Aquatic Insects, Vol. 20 (1998), No. 1, pp. 35–68 0165-0424/98/2001-0035$12.00

Phylogenetic Systematics and Biogeography of the Neoephemeridae (Ephemeroptera: Pannota)

Y.J. BAE and W.P. McCAFFERTY

Y.J. BAE and W.P. McCAFFERTY: Phylogenetic Systematics and Biogeography of the Neoephemeridae (Ephemeroptera: Pannota).

Aquatic Insects, Vol. (20), No. 1, pp. 35–68.

A revision of species of the pannote Holarctic and Oriental mayfly family Neoephemeridae is presented. Three genera are recognized in a strictly phylogenetic classification. *Potamanthellus* [=*Neoephemeropsis* Ulmer syn. n.] includes *P. caenoides* (Ulmer) comb. n., *P. amabilis* (Eaton) [=*N. cuaraoensis* Dang syn. n.], *P. ganges* sp. n., *P. chinensis* (Hsu) [=*P. rarus* (Tiunova and Levanidova) syn. n.], *P. edmundsi* sp. n., and the Oligocene fossil *Potamanthellus rubiensis* Lewis. *Neoephemera* [=*Leucorhoenanthus* Lestage syn. n.] includes *N. maxima* (Joly), *N. purpurea* (Traver), *N. youngi* Berner, *N. bicolor* McDunnough, and *N. compressa* Berner. *Ochernova* gen. n., includes *O. tshernovae* (Kazlauskas) comb. n. Taxa are described, illustrated and keyed. Species cladistics and biogeography are presented.

Keywords: Ephemeroptera, Neoephemeridae, species revision, phylogeny, biogeography.

Y.J. BAE, Department of Biology, Seoul Women's University, 126 Kongnung 2-dong, Nowon-gu, Seoul 139–774, Korea.
W.P. McCAFFERTY, Department of Entomology, Purdue University, West Lafayette, IN 47907, USA.

INTRODUCTION

The family Neoephemeridae is a small group of pannote mayflies (11 extant nominal species) that is widespread in the Holarctic and Oriental regions (Figs. 1, 2). Larvae of Neoephemeridae are found from mountain torrents to large streams and rivers, being either clingers on erosional substrates or sprawlers on depositional substrates.

The Neoephemeridae is a distinct monophyletic group of mayflies (McCafferty and Edmunds, 1979), but the taxonomy of its members has been problematic. Much of this is attributable to what historically has been viewed as apparently incongruent larval and adult stages. This has been explained in terms of differential rates of evolution in these two stages (e.g., Edmunds, 1965). Neoephemerid larvae (Fig. 3) are similar to caenid mayflies in that they have a pair of large, subquadrate, operculate gills on abdominal segment 2. Adults, on the other hand, are similar to potamanthid mayflies, having similar wing venation (esp., basally arched MP_2 and CuA, forked A_1 in forewings) (Figs. 18–21). Bae and McCafferty (1991) clearly delimited both stages of Neoephemeridae and Potamanthidae.

The first known larva of Neoephemeridae was described from Europe by Joly (1870) as *Caenis maxima*. Eaton (1881, 1884) considered this species as *Tricorythus* (?), but grouped it with *Caenis*. Eaton's "Section 7: type of Caenis" was equivalent to the family Caenidae subsequently used by Jacobsen and Bianchi (1905), Klapálek (1909), and Handlirsch (1925).

Eaton (1892) described the first neoephemerid adult from southeast Asia as *Rhoenanthus amabilis* (grouped with potamanthids). Ulmer (1919) described another adult as *Rhoenanthus macedonicus* from Europe. Lestage (1930) placed all neoephemerids in the Potamanthidae because he used only adult characters; this classification was followed by Ulmer (1932) and Hsu (1936–1937). McDunnough (1925) described a neoephemerid genus, *Neoephemera* (type: *N. bicolor* McDunnough), from North America for the first time and placed it in Ephemeridae. Traver (1935) associated the larval and adult stages of neoephemerids, added *Oreianthus* (type: *O. purpureus* Traver), and established the subfamily Neoephemerinae (in Ephemeridae) for *Oreianthus* and *Neoephemera.* Burks (1953) synonymized *Oreianthus* with *Neoephemera* and was the first to recognize neoephemerids at the familial rank.

Lestage (1930) described genera of neoephemerids as *Potamanthellus* (type: *P. horai* Lestage), *Rhoenanthodes* (type: *R. amabilis*), and *Leucorhoenanthus* (type: *R. macedonicus*). Ulmer (1932) synonymized *Rhoenanthodes* with *Potamanthellus*. Ulmer (1939) added *Neoephemeropsis* (type: *N. caenoides* Ulmer), and Demoulin (1961) inadvertently described *Caenomera* (type: *C. maxima*) as a subgenus of *Neoephemera* but shortly thereafter (Demoulin, 1962) realized it was a synonym of what he considered *Neoephemera* (subgenus *Leucorhoenanthus*). *Neoephemera youngi* and *N. compressa* were described from North America by Berner (1953, 1956), and Berner (1956) revised North American *Neoephemera*. *Potamanthellus horai, P. chinensis* Hsu (1935–1936), *N. caenoides,* and *N. rarus* Tiunova and Levanidova (1989) were described from east Asia. *Neoephemera tshernovae* Kazlauskas (1963) was described from central Asia. The only known fossil neoephemerid, *P. rubiensis* Lewis (1977), was described from the Oligocene of Montana.

Although Neoephemeridae historically has been classified in different superfamilies of mayflies (Edmunds and Traver, 1954; Demoulin, 1958; Tshernova, 1960, 1970; Edmunds, 1962; Landa, 1969; McCafferty and Edmunds, 1979; Landa and Soldán, 1985; McCafferty 1991), McCafferty and Edmunds (1979) showed it to be a group of pannote mayflies. Pannote mayflies have most recently been regarded as an infraorder of the suborder Rectracheata by McCafferty (1991).

The purposes of this study are to revise the species of the family, to hypothesize their phylogeny, to devise a strictly phylogenetic generic classification of them, and to hypothesize their historical biogeography. Analytical methods employed are essentially described by Bae and McCafferty (1991). Acronyms of collections cited frequently are BM (British Museum), FAMU (Florida A & M Univ.), HAM (Hamburg Museum), INHS (Illinois Natural History Survey), PERC

Fig. 1. Distribution of Neoephemeridae.

(Purdue Entomological Research Collection), SWU (Seoul Women's University), UU (Univ. of Utah), and ZIP (Zoological Institute of St. Petersburg). Most UU material will soon be deposited at PERC. Materials examined, other than types, are summarized with only numbers, stages (M = male adult, F = female adult, s = subimago, L = larva), countries of origin, and places of deposition. More detailed data are available upon request.

ACCOUNTS OF TAXA

Family **Neoephemeridae** Traver

Group II, Series III, Section 7 (Type of Caenis): Eaton, 1883:137.
Caenidinae (in part): Jacobsen and Bianchi, 1905: 874; Handlirsch, 1925:421.
Caenidae (in part): Klapálek, 1909:14.
Caeninae (Baetidae) (in part): Lestage, 1917:370.
Potamanthidae (in part): Ulmer, 1920:110; Ulmer, 1932:209.
Potamanthidiens (in part): Lestage, 1930:109.
Neoephemerinae (Ephemeridae) Traver, 1935:288.
Potamanthinae (Ephemeridae) (in part): Hsu, 1936–37:131.
Neoephemeridae: Burks, 1953:42.
Potamanthinae (Potamanthidae) (in part): Edmunds and Traver, 1954:239; Demoulin, 1958:7.

Larva. Labrum with bipectinate-hairlike and furcate-stout setae dorsally and sometimes rowed along anterior margin; anterior margin slightly to greatly emarginate. Mandibles with simple stout setae on dorsolateral area; outer and inner incisor of right mandible trifurcate and bifurcate, respectively; outer and inner incisor of left mandible quadrifurcate and trifurcate, respectively. Maxillae (Figs. 4–7) with dense hairlike setae on crown; palpi 3-segmented. Hypopharynx moderately divergent laterally. Labial palpi 3-segmented. Hindwingpads present.

Tarsal claws well developed (0.3–0.6× length of tarsus), edentate, and hooked. Abdominal tergum 1–2 and 6–8 with posteromedian tubercle (6–8 sometimes rudimentary); posterolateral projections of abdominal segment 6–9 well developed (9 greatest, sometimes curved downward). Gills present on abdominal segments 1–6. Gills 1 (Fig. 17) filiform, 2-segmented, anterolaterally oriented, and with sparse to dense hairlike setae. Gills 2 (Figs. 8, 9) operculate (with underlying fringed lamella), somewhat dome-shaped, subquadrate, plate pair not overlapping but meeting medially, with row of hairlike setae along median margin, with marginal membrane posteriorly, and dorsally with diagonal ridge from anterolateral to posteromedian corner (in 2 species diagonal ridge absent). Gills 3–5 double; dorsal lamellae "kidney-shaped," with row of fringes on medial margin and row of tufts of fringes on lateral margin; ventral lamellae smaller, with row of marginal fringes. Gills 6 single, reduced, curved inward, and with row of marginal fringes. Terminal filament subequal to cerci.

Adult. Furcasternum divided by distinct median depression. Forewings (Figs. 18, 20) with stigmatic area not anastomosed to moderately anastomosed; MA forked at about midlength; MP_2 originating at base of MP_1, slightly to greatly arched basally; CuA slightly to greatly arched basally, with 2–4 long intercalaries (1–3 of them forked); A_1 with 1–2 veinlets (angle between A_1 and veinlets 70–90°), and with intercalary vein between CuP and A_1 basally arched and attaching to A_1 (intercalary sometimes missing). Hindwings (Figs. 19, 21) with round to acute costal projection basally. Forelegs relatively short, 0.7–0.9× length of body. Claws dissimilar. Penes slightly furcate (Figs. 25, 26) or atrophied (Figs. 22–24). Terminal filament either subequal to cerci or rudimentary (ca. 0.02–0.09× length of cerci).

Egg. Chorion (Figs. 28–33) with numerous tiny tubercles or sparse peglike tubercles, or without tubercles. Polar caps present (Koss and Edmunds, 1974) or absent. Knob-terminated coiled threads absent. Micropyle (Fig. 33) single, tagenoform; micropylar opening and micropylar canal located at midlength and vertical to long axis of egg. Sperm guide somewhat oval; long axis ca. 0.019 mm; short axis ca. 0.015 mm.

