

New Fossil Mayfly in Amber and Its Relationships among Extant Ephemeridae (Ephemeroptera)

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ABSTRACT *Denina dubiloca*, n. gen. and n. sp. is established for a male adult mayfly of the family Ephemeridae fossilized in Baltic amber and deposited in the Paleontological Institute of the USSR Academy of Sciences. The new genus dates to the Eocene. Although Palearctic, the precise type locality is uncertain because of the lack of locale data. Its evolutionary affinities are clearly with an extant complex of genera that includes *Hexagenia*, *Litobrancha*, *Eatonigenia*, and *Eatonica*, and it is most closely related to the New World genus *Hexagenia*. A cladistic analysis shows *Denina* to be a relatively plesiomorphic and early derived lineage in this complex and substantiates a Northern Hemisphere origin of the complex. It also strengthens the theory that the Palingeniidae is derived from an ancestor shared by this complex.

KEY WORDS *Denina dubiloca*, Ephemeridae, fossil, amber

NINA SINITSHENKOVA of the Paleontological Institute of the USSR Academy of Sciences, Moscow, graciously sent to me a fossil mayfly that had been remarkably well preserved in amber. This male adult specimen represents a new genus and species of the extant family Ephemeridae. The new taxon holds a key evolutionary position and, thus, allows a more definitive interpretation of the phylogeny and biogeography of the Ephemeridae. It is with great pleasure that I name the genus for Nina Sinitshenkova.

Denina, n. gen. (Fig. 1-6)

Male Adult. Compound eyes (Fig. 2) appearing unicolorous but with dark median band separating eyes into upper and lower halves; median margins convergent dorsally in facial view. Transverse shelf of face (Fig. 2) below antennae not extended as far as nasal carina.

Mesoscutellum approximately truncate posteriorly in dorsal view. Fore wings (Fig. 3) with cross-veins not crowded near bullae; R_{3a} more than $\frac{1}{2}$ length of IR_2 ; A_1 not sinuate and not paralleling curvature of CuP; two veinlets connecting A_1 and anal margin; A_2 divergent with A_1 for approximately distal $\frac{1}{3}$. Hind wings (Fig. 4) with two marginal intercalaries between R_2 and IR_3 , longest slightly less than $\frac{1}{2}$ length of IR_3 ; one marginal intercalary between IR_3 and R_{4+5} , slightly less than $\frac{1}{4}$ length of IR_3 .

Genitalia (Fig. 5 and 6) with posterior margin of subgenital plate straight; forceps four-segmented, second segment curved slightly in proximal $\frac{1}{2}$ and attaching at distal aspect of apex of basal segment rather than dorsal aspect of basal segment;

penes separated to base at posterior margin of subgenital plate, narrow, elongate, projecting distally beyond basal segment of forceps, slightly curved medially, and pointed at apices. Median caudal filament (Fig. 5 and 6) ca. $\frac{1}{10}$ body length.

Type Species. The type species of the monotypic genus *Denina* is *Denina dubiloca*, n. sp.

Denina dubiloca McCafferty, n. sp. (Fig. 1-6)

Male Adult. Body (Fig. 1) 18 mm long; compound eyes (Fig. 2) 1.5 mm wide, separated by 0.5 mm dorsally; fore wings (Fig. 3) 15 mm long; hind wings (Fig. 4) 7 mm long; measurements and segment ratios of fore legs unknown; genital forceps (Fig. 5 and 6) 1.9 mm long; penes (Fig. 6) 1 mm long measured along lateral aspect; cerci length unknown; median terminal filament (Fig. 5 and 6) 1.8 mm long. Abdominal color pattern difficult to discern except tergites 9 and 10 dark, each with pair of submedian light stripes, those on tergite 10 in basal $\frac{1}{3}$ and those on tergite 9 in median $\frac{1}{2}$.

Holotype. Male adult in Baltic amber (specimen entire, except fore legs missing); collection and locale data unknown; deposited in the Paleontological Institute of the USSR Academy of Science, Moscow, Collection Number 363/61.

Etymology. The genus name *Denina* is Latin feminine (from Nina) in honor of Nina Sinitshenkova. The specific epithet *dubiloca* is feminine and a combination of letters derived from the Latin *dubius* and *locus*, an allusion to the uncertain type locality of the species.

Discussion. The wing venation as well as all other features of *Denina* clearly show that it belongs to the family Ephemeridae and furthermore



Fig. 1 and 2. *D. dubiloca* male adult, within amber. (1) Whole body. (2) Head and thorax.

Fig. 3 and 4. *D. dubiloca* male adult, within amber. (3) Fore and hind wing. (4) Hind wing and anal area of fore wing.

is closely related to the complex of extant genera within the Ephemeridae made up of *Hexagenia* Walsh (Nearctic and Neotropical), *Litobrancha* McCafferty (Holarctic), *Eatonigenia* Ulmer (Oriental), and *Eatonica* Navas (Afrotropical). Relationships within this complex have been discussed previously by McCafferty (1973) and McCafferty & Sinitshenkova (1983). These genera all share the apomorphic loss of the median caudal filament in the male adult and numerous larval synapomorphies. In *Denina*, however, unlike in other genera of this complex, the median caudal filament is not entirely lost but is reduced to ca. $\frac{1}{10}$ of the body length. This seems to represent an intermediate state between the fully developed median caudal filament of the more ancestral lineages represented by *Ephemera* L. and *Ichthybotus* Eaton and those with a completely reduced median caudal filament.

The wing venation of *Denina* is relatively plesiomorphic for the family. It does not demonstrate the apomorphic venation in the hind wing of *Ephemera* and *Afromera* Demoulin, where the MP_2 vein is attached basally to CuA . The shape of the mesoscutellum is also plesiomorphic for the family, being truncate apically.

