

PALAEOMETROPUS Sinitshenkova,
NEW GENUS

Diagnosis: Subadult, male. Middle femur longer than tibia; hind femur slightly shorter than tibia, almost 0.5 times as long as tibia and tarsus together. Forceps four-segmented, first joint long, two apical segments short, styliger with deep angular cut at the middle. Monotypic.

Palaeometropus is distinguished both from the living genus *Ametropus* and the Baltic amber *Brevitibia* (Demoulin, 1968) by the longer hind tibia (*Ametropus* and *Brevitibia* have the hind tibia shorter than the tarsus) and a short terminal segment of the hind tarsus. It is distinguished from *Brevitibia* also by the relatively shorter hind femur (only 0.5 of the combined length of the tibia and tarsus, while in *Brevitibia* this ratio is 0.75).

Type species: *P. cassus* Sinitshenkova, sp.nov.; Late Cretaceous, Turonian; New Jersey, USA.

Etymology: The generic name *Palaeometropus* is from *palaeos* (Greek) - ancient, and the generic name *Ametropus*.

Discussion: This specimen is referred to the family Ametropodidae on the basis of the following features: the mid and hind femora long, tarsi five-segmented, the first tarsus fused with the tibia, the claws on the hind tarsi different in shape from other claws, the male genitalia of characteristic ametropodid structure. For the family Ametropodidae the presence of three caudal filaments is characteristic. On the studied specimen two cerci are present but the paracercus has probably been broken, because its large basal segments are very visible but the remaining portion is absent. *Palaeometropus* is the third genus of this small family, the second extinct genus, and the first one known from the Cretaceous.

Palaeometropus cassus Sinitshenkova, new species
Figs. 14-16

Description: Subadult, male. Skin dark brown. Segments of mid tarsi decrease in length (from proximal to terminal segments) (1, 2, 3, 4, 5). Ninth abdominal tergite as well as sternite with posterior angles projected backwards, last tergite broadly rounded.

Measurements (in mm): fragment length 5.3, probable total body length ca. 7.5; middle leg: femur length 1.3, tibia length 1.1; hind leg: femur length 1.1, tibia length 1.3, tarsus length 0.9.

Types: Holotype: AMNH NJ-560. The dried moulting skin of a subadult male enclosed in amber lacks the head and pronotum, with the wing pads crumpled; abdomen plus hind and partial middle legs are well preserved; cerci well preserved, paracercus lost, except for the very base. U.S.A., New Jersey: Middlesex Co. Sayreville, White Oaks Pit. 1996, coll. Keith Luzzi. Late Cretaceous, Turonian.

Etymology: The specific name *cassus* (Latin) - empty.

Discussion

The New Jersey mayfly assemblage is probably comprised of entirely lotic taxa. The modern Ametropodidae inhabit large rivers with sandy bottoms. The modern Heptageniidae are mostly strongly rheophilic, occasionally occurring also in lake shores where there is sufficient wave action, but some aberrant and probably less advanced genera develop in large rivers (Edmunds *et al.*, 1979). The living Polymitarciidae include both running (especially medium-sized to large rivers) and standing water dwellers, with nymphs burrowing either in bottom sediments or in submerged wood. Finally, the extinct family Australiphemeridae was previously known only from the Crato Formation in Brazil, where the basin of sedimentation is believed to have been a saline lake lacking aquatic insects, and insect remains are interpreted as river drift (Maisey,

1990). The stratigraphic division of Santana Formation is accepted here after D. Martill and P. Wilby (in Martill, 1993) who return the Crato Member to formation status. Thus all New Jersey mayflies may have had similar paleoecology probably living in a rather large river with widespread sandy bottoms and submerged wood (the latter is the most probable substrate for heptageniid nymphs in large rivers). The environment of the Mesozoic river might be similar to that of a modern north Florida blackwater river described in detail by Peters and Jones, 1973. Among 14 mayfly families inhabiting this kind of river, there are Heptageniidae, Polymitarcyidae, Ametropodidae, and Ephemeridae (the latter is probably not only phylogenetically but also ecologically similar to Australiphemeridae). Moreover, one more family, Leptophlebiidae, has recently been found in the New Jersey amber (Peters and Peters, 2000, this volume) and well represented in a blackwater river. So, all families represented in the New Jersey amber (or, at least, their relatives) occur together in a single modern Coastal Plain river. Almost certainly, the fauna of the New Jersey Cretaceous river included more mayflies than discovered now.