Diagnosis. The larvae of Neoephemeridae have unique subquadrate operculate gills (Figs. 8, 9) on the second abdominal segment that do not overlap but are juxtaposed medially. The operculate gills also possess a single diagonal ridge dorsally (in two species, diagonal ridge is reduced). These characters easily distinguish them from Caenidae, Tricorythidae, Ephemerellidae, and other Ephemeroptera. Adults are distinguished by the combination of the following characters: MP_2 and CuA veins of forewings (Figs. 18, 20) arched basally (as in Ephemeroidea), and A_1 vein of forewings possessing 1–2 veinlets (angle between A_1 stem and veinlets almost right-angled), and either slightly furcate (Figs. 25, 26) or atrophied penes (Figs. 22–24).

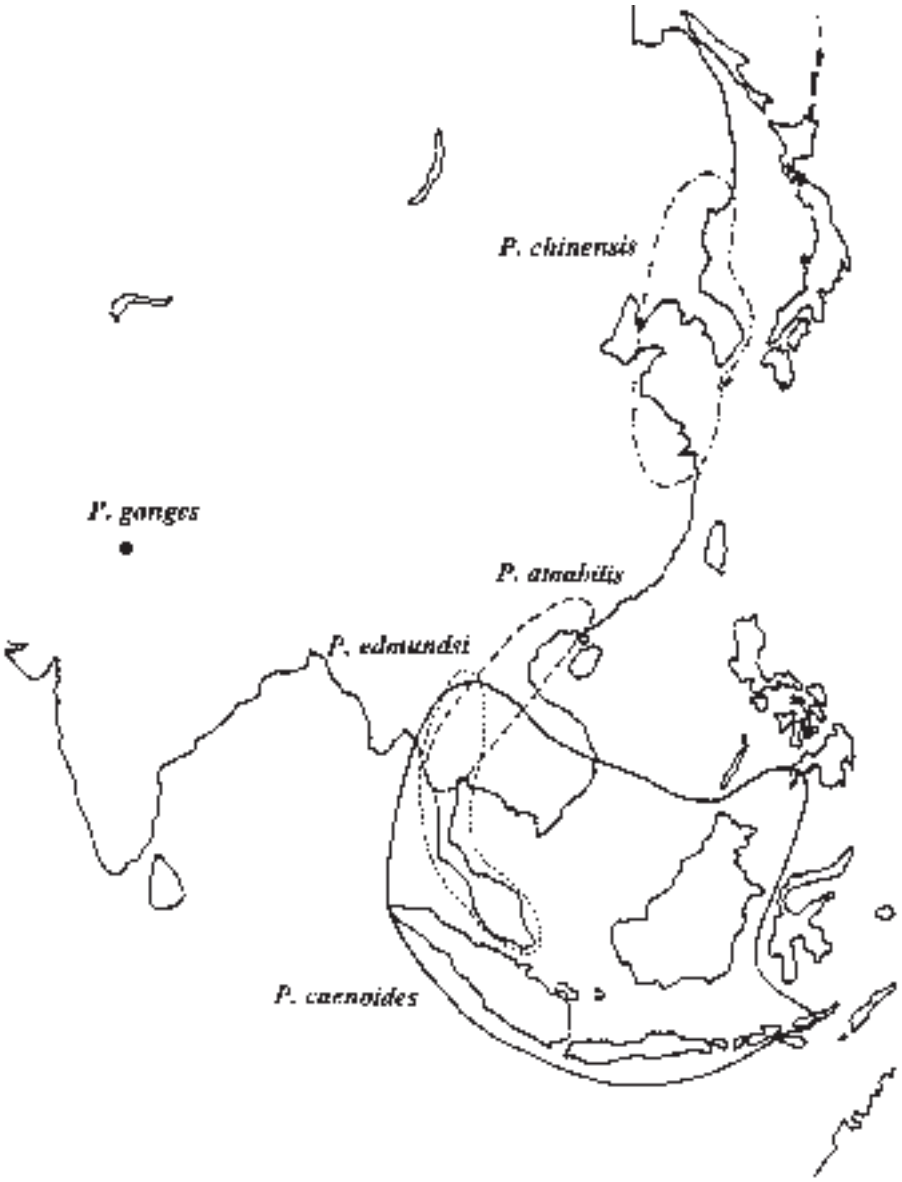


Fig. 2. Distribution of *Potamanthellus* spp.

Genus ***Potamanthellus*** Lestage

Potamanthellus Lestage, 1930:120. Type: *Potamanthellus horai* Lestage, 1930 [= *Potamanthellus amabilis* (Eaton)], by original designation.

Rhoenanthodes Lestage, 1930:136. Type: *Rhoenanthus amabilis* Eaton, 1892 [= *P. amabilis* (Eaton)], by original designation. = *Potamanthellus*: Ulmer, 1932.
Neoephemeropsis Ulmer, 1939:483, **syn. n**. Type: *Neoephemeropsis caenoides* Ulmer, 1939, by original designation.

Larva. Head: Anterior margin of labrum moderately emarginate. Maxillary palpi (Figs. 4, 5) long and slender (terminal segment 1.1–2.0× length of 2nd segment), with dense hairlike setae. Labial palpi (Figs. 4, 5) long and slender (terminal segment 1.0–1.5× length of 2nd segment), with dense hairlike setae. Thorax: Pronotum (Fig. 3) with anterolateral corners round (without projections), without setal fields; lateral margins not greatly expanded. Mesonotum with anterolateral margins not greatly expanded. Legs short (mid- and hindtibiae shorter than mid- and hindfemora). Abdomen: Operculate gills (Fig. 8) with tiny light spots; dorsal surface with dense stout-furcate setae. Caudal filaments (Fig. 14) 0.4–0.7× length of body, with longitudinal rows of long hairlike setae laterally on terminal filament and medially on cerci.

Adult. Head: Compound eyes of male separated by space 0.04–0.15x dorsal diameter of one compound eye. Thorax: Wings with various purplish brown markings. Hindwings (Fig. 19) with round basal costal projection. Abdomen: Segment 6–8 without posterolateral projections. Male genital forceps (Figs. 22–24) 3-segmented, rudimentary. Male and female with terminal filament minute. Male cerci relatively long, 2.2–4.5× length of body.

Distribution. Eastern Palearctic; Oriental; Western Nearctic (Oligocene).

Diagnosis. The larvae of *Potamanthellus* are distinguished from those of *Neoephemera* and *Ochernova* by their densely setate mouthparts (Figs. 4, 5), by their lack of well developed lateral expansions of the pronotum and mesonotum (Fig. 3), and by their possession of rows of long setae on the caudal filaments (Fig. 14). The adults of *Potamanthellus* are distinguished from those of *Neoephemera* by purplish markings on wings (Figs. 18, 19) and body, and their atrophied male genitalia (Figs. 22–24).

Remarks. We regard *Neoephemeropsis caenoides* Ulmer (1939) comb. n. as a member of *Potamanthellus*, and therefore *Neoephemeropsis* as a junior synonym of *Potamanthellus*. Although *P. caenoides* is derived at the base of the *Potamanthellus* clade (Fig. 34), its characterization does not warrant generic recognition apart from *Potamanthellus*.

Potamanthellus amabilis (Eaton) (Figs. 12, 16, 22, 29, 32)

Rhoenanthus amabilis Eaton, 1892:188: M (Lectotype: Kimmins, 1960, Burma, BM).
Potamanthellus horai Lestage, 1930:120: Ms Holotype, Vietnam, HAM. = *amabilis*: Ulmer, 1932.
Rhoenanthodes amabilis (Eaton): Lestage, 1930:136.

Potamanthellus amabilis (Eaton): Ulmer, 1932:211.
Neoephemeropsis cuaraoensis Dang, 1967:160, **syn. n.**: L (Vietnam).

Mature Larva. Dimensions (mm): Length of body 9.5; basal segment of antennae 0.15; flagellum of antennae 3.00; dorsal diameter of male compound eyes 0.45; 1st, 2nd, 3rd segment of maxillary palpi 0.20, 0.18, 0.20; 1st, 2nd, 3rd segment of labial palpi 0.25, 0.15, 0.18; femur, tibia, tarsus, claw of forelegs 1.20, 0.85, 0.95, 0.35; femur, tibia, tarsus, claw of midlegs 1.15, 0.90, 0.75, 0.35; femur, tibia, tarsus, claw of hindlegs 1.50, 1.25, 0.50, 0.35; length and width of operculate gills 1.13 and 1.13; caudal filaments 7.3. Head: Antennae pale. Labrum with dense, hairlike and stout setae anterodorsally. Terminal segment of maxillary palpi (Fig. 12) ca. 1.1× length of 2nd segment. Terminal segment of labial palpi ca. 1.2× length of 2nd segment. Thorax: Forefemora without dorsal, transverse row of simple-stout setae. Abdomen: Terga purplish brown with light markings. Posteromedian tubercle on abdominal tergum 1 minute, on tergum 2 distinct, and on tergum 6–8 rudimentary. Posterolateral projections moderately acute. Operculate gills dark purplish brown with tiny light spots; diagonal ridge present, indistinct. Caudal filaments (Fig. 16) ca. 0.8× length of body; rows of hairlike setae poorly developed.

Adult. Male dimensions (mm): Body length 7.6; dorsal diameter of compound eyes 0.75; forewings length 7.1; forewings width 3.3; hindwings length 2.3; hindwings width 1.5; femur, tibia, tarsal segment 1, 2, 3, 4, 5, and claw of forelegs 1.38, 1.88, 0.13, 0.68, 0.58, 0.38, 0.33, and 0.15; femur, tibia, and tarsus of midlegs 1.15, 0.88, and 0.70, hindlegs 1.38, 1.25, and 0.75; segment 1, 2, and 3 of forceps 0.125, 0.013, and 0.013; penis 0.125; cerci 19.5. Female lengths: Body 7.8; forewings 8.3; cerci 12.5. Head: Distance between compound eyes 0.05× dorsal diameter of eye. Thorax: purplish brown with irregular dark markings (lighter in female). Forewings with purplish markings; veins dark purplish brown; crossveins between C and Sc ca. 23, between Sc and R_1 ca. 20; CuA moderately arched basally, with 2–3 intercalaries (2–3 forked); A_1 with 2 veinlets and often with arched intercalary between CuP and A_1 basally attached to A_1; angle between veinlets and A_1 70–80°. Abdomen: Terga purplish brown with light markings, and with dark lateral stripes. Male genitalia as in Fig. 22.

Distribution. Oriental (Burma, southern China, Thailand, Vietnam).

Diagnosis. The larvae of *P. amabilis* are distinguished from other *Potamanthellus* spp. by the combination of a rudimentary diagonal ridge on the operculate gills, rudimentary tubercles on abdominal terga 6–8, lack of a setal row on the dorsal forefemora, relatively small body size, and relatively long caudal filaments that possess weakly developed lateral setae. Adults of *P. amabilis* are distinguished by the combination of heavily maculated wings, relatively small body size (<8 mm), and A_1 of the forewings that possesses two veinlets (angle between A1 and veinlets 70–80°).

