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Litobrancha from the Oligocene in Eastern Asia (Ephemeroptera: Ephemeridae)[1]

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ABSTRACT A burrowing mayfly, *Litobrancha palearctica* n.sp., is described from a larval fossil taken in Oligocene deposits from Sikhote Alin, USSR. The discovery lends geographic support to the hypothesized phyletic position of *Litobrancha* as intermediate between the New World *Hexagenia* and the Old World *Eatonigenia*. The historical age of *Litobrancha* is significant because it accommodates a theorized paleo-panboreal or Arcto-Tertiary distribution.

Known tertiary mayflies have been considered to be similar to the recent ephemeropteran fauna (Needham et al. 1935). The few fossils of the extant family Ephemeridae are known only from this period, specifically the Oligocene epoch. Scudder (1890) described five larval fossils from the Florissant Basin of Colorado as *Ephemera*. Although these are evidently burrowing ephemeroids, their generic identification remains provisional. Demoulin (1968) described an adult mayfly fossil from Baltic amber, placed it in the Ephemeridae, but could not place it to genus. Lewis (1978) discovered a larval fossil from the Ruby River Basin of Montana and tentatively assigned it to the genus *Hexagenia*. These data have been too scant to have influenced thinking on the phylogeny of the Ephemeridae.

An important fossil ephemerid larva, however, was recently discovered from Oligocene deposits in the Primorsky Province of far eastern USSR (Sikhote Alin). This material was made available to W.P.M. through the auspices of the Paleontological Institute of the USSR Academy of Sciences and of N.S. The remains demonstrate characteristics previously found to be of phyletic worth in studying extant ephemerids, and, as will be shown below, the mayfly provides a "link" between advanced ephemerid genera of the Old and New World.

Litobrancha palearctica n.sp.
(Fig. 1–4, 6, 8, 9)

Described from an incomplete larva (Fig. 1–3): femur, tibia, and tarsus of both forelegs; right and left mandibular tusks; femur, tibia, and tarsus of middle and hind leg.

The ventral aspect of the larva is indicated in Fig. 1 (the left leg and tusk are to the right). Due to the origin of the tarsi and asymmetric shape of the tibiae of ephemerid forelegs, a right and left leg can never be confused, no matter in what position they are found (like human hands). The forelegs have undergone a ca. 90° rotation, since their broadened outer surfaces face ventrally. This rotation can be easily and exactly simulated by slightly depressing specimens of ephemerid larvae.

Specimen 20 mm from anteriorly directed tip of foreleg to posteriorly directed tip of hind leg.

Mandibular tusks relatively short and stout (Fig. 1 and 4), appearing convergent apically but probably slightly upcurved and not convergent (depression of head causes slight inward rotation of tusks by opening mandibles, and aspect seen agrees with medioventral aspect of tusks of related extant species); curvature gradual; lateral row of hairs present; shorter row of ventral hairs present; apical row of short hairs medially; no spurs evident.

Forelegs (Fig. 1 and 6) with expanded tibiae and typical ephemerid setaceousness; tibiae sculptured apically with prominent, pointed dorsolateral process followed ventrally by less prominent but distinct outward rounding, margin then more-or-less smooth and straight to ventral margin (ca. one-third apical marginal length), tips of comb setae of medioventral margin somewhat evident on fossil along straight part of margin, giving area false, slightly serrate appearance; tarsal claws well developed. Middle and hind legs as in Fig. 2, 3, 8, and 9.

Material

Specimens 3429/1614± (Paleontological Institute of the USSR Academy of Sciences, Moscow) taken from Oligocene shale deposits: USSR, Sikhote Alin, northeast of Primorsky Kraj, basin of the upper Bikin River, the Bolshaja Svetlovodnaja River (formerly Biamo), 40 km above its confluence with the Ulunga River. Based on geological and paleontological data, this locality appears to represent a previous cold-water lake inhabited by a number of aquatic Heteroptera. *Litobrancha palearctica* did not originate from the lake but drifted there from a running-water tributary.

Systematics and Biogeography

All available characteristics of *L. palearctica* agree with other ephemerid larvae. The tibial process of the hind leg (Fig. 9) is particularly diagnostic in this respect. The general shapes of the legs (especially the forelegs) and the apparent lack of tusk spurs are typical of an advanced group of ephemerid genera that includes *Hexagenia, Litobrancha, Eatonigenia,* and *Eatonica*. The size and curvature of the mandibular tusks furthermore indicate a relationship to the next advanced grouping of ephemerids that excludes *Hexagenia* but includes *Litobrancha, Eatonigenia,* and *Eatonica*.