Because each of the five specimens available represents a different family, the diversity of the original mayfly fauna should be high. This is in strong contrast with the Taymyr amber assemblages. The richest of these originates from the Late Santonian Yantardakh site at Maymecha River, and is clearly dominated by a single species of Siphonuridae, *Cretoneta zherichini* Tshernova, constituting more than 33% of the entire collection (32 out of the total 89 mayfly specimens including the unidentifiable ones). Moreover, all Taymyr amber mayflies belong to only 3 families (Siphonuridae, Baetidae, and Palaeoanthidae: Kluge, 1993, 1997). The family Palaeoanthidae described by Kluge has been recently placed as a junior synonym of the family Australiphemeridae (McCafferty, 1997). If so, this is the only family common for the Taymyr and New Jersey ambers. This contrast may be explained either by zoogeographical (a latitudinal diversity gradient) or by ecological reasons (e.g., habitat diversity in Late Cretaceous Taymyr rivers was lower than in New Jersey). Since the Taymyr mayflies are found in

several sites, including some situated very far apart, and probably originating from a different river basin, the former explanation - latitude - seems to be more plausible.

It is noteworthy that the mayfly families in the New Jersey amber (Polymitarcyidae, Australiphemeridae, Heptageniidae and Ametropodidae) are considerably different from those in the Taymyr amber (Palaeoanthidae, Siphonuridae, and Baetidae). This may be additional evidence of pronounced zoogeographic differences between the Siberian-Canadian and the Euro-Chinese realms in the Late Cretaceous. The general distribution of mayflies at this time is poorly known, but an interesting distributional pattern of Polymitarcyidae should be noted. Presumed polymitarcyid ichnofossils, *Asthenopodichnium* (Thenius, 1979), have been discovered in the Central Asian province of the Euro-Chinese realm in Uzbekistan (Nessov, 1988) (fig. 17). As mentioned above, similar ichnofossils also occur at the Amur River. This find, previously unrecorded in the literature, was made by Dr. Yu. L. Bolotsky near Blagoveshchensk. The wood burrowed by mayfly nymphs is buried together with dinosaurs and tortoises of Maastrichtian age (Nessov, 1995). This site is located within the Siberian-Canadian realm, but at its extreme southern part it is close to the borderline between it and the Euro-Chinese realm (Vakhrameev, 1988). On the other hand, though fossilized wood is common in Taymyr amber sites and shows some insect damage (Zherikhin and Sukatsheva, 1973; Zherikhin, 1978), no *Asthenopodichnium* or similar trace fossils have been found (V.V. Zherikhin, pers. comm.). The Early Cretaceous polymitarcyid genera *Caririnympa* and *Pristiplocia* are known only from Brazil (Martins-Neto and Caldos, 1990; McCafferty, 1990). Thus, the Cretaceous finds of the family are nearly restricted to tropical and subtropical areas of this time. Nowadays Polymitarcyidae are rather widely distributed in temperate areas of Eurasia, but the majority of taxa, including all wood-boring genera, are restricted to warm climatic regions.

The family Siphonuridae, which is taken here in the broad sense equivalent to the infraorder Imprimata of McCafferty's (1991) system, on the

contrary, is distributed now mostly in temperate areas in the northern and southern hemispheres. This bipolar distributional pattern may be ancient and probably existed by the Cretaceous or at least suggests a more cosmopolitan distribution in the past. Siphonurids are the numerically dominant group in the Taymyr amber assemblages, but are not found in New Jersey amber. In the Late Early Cretaceous few siphonurid remains occur in Brazil (McCafferty, 1990) while in the cold temperate Koonwarra assemblage in Victoria, Australia, this is the only family of mayflies represented by abundant nymphs of 3 genera (Jell and Duncan, 1986). The siphonurids are also well represented in the Jurassic and Lower Cretaceous of Siberia (Sinitshenkova, 1985, 1990). This family is certainly ancient and represents probably the most generalized type among the living mayflies (McCafferty, 1991).

As discussed above, there is some similarity between the Late Early Cretaceous fauna of Brazil and the Early Late Cretaceous fauna of New Jersey. They share two families, Polymitarciidae and Australiphemeridae. This similarity may be due to the warm climate in both areas. In general though, both assemblages are clearly very different in composition, with the Brazilian assemblage strongly dominated by the hexagenitid genus *Protoligoneuria* Demoulin. The extinct family Hexagenitidae is extremely common in many Jurassic and especially Early Cretaceous assemblages but no hexagenitids are known from the Late Cretaceous.