Remarks. Based on comparisons of the type and non-type materials of *P. amabilis* and *P. horai*, we reconfirm Ulmer's (1932) synonymy of them. Based on reared material, we provide the first larval description of *P. amabilis* and redescribe the adult. We provisionally place *P. cuaraoensis* Dang (1967) as a junior subjective synonym of *P. amabilis* because characteristics noted by Dang, including the rudimentary abdominal tubercles, appear conspecific. Most mature larvae of *P. amabilis* were found in muddy overflow pools of Thai rivers, but some younger larvae were collected in mid channels by W. L. Peters (pers. comm.). All larval materials we have examined were covered with thick muddy debris. Adults were collected in March and November, with females more abundant than males at light.

Material examined. LECTOTYPE (*Rhoenanthus amabilis* Eaton, 1892): M, pinned, labeled as det. Kimmins, 1958, BAE-34), [BURMA], Tenasserim Valley (date and collector missing), BM. HOLOTYPE (*Potamanthellus horai* Lestage, 1930): Ms pinned, BAE-282, Tonkin [VIETNAM], Cho-moi , III–1896, Roget (also labeled as Mug., Paris, 1923; Coll., Ulmer, Eing. Nr. 6–63; Z.M.H. Hamburg), HAM. Other materials: 1M (reared), 21F, 1Fs, 17L, 1L exuviae (reared); CHINA (Kwangtung), THAILAND (Chiengmai); Berlin Museum, FAMU, UU.

Potamanthellus caenoides (Ulmer) comb. n. (Fig. 23)

Neoephemeropsis caenoides Ulmer, 1939:485: F (**Lectotype** designated here), Ms, Sumatra, HAM. L: Ulmer, 1939:606.

Mature Larva. Dimensions (mm): Length of body 6.5; basal segment of antennae 0.13; flagellum of antennae 2.30; dorsal diameter of male compound eyes 0.43; 1st, 2nd, 3rd segment of maxillary palpi 0.18, 0.13, 0.25; 1st, 2nd, 3rd segment of labial palpi 0.25, 0.15, 0.23; femur, tibia, tarsus, claw of forelegs 1.08, 0.75, 0.75, 0.25; femur, tibia, tarsus, claw of midlegs 1.00, 0.88, 0.68, 0.30; femur, tibia, tarsus, claw of hindlegs 1.38, 1.20, 0.75, 0.33; length and width of operculate gills 1.05 and 0.93; caudal filaments 3.5. Head: Antennae pale. Labrum with dense hairlike and stout setae anterodorsally. Terminal segment of maxillary palpi ca. 2.0× length of 2nd segment. Terminal segment of labial palpi ca. 1.5× length of 2nd segment. Thorax: Legs with broad purplish brown band on femora, tibiae, tarsi, and claws. Forefemora with subapical, dorsal, transverse row of 7–8 simple-stout setae. Abdomen: Terga purplish brown with light markings. Posteromedian tubercle on abdominal terga 1–2 and 6–8 distinct. Posterolateral projections moderately acute. Operculate gills dark purplish brown with tiny light spots; diagonal ridge distinct. Caudal filaments ca. 0.5× length of body; rows of hairlike setae strongly developed.

*Adult***.** Dimensions (mm): Body length 6.1; dorsal diameter of compound eyes 0.78; forewings length 6.0; forewings width 3.2. Female lengths: Body 6.7; forewings 7.8. Head: Distance between compound eyes 0.01× dorsal diameter of eye. Thorax: dark purplish brown. Forewings lightly purplish stained basally and

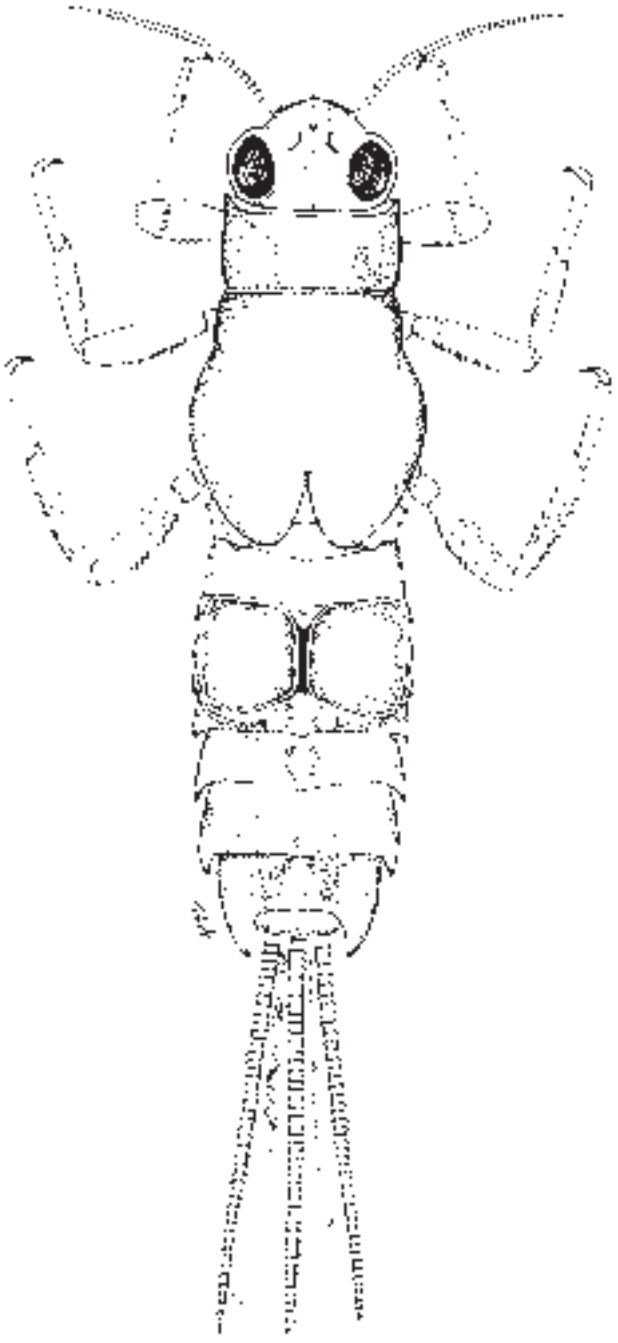


Fig. 3. *Potamanthellus edmundsi,* larval habitus.

near crossveins; veins lightly purplish stained; crossveins between C and Sc ca. 16, between Sc and R1 ca. 11; CuA slightly arched basally, with two intercalaries (one forked); A_1 with one veinlet and without intercalary between CuP and A_1; angle between veinlet and A_1 almost 90°. Abdomen: Terga purplish brown with poorly defined dark markings. Male genitalia as in Fig. 23.

Distribution. Oriental (Indonesia: Sumatra, Java, Bali, Lombok, Flores; Malaysia: Malay peninsula, Sabah, Sarawak; Philippines: Mindanao; Thailand)

Diagnosis. The larvae of *P. caenoides* are distinguished from other *Potamanthellus* spp. by the combination of a distinct diagonal ridge on operculate gills, distinct tubercles on abdominal terga 6–8, a setal row on the dorsal forefemora, relatively small body size (<8 mm), and relatively short caudal filaments that possess strongly developed lateral setae. The adults are distinguished by the combination of a strongly furcate genitalia (Fig. 23), weakly maculated wings, relatively small body size (<8 mm), and A1 of forewings that possesses a single veinlet (angle between A1 and veinlet almost 90°).

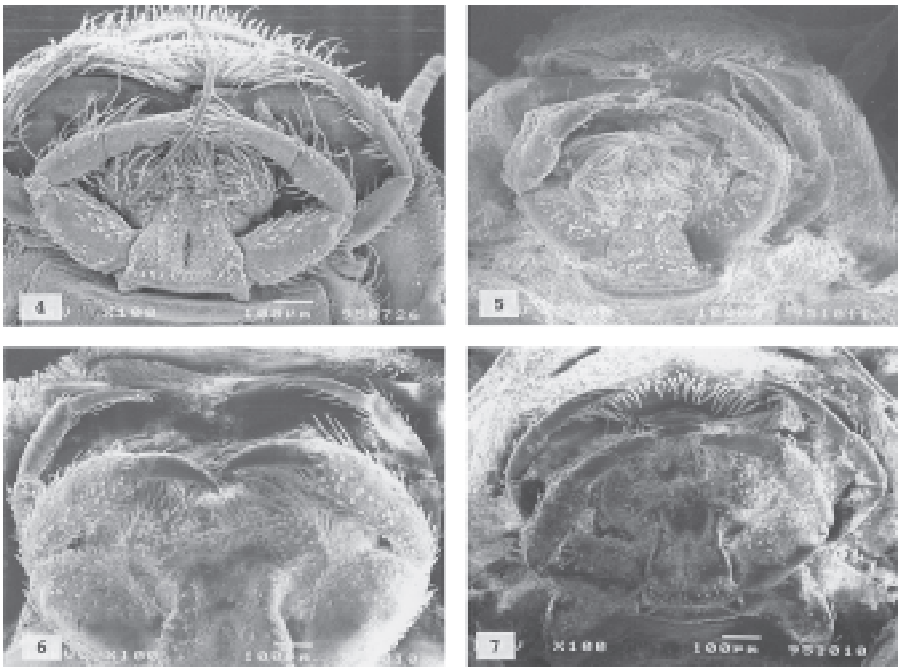
Remarks. We describe the male adult of *P. caenoides* (from Sarawak) for the first time. Larva, male subimago, and female adult were well illustrated by Ulmer (1939). Preserved larval specimens examined were covered with muddy debris; and live larvae have been taken in *Saraca* root balls in a Malaysian river by Edmunds (pers. comm.). Adults were collected throughout the year, indicative of a continuous emergence behavior common in tropical and subtropical southeast Asia.

Material examined. LECTOTYPE DESIGNATION: F (alcohol, legs except left hindleg, terminal filament, and 1 cercus absent, BAE-283), [INDONESIA], SUMATRA, Korintji-See (Korintj) Suc, mabra, VII.1915, leg. E. Jacobson (also labeled as *Neoephemeropsis caenoides* Ulmer, Type F, Zool. Mus. Hamburg, Coll. G. Ulmer, Eing. Nr. 6–1963), HAM. PARALECTOTYPES: 1 F (alcohol, damaged, BAE-284), same data as Lectotype, HAM; 1 Ms (alcohol, damaged, BAE-285), [INDONESIA], JAVA, Nongkodjadjar, Jan. 1911, E. Jacobson, HAM; 1 mature, 3 mid-grown, and 1 early instar L (alcohol, head, mouthparts, gills, and legs on slide, BAE-288), [INDONESIA], S d-SUMATRA, Ranau, Kali Warkak, 4.II.1929 (also labeled as R37d 4.2.29), HAM. Other materials: 1M, 2F, 43L, 1L exuviae; INDONESIA (BALI, FLORES, LOMBOK, SUMATRA), MALAYSIA (SABAH, SARAWAK) PHILIPPINES (MINDANAO), THAILAND (Chiengmai); FAMU, HAM, UU.