Foretibiae of the larvae of Ephemeridae are specific for each genus. The degree of foretibial broadening, the shape of the apical margin of the foretibiae, and the tusk

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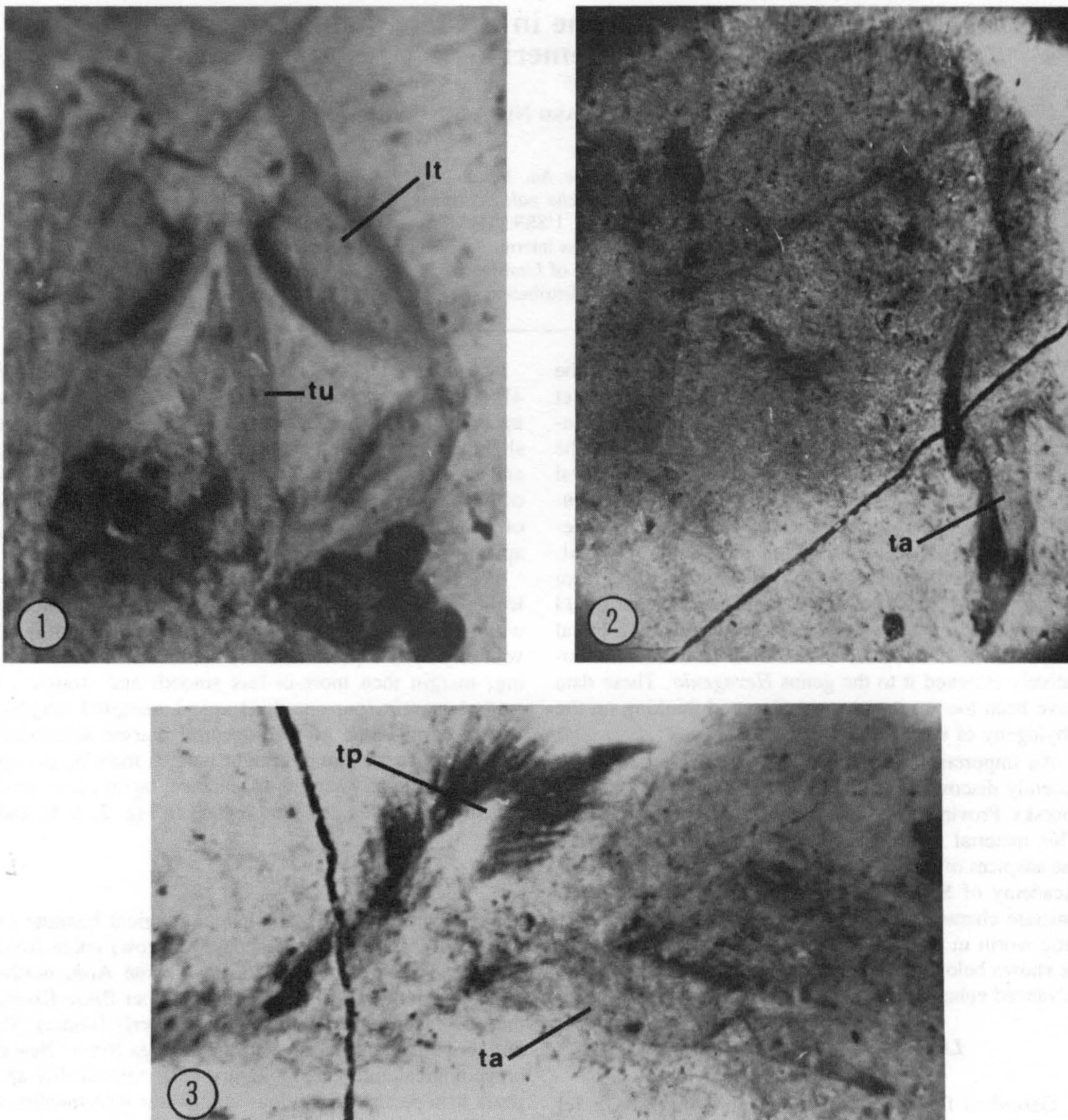

FIG. 1–3.—*L. palearctica*. (1) Forelegs and tusks, ventral aspect. (2) Middle leg. (3) Hind leg. lt, Left tibia; ta, tarsus; tp, tibial process; tu, tusk.

size of *L. palearctica* agree with those of the extant *Litobrancha recurvata* (Morgan) of eastern North America. *Litobrancha palearctica* differs from *L. recurvata* slightly in the apparent shape of the tusks, with its tusks possibly not as upcurved toward the tips and somewhat thicker. In this respect, *L. palearctica* is somewhat similar to *Eatonigenia* and *Eatonica*. The abrupt and more extreme broadening and the rounded ventrodistal margin of the foretibiae of the latter genera are not found in *L. palearactica*. The fossil also lacks the inserted tarsal claws typical of *Eatonigena* and the more elongate dorsodistal process found on the foretibiae of *Eatonica*.