In spite of the strong differences in taxonomic composition and somewhat different age (the main site of the Taymyr amber is Late Santonian and thus younger than the Turonian New Jersey amber), both Late Cretaceous amber assemblages show no obvious differences in their evolutionary advancement. In both cases one family (Australiphemeridae) is extinct, and among living families one is represented by an extinct subfamily (Cretomitarciinae in New Jersey and the baetid subfamily Palaeocloeoninae in Taymyr; Kluge, 1997). In both cases some living families appear for the first time in the fossil record (Ametropodidae and Heptageniidae in New Jersey, Baetidae in Taymyr). In both cases no living genera are represented.

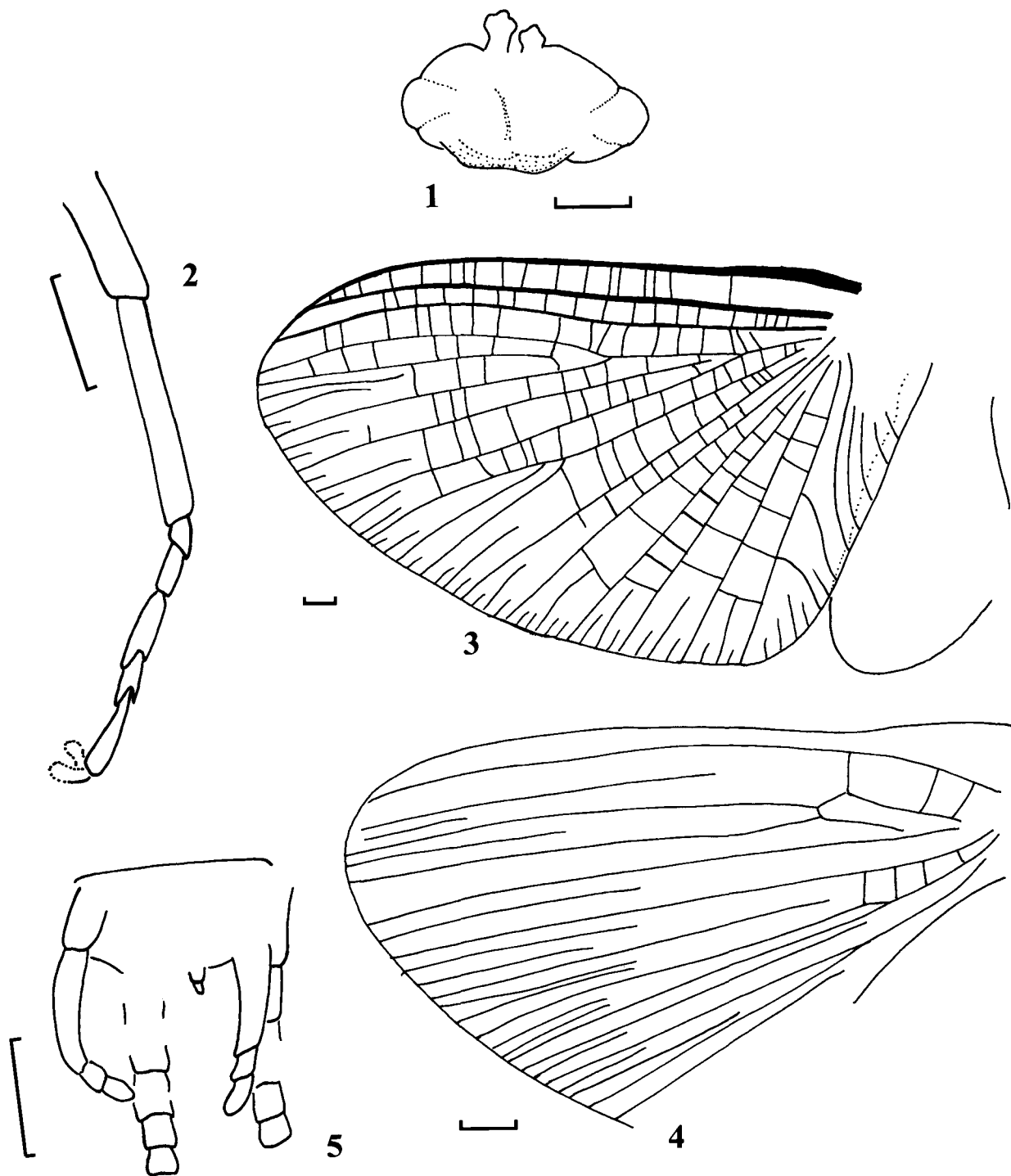
Finally, the New Jersey amber finds indicate the Turonian as the minimum geological age for two living families, Ametropodidae and Heptageniidae. Probably all living families of mayflies occurred in the Late Cretaceous together with a few remnants of entirely Mesozoic families. The main extinction event in the history of Late Mesozoic mayflies was rather near the Early/Late Cretaceous boundary (Albian-Cenomanian), than at the end of the Late Cretaceous (latest Maastrichtian). This is in agreement with the general pattern of insect extinctions described by Zherikhin (1978).