Potamanthellus chinensis (Hsu) (Figs. 4, 8, 10, 14, 18, 19, 24, 28)

Potamanthellus chinensis Hsu, 1935:321: M Holotype, China, (Jiangxi), lost.
Neoephemera KUa Yoon and Bae, 1988:181.
Neoephemeropsis rarus Tiunova and Levanidova, 1989:242, **syn. n.**: L Holotype, Russia (Primorye Territory), ZIP.
Potamanthellus rarus (Tiunova and Levanidova): Tiunova, 1991:136, **syn. n**.

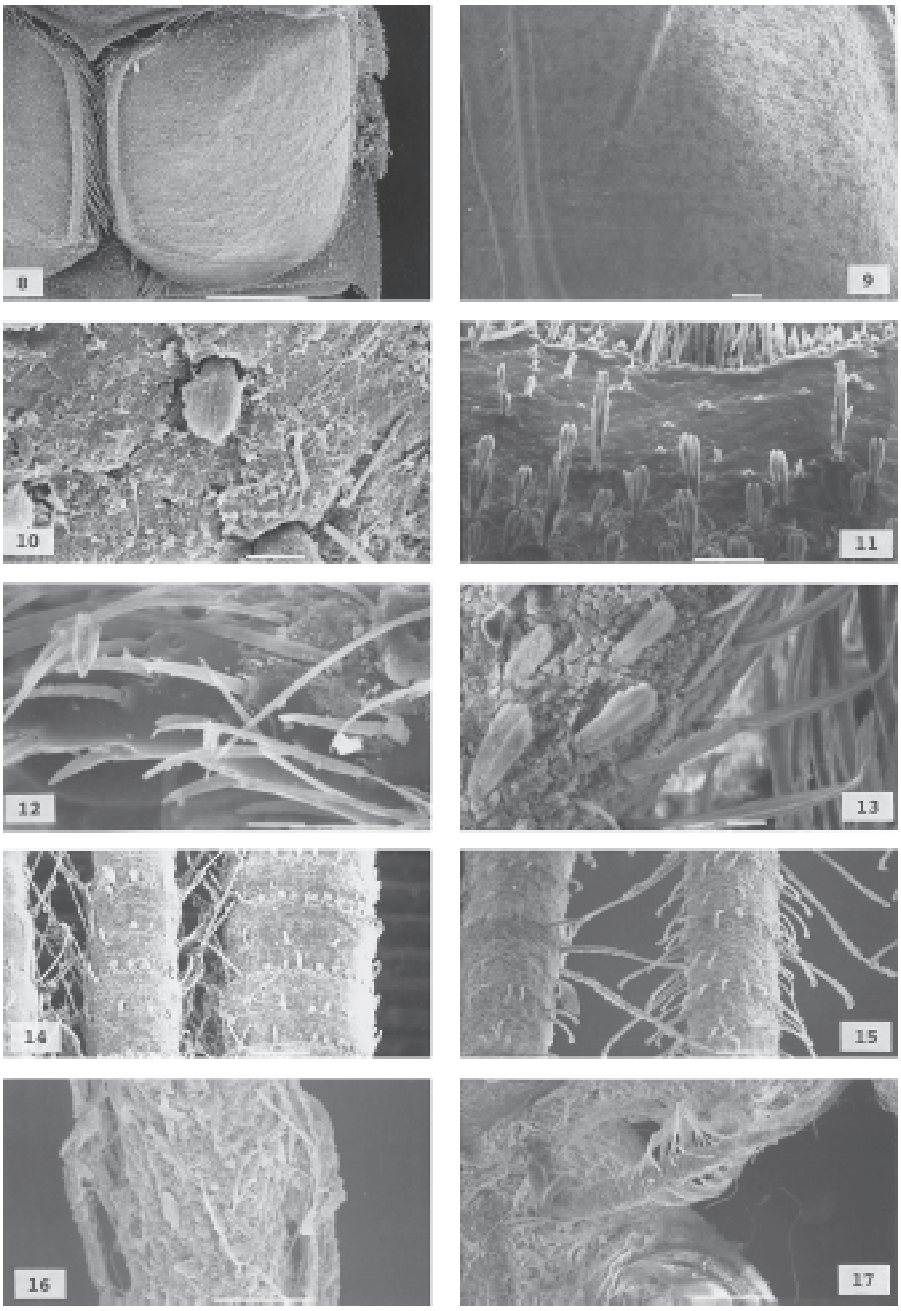
Mature larva. Dimensions (mm): Length of body 12.1; basal segment of antennae 0.2; flagellum of antennae 3.0; dorsal diameter of male compound eyes



Figs. 4–7. Larval mouthparts (bar=0.1mm): 4. *Potamanthellus chinensis*. 5. *P. edmundsi*. 6. *Neoephemera purpurea*. 7. *N. youngi*.

0.63; 1st, 2nd, 3rd segment of maxillary palpi 0.35, 0.25, 0.35; 1st, 2nd, 3rd segment of labial palpi 0.38, 0.30, 0.30; femur, tibia, tarsus, claw of forelegs 1.50, 1.00, 1.10, 0.50; femur, tibia, tarsus, claw of midlegs 1.15, 0.85, 1.00, 0.50; femur, tibia, tarsus, claw of hindlegs 2.00, 1.05, 1.25, 0.50; length and width of operculate gills 1.85 and 1.60; caudal filaments 5.7. Head: Antennae pale. Labrum with dense hairlike setae on anterodorsal margin, and with poorly developed stout setae on dorsal surface. Terminal segment of maxillary palpi (Fig. 4) ca. 1.4× length of 2nd segment. Terminal segment of labial palpi (Fig. 4) ca. 1.0× length of 2nd segment. Thorax: Legs with broad purplish brown band on femora, tibiae, tarsi, and claws. Forefemora without subapical, dorsal, transverse row of simple-stout setae. Abdomen: Terga purplish brown with light markings. Posteromedian tubercle on abdominal tergum 1 small, on tergum 2 distinct, and on tergum 6–8 rudimentary. Posterolateral projections moderately acute. Operculate gills (Figs. 8, 10) dark purplish brown with tiny light spots; diagonal ridge absent. Caudal filaments (Fig. 14) ca. 0.5× length of body; rows of hairlike setae well developed.

Adult. Dimensions (mm): Body length 10.5; dorsal diameter of compound eyes 1.10; forewings length 9.5; forewings width 4.7; hindwings length 3.2;



Figs. 8–9. Operculate gills: 8. *Potamanthellus chinensis* (bar=0.5mm). 9. *Neoephemera youngi* (bar=0.1mm).
Figs. 10–17. Larval setation: 10. Dorsal operculate gill, *P. chinensis* (bar=0.01mm). 11. Dorsal

hindwings width 2.2; femur, tibia, tarsal segment 1, 2, 3, 4, 5, and claw of forelegs 1.38, 2.65, 0.15, 1.10, 1.00, 0.60, 0.40, and 0.15; femur, tibia, and tarsus of midlegs 1.50, 0.75, and 0.90, hindlegs 1.65, 0.90, and 0.90; segments 1, 2, and 3 of forceps 0.225, 0.050, and 0.025; cerci 23.0. Female lengths: Body 12.0; forewings 13.0; cerci 23.5. Head: Distance between compound eyes 0.05× dorsal diameter of eye. Thorax: Pronotum purplish brown; meso- and metanotum light purplish yellow; pleura purplish brown; sterna purplish yellow. Forewings (Fig. 18) with purplish markings; veins dark purplish brown; crossveins between C and Sc ca. 26, between Sc and R1 ca. 25; 2–3 crossveins near bullae somewhat crowded; CuA moderately arched basally, with 3–4 intercalaries (3–4 forked); A_1 with 2 veinlets and often with arched intercalary between CuP and A_1 basally attached to A_1; angle between veinlets and A1 70–80°. Abdomen: Terga purplish brown with poorly defined light markings. Male genitalia as in Fig. 24.

Distribution. Eastern Palearctic (central and northeastern China, Korea, far eastern Russia).

Diagnosis. Larvae of *P. chinensis* are distinguished from other *Potamanthellus* spp. by the combination of the absence of a diagonal ridge on the operculate gills (Fig. 8), presence of rudimentary tubercles on abdominal terga 6–8, lack of a setal row on the dorsal forefemora, relatively large body size (>10 mm), and relatively short caudal filaments that possess strongly developed lateral setae (Fig. 14). Adults are distinguished by the combination of heavily maculated wings (Figs. 18–19), relatively large body size (>10 mm), and A_1 of the forewings that possess two veinlets (angle between A1 and veinlets 70–80°).

Remarks. From the descriptions of Hsu (1935–1936), Tiunova and Levanidova (1989), and Tiunova (1991), our examination of new and type materials of *P. amabilis*, *P. caenoides*, and *P. rarus*, it is apparent that *P. rarus* is conspecific with *P. chinensis*. Genital structure as well as ratio between segments of forceps suggested by Tiunova (1991) to separate those supposed species are not consistent. *Potamanthellus chinensis* is apparently the only large sized (>10 mm) species of the genus found in temperate East Asia, including central and northeastern China, Korea, and Far East Russia. The informal name *Neoephemera* KUa was used by Yoon and Bae (1988) for *P. chinensis* in Korea and thus appears in the synonymy above. In Korea, larvae of *P. chinensis* occur in the lower reaches of streams or large rivers, where current is relatively slow and the substrate is muddy. We have observed them sprawling on the substrate, and they are somewhat tolerant of water pollution. Emergence takes place in June and July.

---

anterior margin of labrum, *N. purpurea* (bar=0.05 mm). 12. Terminal segment of maxillary palp, *P. amabilis* (bar=0.01mm). 13. 2nd segment of labial palp, *N. purpurea* (bar=0.01mm). 14. Caudal filaments, *P. chinensis* (bar=0.1mm). 15. Caudal filaments, N. youngi (bar=0.1mm). 16. Cercus, *P. amabilis* (bar=0.05 mm). 17. Gill 1, *P. amabilis* (bar=0.1mm).

Materials examined. 12M, 56F, 2F (reared), 16L, 2L exuviae (reared); KOREA (Kangwon-do, Kyonggi-do), RUSSIA (Primorye); SWU.