The genitalia of *Denina* show a strong affinity with those of the complex of genera mentioned above, essentially because the penes are narrow, elongate, and pointed as in *Hexagenia rigida*

McDunnough. Although the penes of *D. dubiloca* are almost identical with those of *H. rigida*, the latter species as well as all *Hexagenia* s.s. differ in having wings with more cross venation (see especially anal veinlets) and intercalary venation, a notched mesoscutellum, and a vestigial median caudal filament. The separated and elongate penes lobes apparently evolved in the common ancestor of the complex. They are retained in *Denina* and *Hexagenia* and are more fused basally in *Litobrancha*, *Eatonigenia*, and *Eatonica*. Also, the second segment of the forceps uniquely attaches on the dorsal aspect of the basal segment in these latter three genera. Both *Denina* and *Hexagenia* possess the plesiomorphic apical attachment of the segment.

I can summarize the hypothesized relationships of *Denina* within a phylogeny based on information from male adults as follows. 1) An ephemerid ancestor, in a lineage more apomorphic than lineages including *Ephemera* and *Ichthybotus*, evolved a greatly reduced median caudal filament and separated, elongate penes lobes. The lineage leading to the Palingeniidae probably originated from this ancestor, given the position of *Pentagenia* Walsh (McCafferty 1972, McCafferty & Edmunds 1976) and its elongate penes lobes and short male median caudal filament. 2) From this same ancestor evolved a lineage leading to *Denina*, *Hex-*

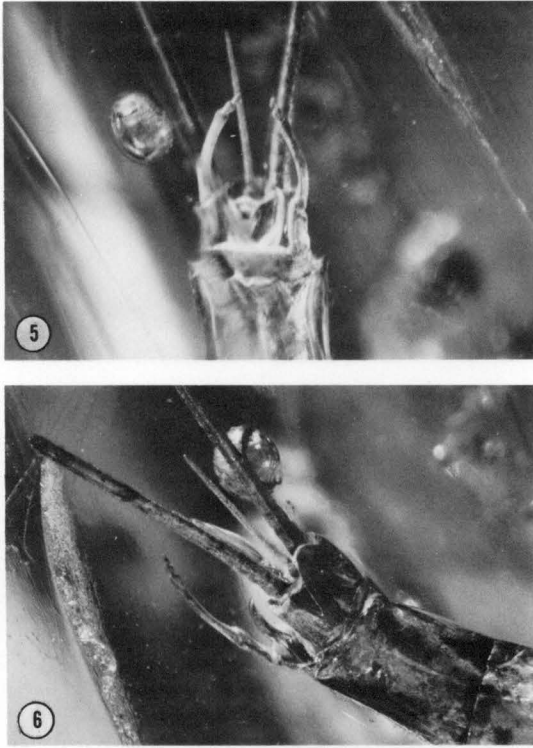


Fig. 5 and 6. *D. dubiloca* male adult, within amber. (5) Genitalia and terminalia, ventral. (6) Genitalia and terminalia, dorsolateral.

agenia, *Litobranchna*, *Eatonigenia*, and *Eatonica*, and in the immediate common ancestor of this group the penes lobes became pointed apically. 3) This ancestor gave rise to *Denina*, which may have essentially resembled the ancestor and subsequently became extinct, and a lineage leading to the immediate ancestor of the remainder of the complex, in which the median caudal filament of the male was completely lost. 4) From that ancestor arose *Hexagenia*, which retained the ancestral genitalia, except that in many species the penes became shorter or strongly hooked, or both, at the apex (see comparative illustrations of Spieth [1941]), and which developed a conspicuously notched apex of the mesoscutellum. Also from that ancestor arose a sister lineage of *Hexagenia* that involved the immediate common ancestor of *Litobranchna*, *Eatonigenia*, and *Eatonica*. 5) In the latter lineage, the penes became fused basally and modified apically, the base of the second segment of the forceps rotated dorsally on the first segment, and the mesoscutellum became narrowed and eventually pointed apically.

The less parsimonious alternative to this hypothesized phylogeny requires an immediate common ancestor of *Hexagenia* and *Denina* (cf. their similar penes), with the median caudal filament being completely lost in the male independently in *Hexagenia* and the immediate common ancestor of

Litobranchna, *Eatonigenia*, and *Eatonica*. Under this alternative, one must not only reconcile the convergent loss of the median caudal filament but also a convergent elongation and separation of the penes lobes in *Hexagenia-Denina* and the Palingeniidae. It seems more likely that the median caudal filament of the male was lost only once in the Ephemeroidea and that the penes went from a basally fused type (as in *Ichthybotus*) to a basally separated type and then subsequently to a basally fused type that otherwise is quite different from the more ancestral penes.

The exact range of the fossil *D. dubiloca* is unknown, but it is assuredly Palearctic. The specimen of amber dates to the Eocene. Given the probable phylogeny, or even the less parsimonious one mentioned, along with the known generic distributions, the fossil establishes an Old World–New World relationship via the Northern Hemisphere early in the evolution of the complex of genera under discussion. The Palearctic distribution of *Denina*, the Nearctic distribution of *Hexagenia* s.s., which is the more ancestral subgenus of *Hexagenia* (McCafferty et al., 1987), and the Holarctic distribution of *Litobranchna*, with its known Palearctic species dating to at least the Oligocene (McCafferty & Sinitshenkova 1983), suggest that the ancestor of the complex was widespread in the Holarctic, with subsequent vicariant events accompanying evolution, or of more localized (probably Palearctic) distribution closely followed by Laurasian dispersal and vicariance.

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