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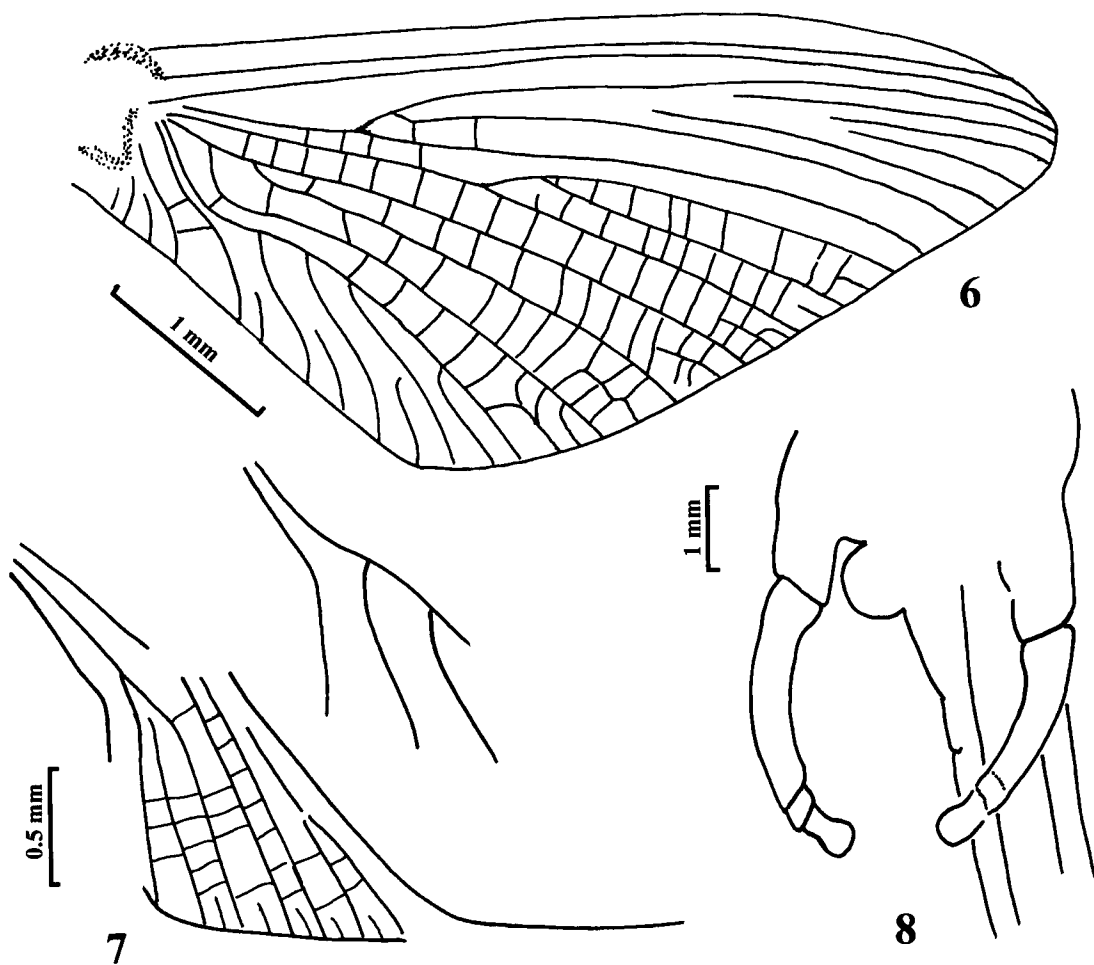
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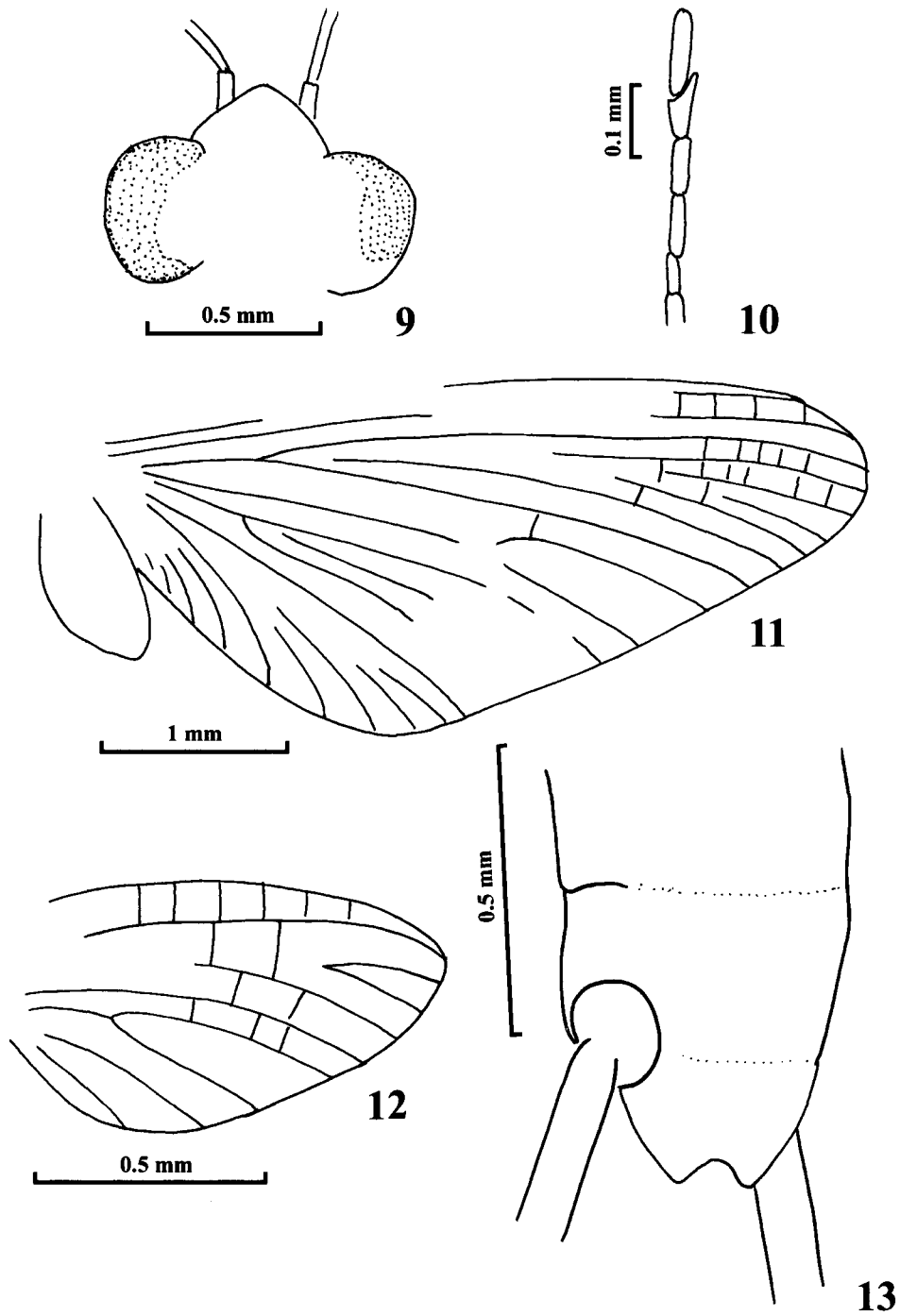
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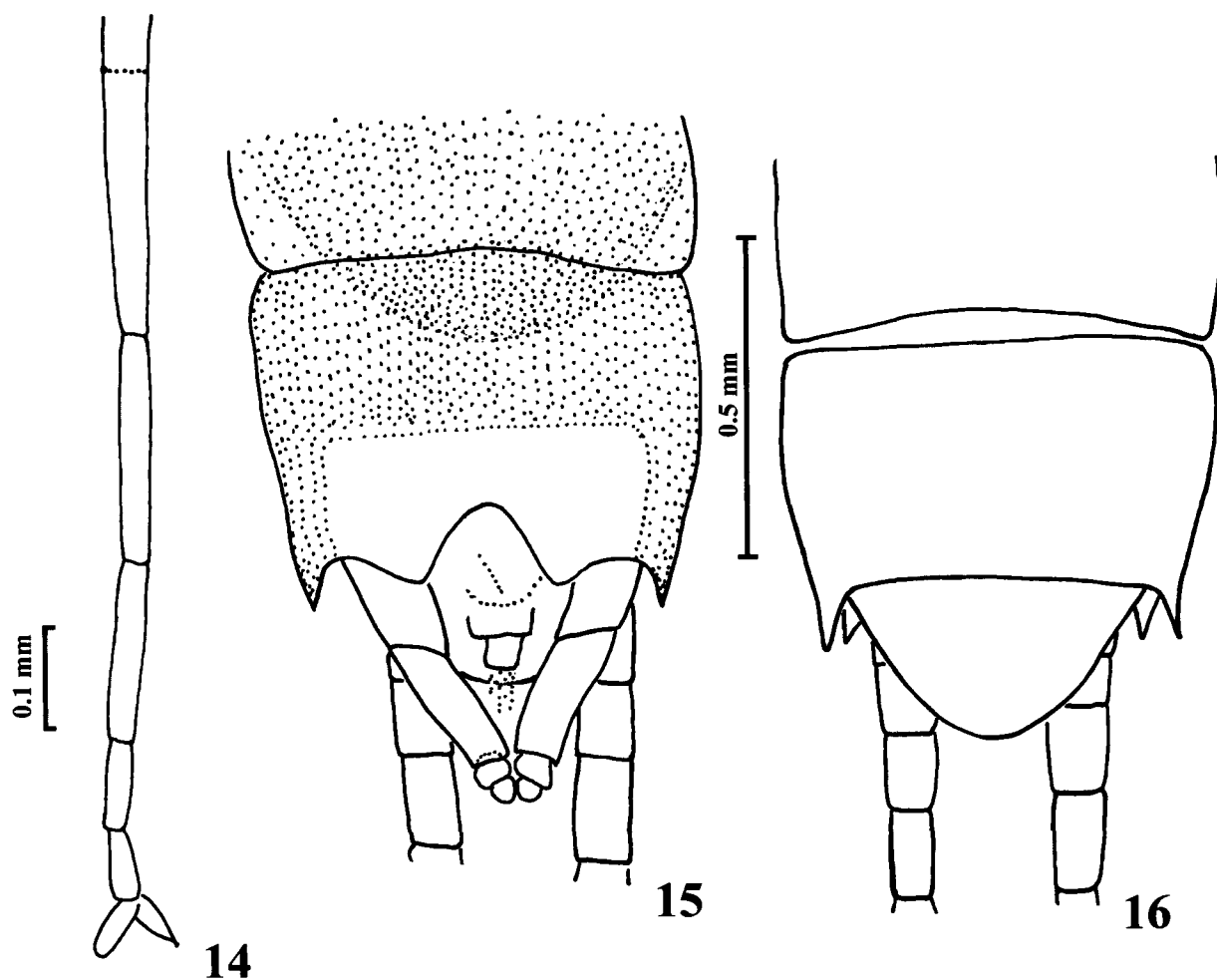
Figs. 1-5. *Cretomitarcys luzzii*, new species (Polymitarcyidae), imago male, holotype, AMNH NJ-257. 1. - head 2. - foreleg 3. - forewing 4. - hind wing 5. - abdomen apex, ventral view, scale 0.1 mm.



Figs. 6-8. *Borephemera goldmani*, new species (Australiphemeridae), imago male, holotype, AMNH NJ-116C. 6 - forewing. 7 - hind wing. 8 - abdomen apex, ventral view.



Figs. 9-13. *Amerogenia macrops*, new species (Heptageniidae), imago female, holotype, AMNH NJ-15. 9 - head. 10 - hind tarsus. 11 - forewing. 12 - fragment of hind wing. 13 - abdomen apex, ventral view.



Figs. 14-16. *Palaeometropus cassus*, new species (Ametropodidae), subadult male, holotype, AMNH NJ-560. 14 - middle leg. 15 - abdomen apex, ventral view. 16 - abdomen apex, dorsal view.

STUDIES ON FOSSILS IN AMBER,
WITH PARTICULAR REFERENCE
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