Potamanthellus edmundsi sp. n. (Figs. 3, 5)

Mature larva. Dimensions (mm): Length of body 10.0; basal segment of antennae 0.15; flagellum of antennae 2.50; dorsal diameter of male compound eyes 0.50; 1st, 2nd, 3rd segment of maxillary palpi 0.25, 0.20, 0.30; 1st, 2nd, 3rd segment of labial palpi 0.30, 0.18, 0.28; femur, tibia, tarsus, claw of forelegs 1.3, 0.9, 0.8, 0.3; femur, tibia, tarsus, claw of midlegs 1.3, 0.9, 0.7, 0.4; femur, tibia, tarsus, claw of hindlegs 1.5, 1.0, 0.9, 0.4; length and width of operculate gills 1.38, 1.25; caudal filaments 5.0. Head: Antennae light purplish brown. Labrum with dense hairlike setae on anterodorsal margin, and with weakly developed stout setae on dorsal surface. Terminal segment of maxillary palpi (Fig. 5) ca. 1.5× length of 2nd segment. Terminal segment of labial palpi (Fig. 5) ca. 1.6× length of 2nd segment. Thorax: Color and setal pattern of legs as in Fig. 3. Abdomen: Terga purplish brown with light markings (Fig. 3). Terga 1–2 with small and distinct posteromedian tubercle; terga 6–8 with rudimentary posteromedian tubercle. Posterolateral projections acute. Operculate gills dark purplish brown with tiny light spots; diagonal ridge absent. Caudal filaments ca. 0.5× length of body; rows of hairlike setae moderately developed.

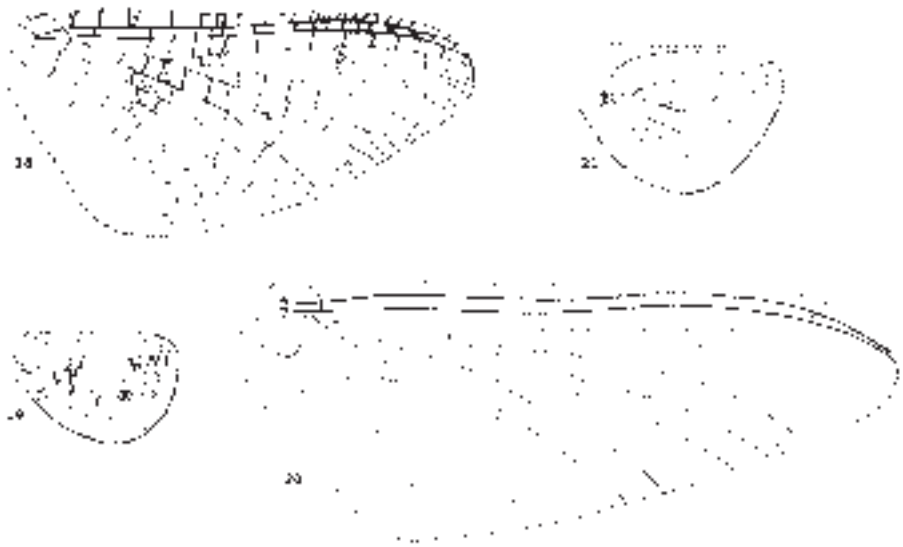
Adult. Unknown.

Distribution. Oriental (Thailand; Malaysia: Malay Peninsula).

Diagnosis. The larvae of *P. edmundsi* are distinguished from other *Potamanthellus* spp. by the combination of the absence of a diagonal ridge on the operculate gills, the presence of rudimentary tubercles on abdominal terga 6–8, very acute posterolateral projections on the abdomen, the presence of a row of setae on the dorsal forefemora, intermediate body size (8–11 mm), and relatively short caudal filaments with lateral rows of setae.

Remarks. This species is a sister species of *P. chinensis* (Fig. 34). Some larvae were found cohabiting with *P. caenoides*. We are honored to name this species after Professor G. F. Edmunds, Jr.

Material examined. HOLOTYPE: male last instar L (BAE-308, alcohol), MALAYSIA, Perak, stream 58 km S Grik (CL 2077), VIII–19–1985, J.T. & D.A. Polhemus, PERC. PARATYPES: 2 last instar L, same data as holotype, SWU; 1 mature L (BAE-310), MALAYSIA, Selangor, Sungai Tua, 6 mi N Batu Caves, IX–14–1978, G.F. & C.H. Edmunds, UU; 1 mature L (BAE-298), MALAYSIA, Gombak R, 6.5 mi N Kuala Lumpur nr Bentong rd, III–8–1969, J.E. Bishop, FAMU; 1 mature L (BAE-299), MALAYSIA, Gombak R, 6.5 mi N Kuala Lumpur nr Bentong rd, IV–3–1969, J.E. Bishop, FAMU; 1 L (BAE-300), MALAYSIA, Gombak R, 4.5 mi N Kuala Lumpur nr Bentong rd, IV–3–1969, J.E. Bishop, FAMU; 1 last instar L (BAE-307), THAILAND, Chengmai Prov., Mae Mao R, SW Fang Hort. Sta. (CL 2200), 500m, VIII–19–1985, J.T. & D.A. Polhemus (UU).



Figs. 18–21. Male adult wings: 18. forewing, *Potamanthellus chinensis*. 19. hindwing, *P. chinensis*. 20. forewing, *Neoephemera purpurea*. 21. hindwing, *N. purpurea*.

Potamanthellus ganges sp. n. (Fig. 27)

Mature larva. Dimensions (mm): Length of thorax 5.2, abdomen 7.2; femur, tibia of forelegs 2.0, 1.2; femur, tibia, tarsus, claw of midlegs 2.1, 1.3, 1.4, 0.6; femur, tibia, tarsus, claw of hindlegs 2.6, 1.8, 1.5, 0.7; length and width of operculate gills 2.00, 1.70; caudal filaments 8.6. Head: (missing). Thorax: Legs dark brown; claws blackish brown. Forefemora without subapical, dorsal, transverse row of setae. Abdomen: Terga and sterna dark brown, slightly purplish tinged, posterior segments darker. Posteromedian tubercle on abdominal tergum 1 small, on tergum 2 distinct, and on terga 6–8 distinct (Fig. 27). Posterolateral projections acute. Operculate gills (Fig. 27) dark brown without markings; diagonal ridge present, indistinct. Caudal filaments ca. 0.6× length of body; rows of hairlike setae poorly developed.

Adult. Unknown.

Distribution. Oriental (India).

Diagnosis. Larvae of *P. ganges* are distinguished from other *Potamanthellus* by the combination of a diagonal ridge on the operculate gills (not as distinct as in *P. caenoides*), distinct tubercles on abdominal terga 6–8, very acute posterolateral projections, the absence of a row of setae on the dorsal forefemora, and relatively large size (ca. 15 mm).

Remarks. This enigmatic species is known from a single larva from India, previously reported by Edmunds and Polhemus (1992) as *Neoephemeropsis* sp. (locality referred as "Kaukuhl River"). The larval specimen was covered with muddy debris, probably indicating its habitat. The name *ganges* is a noun in apposition (Ganges, the river where the type was taken).

Material examined. HOLOTYPE: mature female L (BAE-322, alcohol, head missing), INDIA, Horowar Dist., Kankhal R (trib to Ganges) at Anandamayee Ashram, II–12–1977, R. Koss, PERC.

Potamanthellus rubiensis Lewis

Potamanthellus rubiensis Lewis, 1977: 583: Oligocene L Holotype; Montana; S. E. Lewis collection, St. Cloud State Univ., Minnesota.

Distribution. Western Nearctic (Oligocene only).

Remarks. We were not allowed to examine material of this fossil species (S. Lewis, pers. comm.). It is not known in the adult stage; however, from the larval description (Lewis, 1977), it appears to have been placed correctly in *Potamanthellus*. Its limited characterization does not allow a comparative cladistic analysis, and thus it does not appear in the cladogram (Fig. 34). It is of some significance with respect to our biogeographic analysis because it is the only North American representative of the otherwise Asian genus *Potamanthellus*.

Genus ***Neoephemera*** McDunnough

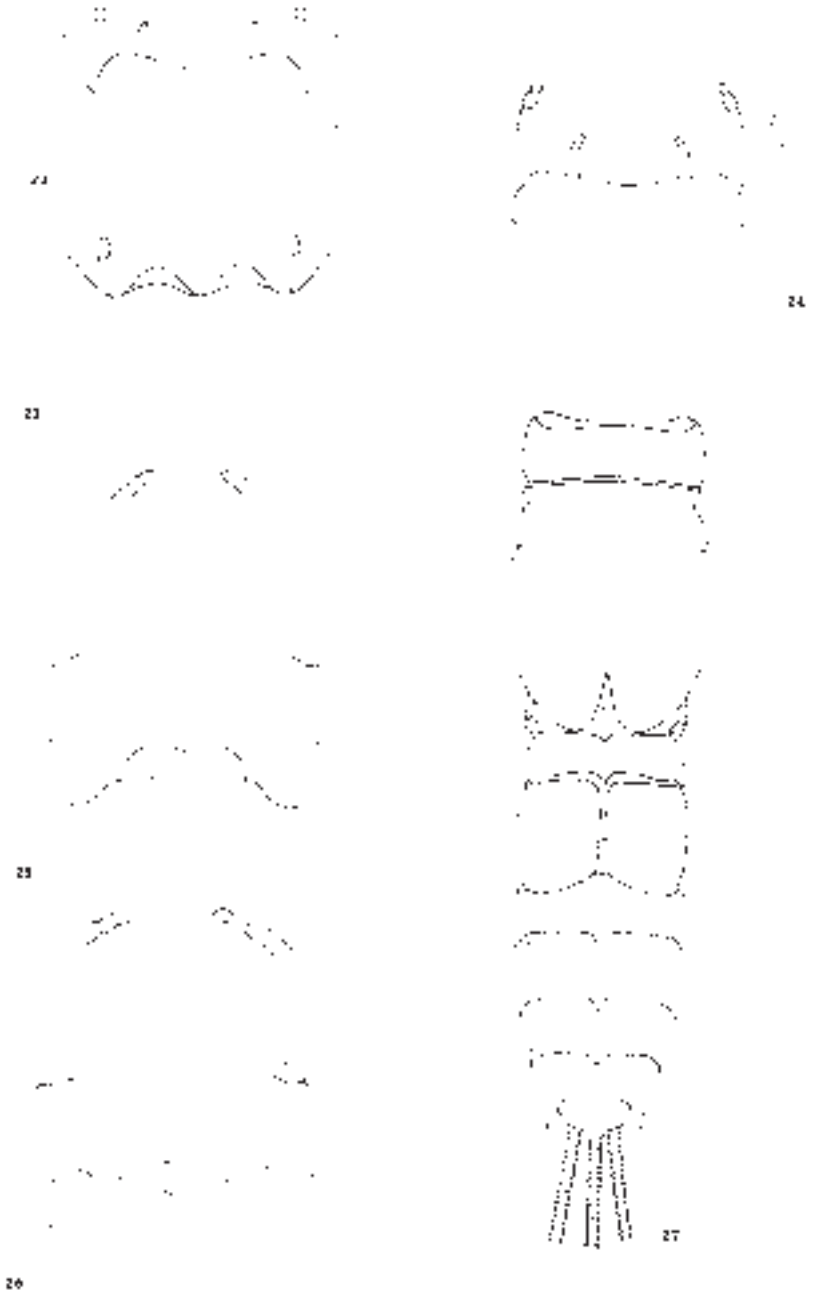
Neoephemera McDunnough, 1925:168. Type: *Neoephemera bicolor* McDunnough, 1925, by original designation.