This new species of *Litobrancha* is an important discovery from the standpoint of phylogeny and biogeography. McCafferty (1971, 1973) indicated that *Litobrancha* was closely related to *Eatonigenia* and was phylogenetically intermediate between *Hexagenia* and *Eatonigenia*. Although numerous characters suggest this relationship, it has previously been difficult to accommodate the geography of the genera in this phylogeny, since *Eatonigenia* is restricted to the Oriental region, *Hexagenia* is restricted to the Western Hemisphere (primarily Nearctic), and *Litobrancha* was known only from eastern North America. McCafferty (1973) stated, "if

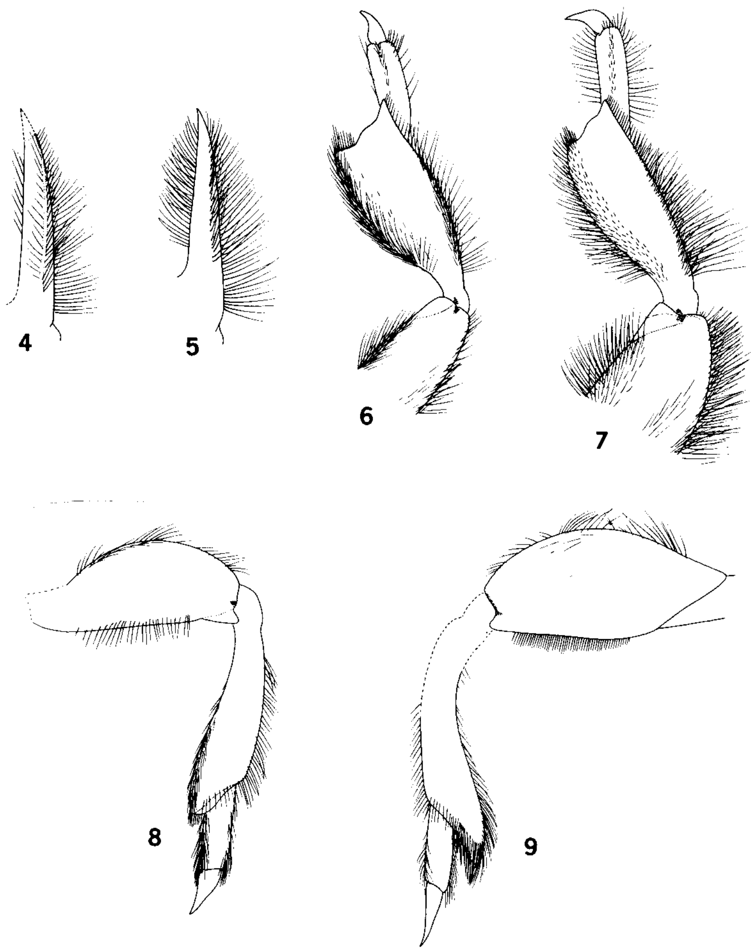

FIG. 4–9.—(4–5) Left tusk, ventral. (4) *L. palearctica*, reconstructed. (5) *L. recurvata*. (6–7) Left foreleg, lateral. (6) *L. palearctica*, reconstructed. (7) *L. recurvata*. (8) Middle leg, *L. palearctica*, reconstructed. (9) Hind leg, *L. palearctica*, reconstructed.

indeed *Eatonigenia* and *Litobrancha* are directly related, then geographic dispersal involving the Nearctic and Oriental Regions must be explained. Granting Holarctic dispersal, the apparent anomaly is that no records of either genus or even a similar type have been established for the Palearctic."

With the discovery of *L. palearctica*, not only has the theorized phylogeny become supportable biogeographically (the phylogeny was predictive), but the existence of *Litobrancha* in the Oligocene suggests the possibility of a previous panboreal distribution followed by vicariance associated with cooling events, or at the very least a trans-Beringia dispersal. The presently known distribution of *Litobrancha* in eastern North America (McCafferty 1975) and eastern Asia is reminiscent of many distribution patterns of both plants and animals that were associated with the Arcto-Tertiary forest (Pielou 1979).

The question as to why *Litobrancha* has apparently not survived in the Palearctic to the present is an interesting one. Perhaps it has. Eaton (see p. 307 in Eaton [1883–1888]) cited one undescribed species of *Hexagenia* as occurring in eastern Siberia, with no other information given; *Litobrancha* adults would have been classified as *Hexagenia* by Eaton at that time. If *Litobrancha* is present is eastern Siberia, it seems surprising that these large mayflies have not been reported again. However, the remoteness of the area and the possibility of a somewhat restricted range and narrow habitat limitations, like those of *Litobrancha* in North America, may explain its absence from collections.

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