Oreianthus Traver, 1931: 104. Type: *Oreianthus purpureus* Traver, 1931, by original designation. = *Neoephemera*: Burks, 1953.

Leucorhoenanthus Lestage, 1930:134, **syn. n**. Type: *Rhoenanthus macedonicus* Ulmer, 1920 [= *Neoephemera maxima* (Joly)], by original designation. = *Neoephemera* (*Leucorhoenanthus*): Demoulin, 1962.

Caenomera Demoulin, 1961:66, **syn. n**. Type: *Caenis maxima* Joly, 1870 [= *N. maxima* (Joly)], by original designation. = *Neoephemera* (*Caenomera*): Demoulin, 1961. = *Neoephemera* (*Leucorhoenanthus*): Demoulin, 1962.

Larva. Head: Anterior margin of labrum slightly emarginate. Maxillary palpi (Figs. 6–7) long and slender (terminal segment 0.7–1.3× length of 2nd segment), with sparse hairlike setae. Labial palpi (Figs. 6–7) long and slender (terminal segment 0.6–1.1× length of 2nd segment), with sparse hairlike setae. Thorax: Pronotum with well developed anterolateral projections; lateral margins greatly expanded. Mesonotum with anterolateral margins greatly expanded. Legs short (mid- and hindtibiae shorter than mid- and hindfemora). Abdomen: Operculate gills (Fig. 9) with or without tiny light spots; dorsal surface without dense stout-furcate setae. Caudal filaments (Fig. 15) 0.8–1.0× length of body, without rows of hairlike setae.



Figs. 22–27. Male genitalia: 22. *Potamanthellus amabilis*. 23. *P. caenoides*. 24. *P. chinensis*. 25. *Neoephemera maxima*. 26. *N. youngi*. Fig. 27. Larval thorax and abdomen: *P. ganges*.

Adult. Head: Compound eyes of male separated by space 0.15–1.15× dorsal diameter of one compound eye. Thorax: Wings without purplish brown markings. Hindwings (Fig. 21) with acute basal costal projection. Abdomen: Segment 6–9 with posterolateral projections. Male genital forceps (Figs. 25, 26) 4-segmented, fully developed. Male and female with terminal filament minute or subequal to cerci. Male cerci 1.2–2.3× length of body.

Distribution. Western and central Palearctic; eastern Nearctic.

Diagnosis. Larvae of *Neoephemera* are distinguished from those of *Ochernova* by their slightly to moderately emarginate labrum, relatively longer terminal segment of maxillary and labial palps (Figs. 6, 7, 13), as well as relatively shorter tibiae and caudal filaments (Fig. 15). They are distinguished from those of *Potamanthellus* by their sparsely setate mouthparts (Figs. 6, 7), well developed lateral expansions of pronotum and mesonotum, and lack of rows of long setae on the caudal filaments (Fig. 15). The adults of *Neoephemera* are distinguished from those of *Potamanthellus* by their stainless wings (Figs. 20, 21) and fully developed male genitalia (Figs. 25, 26).

Remarks. The species *N. maxima* (Joly) comb. n. has been referred to both *Leucorhoenanthus* Lestage (1930) and *Caenomera* Demoulin (1961) (see generic synonymy, above). Although this species occurs at the base of the *Neoephemera* clade (Fig. 34), its characterization does not warrant separate generic or subgeneric recognition.

Neoephemera bicolor McDunnough

Neoephemera bicolor McDunnough, 1925:168: M Holotype, Quebec, CNC. L: Berner, 1956:41.

Distribution. Eastern Nearctic (Canada: Quebec; USA: Indiana, Michigan).

Remarks. We were unable to borrow material of this species, but based on Berner (1956), its larvae [figs. 3, 7 in Berner (1956)] resemble those of *N. compressa* [figs. 4, 6 in Berner (1956)], differing only in minor details. The anterosubmedian tubercles of the pronotum are more widely spaced and are slightly less prominent, and the posterolateral projections of abdomen are slightly shorter and are less strongly curved ventrally. The adults of *N. bicolor* most resemble those of *N. compressa* and *N. youngi*, but they apparently have the unique combined characteristics of a single A_1 veinlet in the forewings, non-annulated tarsi, non-annulated caudal filaments, and intermediate size (McDunnough, 1925; Traver, 1935; Berner, 1956).

Neoephemera compressa Berner

Neoephemera compressa Berner, 1956:34 M (Holotype), F, L; Florida; FAMU.

Mature larva. Dimensions (mm): Length of body 10.2; 1st, 2nd, 3rd segment of maxillary palpi 0.25, 0.23, 0.25; 1st, 2nd, 3rd segment of labial palpi 0.25, 0.25, 0.28; femur, tibia, tarsus, claw of forelegs 1.9, 1.3, 1.1, 0.5; femur, tibia, tarsus, claw of midlegs 2.0, 1.6, 1.2, 0.6; femur, tibia, tarsus, claw of hindlegs 2.3, 1.8, 1.4, 0.7; length and width of operculate gills 1.13 and 1.33; caudal filaments 8.5. Head: Terminal segment of maxillary palpi ca. 1.1× length of 2nd segment. Terminal segment of labial palpi ca. 1.1× length of 2nd segment. Thorax: Pronotum with broad anterior margined by well-developed ridge, without setal fields; anterosubmedian tubercles well developed; anterolateral projections moderately developed and angulate; lateral expansions well developed. Mesonotum with well-developed and angulate anterolateral expansions, and with well-developed anterosubmedian and posteromedian tubercles. Abdomen: Posteromedian tubercle on terga 1–2 and 6–8 well developed. Posterolateral projections of segment 9 curved ventrally. Operculate gills with tiny light spots, without setal fields. Cerci ca. 0.8× body.

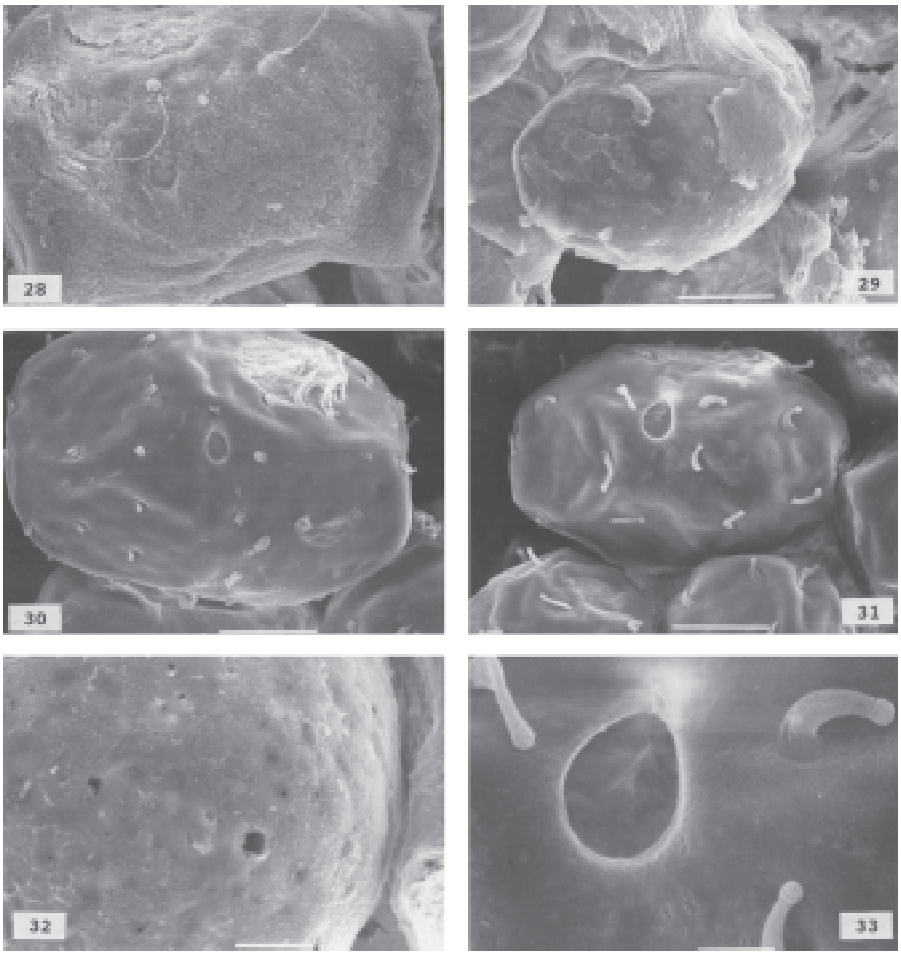
Adult. See description and figures of Berner (1956).

Distribution. Eastern Nearctic (USA: Florida, Georgia).

Diagnosis. The larvae of *N. compressa* are distinguished from other *Neoephemera* by the combination of moderately developed anterolateral projections and well developed anterosubmedian tubercles on the pronotum, well developed anterosubmedian and posteromedian tubercles on the mesonotum, angled anterolateral expansions on the mesonotum, and intermediate size. Adults are distinguished by the combination of a single A_1 veinlet in the forewings, annulated tarsi, non-annulated caudal filaments, and intermediate size. They apparently differ from *N. bicolor* only by heavily stained legs and blackish brown spots laterally and anteromedially on the abdominal sterna (Berner, 1956).

Remarks. This species is most closely related to *N. youngi*. Larvae have been taken from the Coastal Plain regions of southeastern USA, where they inhabit moss covered driftwood or debris in slow to moderately currents of streams (see Berner, 1956).

Material examined. 1 F (reared, with L exuviae); Florida; FAMU.



Figs. 28–33. Eggs: 28. *Potamanthellus chinensis chinensis* (bar=0.01 mm). 29. *P. amabilis* (bar= 0.05 mm). 30. *Neoephemera purpurea* (bar=0.05 mm). 31. *N. youngi* (bar=0.05 mm). 32. *P amabilis* (bar=0.01 mm). 33. *N. youngi* (bar=0.01 mm).

Neoephemera maxima (Joly) (Fig. 25)

Caenis maxima (?) Joly, 1870:142 [Material: L Holotype, France, lost (?)].
Tricorythus (?) sp.: Eaton, 1884:140.
Rhoenanthus macedonicus Ulmer, 1919:14 [M Holotype, Macedonia, HAM].
Leucorhoenanthus macedonicus (Ulmer): Lestage, 1930:135.
Oreianthus maximus (Joly): Traver, 1931:108.
Neoephemera maxima (Joly): Kazlauskas, 1959:158.
Oreianthus macendonicus (Ulmer): Ikonomov, 1960. =*Neoephemera maxima* (Joly): Illies, 1967:214.
Neoephemera (*Caenomera*) *maxima* (Joly): Demoulin, 1961:66.
Neoephemera (*Leucorhoenanthus*) *maxima* (Joly): Demoulin, 1962:369.
Neoephemera (*Leucorhoenanthus*) *macedonica* (Ulmer): Demoulin, 1962:369.
Leucorhoenanthus maximus (Joly): Tshernova et al., 1986:140.

Mature larva. Dimensions (mm): Length of body 7.5; antennae 1.9; dorsal diameter of male compound eyes 0.50; 1st, 2nd, 3rd segment of maxillary palpi 0.33, 0.23, 0.18; 1st, 2nd, 3rd segment of labial palpi 0.28, 0.23, 0.15; femur, tibia, tarsus, claw of forelegs 1.3, 0.9, 0.9, 0.4; femur, tibia, tarsus, claw of midlegs 1.4, 1.1, 0.9, 0.4; femur, tibia, tarsus, claw of hindlegs 1.7, 1.4, 1.0, 0.4; length and width of operculate gills 0.98 and 1.00; caudal filaments 6.5. Head: Head without distinct markings. Terminal segment of maxillary palpi ca. 0.78× length of 2nd segment. Terminal segment of labial palpi ca. 0.67× length of 2nd segment. Thorax: Pronotum with broad anterior margined by well-developed ridge; with dense, stout setae sublaterally near ridge; tubercles absent; anterolateral projections moderately developed and rounded; lateral expansions moderately developed. Mesonotum with moderately developed anterolateral expansions. Abdomen: Posteromedian tubercle on tergum 1 small, on tergum 2 well developed, on terga 6-8 rudimentary, and on tergum 9 absent. Operculate gills without light spots, with dense, stout setae anterodorsally. Cerci ca. 0.8× body.

Adult. Dimensions (mm): Body length 7.5; dorsal diameter of compound eyes 0.50; forewings length 8.4; forewings width 3.6; hindwings length 2.7; hindwings width 1.7; femur, tibia, tarsal segment 1, 2, 3, 4, 5, and claw of forelegs 1.48, 2.93, 0.13, 0.90, 0.60, 0.62, 0.38, and 0.13; femur, tibia, and tarsus of midlegs 1.40, 1.13, and 0.75, hindlegs 1.75, 1.55, and 0.75; segment 1, 2, 3, and 4 of forceps 0.225, 0.350, 0.017, and 0.033; penis 0.075; cerci 18.0. Female lengths: Body 9.0; forewings 8.5; hindwings 3.0; cerci 12.7. Head: dark purplish brown (lighter in female). Distance between compound eyes 1.15× dorsal diameter of eye. Thorax: dark purplish brown (slightly lighter in female); membranous area light yellow. Forewing veins hyaline; MAs ca. 1.1–1.2× length of MA_1; CuA with two intercalaries (one forked); A_1 with 2 veinlets and often with arched intercalary between CuP and A_1 basally attached to A_1. Hindwing veins hyaline. Forelegs femora light yellow; tibiae dark purplish brown; tarsi light brown; claws light brown. Mid- and hindlegs light yellow; claws dark purplish brown. Abdomen: Terga light yellow; posterior half of tergum 7 and terga 8–9 blackish brown (except median and lateral narrow area); tergum 10 blackish brown (except lateral narrow area). Male genitalia as in Fig. 25; terminal forceps segment not clearly articulated with segment 3. Cerci ca. 2.4× length of body in male, 1.4× body in female, not annulated. Terminal filament 0.03–0.07× length of body.

Distribution. Western Palearctic (France, Hungary, Poland, Yugoslavia, Lithuania).

Diagnosis. Larvae of *N. maxima* are distinguished from other *Neoephemera* by the absence of thoracic tubercles and acute anterolateral projections. Adults are easily distinguished by their rudimentary terminal filament and the blackish brown markings on abdominal terga 7–10.

Remarks. Types of *C. maxima* are not in the Toulouse Museum (A. Thomas, pers. comm.) or Paris Museum (J. Legrand, pers. comm.), and Eaton's materials are not in the British Museum (D. T. Goodger, pers. comm.). This is the only neoephemerid in Europe and the only species of *Neoephemera* in the Palearctic. Its distribution is now very localized, not having been found recently in Toulouse (type locality) (A. Thomas, pers. comm.), Hungary and Slovakia (S. Andrikovics, pers. comm.), Italy (C. Belfiore, pers. comm.), Switzerland (M. Sartori, pers. comm.), or Germany (D. Braasch, pers. comm.; U. Jacob, pers. comm.). Demoulin (1962) intimated that *N. macedonica* may prove to be a synonym of *N. maxima*. The only published consideration of such is the rather obscure footnote in Illies (1967) (see synonymy, above) in a list of European Ephemeroptera. It is clear from our analysis that the synonymy is correct. Larvae inhabit rivers or streams where current is slow and substrate is covered with detritus, algae, mosses, and other macrophytes in the summer (Jazdzewska, 1975; Kazlauskas, 1959). Mature larvae have been taken from April to May and reared adults from May to June (Jazdzewska, 1975). Jacob (pers. comm.) has observed adults of this species swarming early in the morning over the middle of large rivers.

Material examined. HOLOTYPE (*Rhoenanthus macedonicus* Ulmer, 1919): M (pinned, BAE-281), Mazedonien [MACEDONIA], Gradsco, VI.1917, W. Schröder leg., ded. 30.6.1917 (also labeled as G. Ulmer determ., 1917–23; *Rhoenanthus macedonicus* Ulmer, Type!; *Neoephemera maxima* Joly, 1975, det. Jacob, 1975; Z.M.H, Hamburg) (HAM). Other materials examined: 1 M (reared), 1 Ms (reared), 1 F (reared), 2 L, 3 L exuviae (reared); LITHUANIA, POLAND; Jazdzewska Collection, ZIP.

Neoephemera purpurea (Traver) (Figs. 6, 11, 13, 20, 21, 30)

Oreianthus purpureus Traver, 1931:105: F (Holotype), L; North Carolina; CU.
Neoephemera purpurea (Traver): Burks, 1953:43.

Mature larva. Dimensions (mm): Length of body 16.5; dorsal diameter of male compound eyes 0.75; 1st, 2nd, 3rd segment of maxillary palpi 0.28, 0.30, 0.28; 1st, 2nd, 3rd segment of labial palpi 0.40, 0.45, 0.28; femur, tibia, tarsus, claw of forelegs 2.4, 1.7, 1.5, 0.5; femur, tibia, tarsus, claw of midlegs 2.7, 2.5, 1.5, 0.5; femur, tibia, tarsus, claw of hindlegs 3.4, 3.2, 1.5, 0.6; length and width of operculate gills 1.83 and 1.88; caudal filaments 9.0. Head: Terminal segment of maxillary palpi (Fig. 6) ca. 1.92× length of 2nd segment. Terminal segment of labial palpi (Fig. 6) ca. 0.61× length of 2nd segment. Thorax: Pronotum with broad anterior margin not developed into ridge, without setal fields; tubercles rudimentary; anterolateral projections well developed and angulate; lateral expansions well developed. Mesonotum with well-developed and rounded anterolateral expansions. Abdomen: Posteromedian tubercle on terga 1–2 well developed, on terga 6–7 small, and on tergum 8 rudimentary. Operculate gills with tiny light spots, without setal fields. Cerci ca. 0.6× body.

Adult. Dimensions (mm): Body length 13.1; dorsal diameter of compound eyes 1.63; forewings length 13.3; forewings width 5.2; femur, tibia, tarsal segment 1, 2, 3, 4, 5, and claw of forelegs 2.7, 4.1, 0.2, 1.4, 1.3, 0.7, 0.5, and 0.3; femur, tibia, and tarsus of midlegs 2.7, 2.8, and 1.5, of hindlegs 3.5, 3.5, and 1.0; segment 1, 2, 3, and 4 of forceps 0.500, 1.000, 0.075, and 0.100; caudal filaments 20.2. Female lengths: Body 15.0; forewings 16.5; femur, tibia, and tarsus of forelegs 2.8, 2.3, and 1.8; femur, tibia, and tarsus of midlegs 3.2, 3.1, and 1.7, of hindlegs 4.2, 4.0, and 1.8; caudal filaments 22.0. Head: dark brown. Distance between compound eyes ca. 0.15× dorsal diameter of eye. Thorax: Pronotum dark brown; meso- and metanotum purplish brown; pleura light purplish brown; sterna purplish brown. Forewings (Fig. 20) with longitudinal veins purplish black; crossveins purplish brown; MAs ca. 0.7× length of MA_1; CuA with two forked intercalaries; A_1 with two veinlets (one incomplete) and usually with one arched intercalary between CuP and A_1 basally attached to A_1. Hindwing (Fig. 21) veins purplish black to light brown. Forefemora purplish brown; foretibiae dark purplish brown; foretarsi and foreclaws light brown; midlegs and hindlegs purplish brown with light marking on each tarsal segment 1. Abdomen: Terga brown to purplish brown; sterna light brown to brown. Male genitalia as in Fig. 26; terminal forceps segment articulated with segment 3. Cerci and terminal filament ca. 1.5× length of body, not annulated.

Distribution. Eastern Nearctic (USA: Georgia, North Carolina, South Carolina, Tennessee, Virginia, West Virginia).

Diagnosis. Larvae of *N. purpurea* are distinguished from other North American *Neoephemera* by the combination of greatly developed anterolateral projections and rudimentary anterosubmedian tubercles on the pronotum, round anterolateral expansions on the mesonotum, and large size. Adults are distinguished by the combination of pigmented veins of wings, two A_1 veinlets in the forewings (one often incomplete), non-annulated tarsi and caudal filaments, and large size.

Remarks. This Appalachian Mountains species develops in slow to swift currents, under stones, debris dams, or root banks (see Traver, 1937; Berner, 1956).

Material examined. 1M, 1M (reared), 2F, 1Fs, 1L, 1L exuviae (reared); SOUTH CAROLINA; FAMU, PERC.

Neoephemera youngi Berner (Figs. 7, 9, 15, 26, 31, 33)

Oreianthus sp. No. 1 Traver, 1937:83: L.
Neoephemera youngi Berner, 1953:145: M (Holotype), F; Georgia; FAMU.

Mature larva. Dimensions (mm): Length of body 8.1–11.0; dorsal diameter of male compound eyes 0.53; 1st, 2nd, 3rd segment of maxillary palpi 0.20, 0.20,

0.25; 1st, 2nd, 3rd segment of labial palpi 0.25, 0.25, 0.25; femur, tibia, tarsus, claw of forelegs 1.8, 1.1, 1.1, 0.6; femur, tibia, tarsus, claw of midlegs 1.9, 1.9, 1.7, 0.6; femur, tibia, tarsus, claw of hindlegs 2.2, 1.8, 1.3, 0.6; length and width of operculate gills 1.25 and 1.38; caudal filaments 8.0–9.0. Head: Terminal segment of maxillary palpi (Fig. 7) ca. 1.25× length of 2nd segment. Terminal segment of labial palpi (Fig. 7) ca. 1.00× length of 2nd segment. Thorax: Pronotum with broad anterior not margined by well-developed ridge, without setal fields; tubercles rudimentary; anterolateral projections moderately developed and angulate; lateral expansions well developed. Mesonotum with well-developed and rounded anterolateral expansions. Abdomen: Posteromedian tubercle on terga 1–2 well developed, and on terga 6–8 rudimentary. Posterolateral projections of segment 9 curved ventrally. Operculate gills (Fig. 9) with tiny light spots, without setal fields. Cerci (Fig. 15) ca. 0.9× body.

Adult. Dimensions (mm): Body length 7.0; dorsal diameter of compound eyes 0.90; forewings length 7.9; forewings width 2.9; hindwings length 2.1; hindwings width 1.6; femur, tibia, tarsal segment 1, 2, 3, 4, 5, and claw of forelegs 1.00, 1.90, 0.08, 0.60, 0.53, 0.35, 0.30, and 0.15; femur, tibia, and tarsus of midlegs 1.38, 1.13, and 0.75, of hindlegs 1.68, 1.25, and 0.75; segment 1, 2, 3, and 4 of forceps 0.225, 0.500, 0.050, and 0.050; caudal filaments 8.8. Female lengths: Body 7.7; forewings 9.2; hindwings 2.3; femur, tibia, and tarsus of forelegs 1.55, 1.13, and 0.88; femur, tibia, and tarsus of midlegs 1.55, 1.25, and 0.88, of hindlegs 1.93, 1.63, and 0.88; caudal filaments 9.0. Head: purplish brown with light spots. Distance between compound eyes ca. 0.25× dorsal diameter of eye. Thorax: shiny dark purplish brown; pronotum with dark lateral stripes. Forewing veins hyaline; MAs ca. 1.2–1.5× length of MA_1; CuA with two intercalaries (one forked); A_1 with 1 veinlet and usually without arched intercalary between CuP and A_1 basally attaching to A_1. Hindwing veins hyaline. Legs white with purplish brown markings on apex of femora, midlength of tibiae, and apex of each tarsal segment; claws purplish brown. Abdomen: Terga dark purplish brown with numerous light spots; sterna light with dark anterolateral spots. Male genitalia as in Fig. 26; terminal forceps segment articulated with segment 3. Caudal filaments ca. 1.2× length of body, annulated.

Distribution. Eastern Nearctic (USA: Alabama, Florida, Georgia, South Carolina).

Diagnosis. Larvae of *N. youngi* are distinguished from other North American *Neoephemera* by the combination of moderately developed anterolateral projections and rudimentary anterosubmedian tubercles on the pronotum, round anterolateral expansions on the mesonotum, and intermediate size. Adults are distinguished by the combination of a single A_1 veinlet in the forewings, annulated tarsi and caudal filaments, and intermediate size.

Remarks. Larvae develop in the slow to moderately swift streams among plant debris or roots (see Berner, 1950). Berner and Pescador (1988) reviewed detailed unpublished data from Jones (1977) regarding the biology of this species.

Material examined. 1M, 20F, 3F (reared), 4L, 3L exuviae (reared); ALABAMA, GEORGIA, FLORIDA, SOUTH CAROLINA; FAMU, INHS, PERC.

Genus ***Ochernova*** gen. n.

Type: *Neoephemera tshernovae* Kazlauskas, 1963.

Larva. Head: Anterior margin of labrum deeply emarginate. Maxillary palpi short and stout (terminal segment ca. 0.35× length of 2nd segment), with few hairlike setae. Labial palpi short and stout (terminal segment ca. 0.39× length of 2nd segment), with few hairlike setae. Thorax: Pronotum with slightly developed anterolateral projections; lateral margins slightly expanded. Mesonotum with anterolateral margins slightly expanded. Legs long and slender; mid- and hindtibiae, respectively, longer than mid- and hindfemora. Abdomen: Operculate gills without tiny white spots; dorsal surface without stout-furcate setae. Caudal filaments longer than body length, ca. 1.4× length of body, without rows of hairlike setae.

Adult. Unknown.

Distribution. Central Palearctic (Tadzhikistan, Uzbekistan).

Diagnosis. The larvae of *Ochernova* are distinguished from those of *Neoephemera* by their relatively long legs and caudal filaments, relatively short and stout maxillary and labial palpi, and greatly notched labrum. They are distinguished from *Potamanthellus* by their sparsely setate mouthparts, well-developed lateral expansions of the pronotum and mesonotum, and lack of rows of long setae on the caudal filaments.

Remarks. *Ochernova* is a highly distinctive sister lineage to that of *Neoephemera* (Fig. 34). The genus group name is in honor of the late Dr. O. A. Tshernova, who pioneered mayfly systematics in much of the Asian Palearctic.

Ochernova tshernovae (Kazlauskas) comb. n.

Neoephemera tshernovae Kazlauskas, 1963:582: L Holotype, Uzbekistan, ZIP.

Mature larva. Dimensions (mm): Length of body 10.8; basal segment of antennae 0.15; flagellum of antennae ca. 2.0; dorsal diameter of female compound eyes 0.28; 1st, 2nd, 3rd segment of maxillary palpi 0.38, 0.50, 0.18; 1st,

2nd, 3rd segment of labial palpi 0.45, 0.45, 0.18; femur, tibia, tarsus, claw of forelegs 2.7, 2.4, 1.1, 0.4; femur, tibia, tarsus, claw of midlegs 2.8, 3.2, 1.1, 0.5; femur, tibia, tarsus, claw of hindlegs 3.5, 4.3, 1.2, 0.5; length and width of operculate gills 2.00 and 1.25; caudal filaments 15.0. Head: Head globular, purplish brown, covered with numerous tiny spots; vertex slightly darker, without markings or tubercles; clypeal margin round, with row of hairlike setae. Labrum with hairlike and stout setae anterodorsally. Basal and 2nd segment of labial palpi relatively long and broad. Glossae and paraglossae pointed; paraglossae longer than glossae. Thorax: purplish brown, without markings, covered with numerous tiny spots. Pronotum with broad anterior margined by well-developed ridge, without setal fields, poorly developed anterolaterally and laterally. Legs without distinct markings or armature; forelegs, midlegs, and hindlegs ca. 0.6×, 0.7×, and 0.9× length of body, respectively. Abdomen: terga purplish brown, without markings, covered with numerous tiny spots. Posteromedian tubercle on abdominal tergum 1 absent, on tergum 2 small, on tergum 6 absent, on tergum 7 small, on tergum 8 rudimentary, and on tergum 9 absent. Posterolateral projections of abdominal segment 7–9 moderately developed. Operculate gills somewhat rectangular, purplish brown; diagonal ridge distinct. Posterior margin of tergum 10 with large median process.

Adult. Unknown.

Distribution. Central Palearctic (Tadzhikistan, Uzbekistan).

Remarks. *Ochernova tshernovae* is the only known species. Larvae have been found in the moss on driftwood in streams (N. Kluge, pers. comm.).

Material examined. 1L; TADZHIKISTAN; ZIP.

KEY TO GENERA AND SPECIES

Known larvae.

1. Pronotum with anterolateral projections. Mesonotum with anterolateral expansions. Mouthparts with sparse setae (Figs. 6, 7). Caudal filaments without longitudinal rows of setae (Fig. 15). 2
1'. Pronotum without anterolateral projections (Fig. 3). Mesonotum without anterolateral expansions (Fig. 3). Mouthparts relatively setaceous (Figs. 4, 5). Caudal filaments with rows of lateral setae (Fig. 3, 14). Genus *Potamanthellus*, 7
2. Hindtibiae slightly longer than hindfemora. Caudal filaments nearly 1.5× length of body. Segment 3 of maxillary and labial palpi short (<0.4× length of segment 2). Genus *Ochernova* gen. n., *O. tshernovae* comb. n.
2'. Hindtibiae as long as, or shorter than, hindfemora. Caudal filaments shorter than body. Segment 3 of maxillary and labial palpi relatively long (>0.6× length of segment 2). Genus *Neoephemera*, 3
3. Pronotum without anterosubmedian tubercles. *N. maxima*
3'. Pronotum with anterosubmedian tubercles. 4
4. Pronotum with well-developed anterolateral projections. Mature body 14–17 mm. *N. purpurea*
4'. Pronotum with moderately developed anterolateral projections. Mature body 8–11 mm. 5

5. Pronotum with rudimentary anterosubmedian tubercles. Mesonotum with round anterolateral expansions and without anterosubmedian tubercles. Abdominal terga 6–8 with rudimentary posteromedian tubercle. *N. youngi*
5'. Pronotum with distinct anterosubmedian tubercles. Mesonotum with pointed anterolateral expansions and with anterosubmedian tubercles. Abdominal terga 6–8 with distinct posteromedian tubercle. 6
6. Anterosubmedian tubercles of pronotum approximate. *N. compressa*
6'. Anterosubmedian tubercles of pronotum well separated. *N. bicolor*
7. Operculate gills without diagonal ridge (Fig. 3). 8
7'. Operculate gills with diagonal ridge. 9
8. Dorsal forefemora with transverse row of setae (Fig. 3). Mature body 8–11 mm. *P. edmundsi* sp. n.
8'. Dorsal forefemora without transverse row of setae. Mature body >12 mm. *P. chinensis*
9. Abdominal terga 6–8 with rudimentary posteromedian tubercle. *P. amabilis*
9'. Abdominal terga 6–8 with distinct posteromedian tubercle. 10
10. Dorsal forefemora with transverse row of setae. Mature body 6–8 mm. *P. caenoides*
10'. Dorsal forefemora without transverse row of setae. Mature body ca. 15 mm. *P. ganges* sp. n.

Known adults.

1. Wings without markings; basal C-Sc crossveins of forewings reduced (Fig. 20). Penes furcate, not separated beyond subgenital plate; forceps fully developed, 4-segmented; segment 1 ca. 0.5× length of segment 2 (Figs. 25, 26). *Neoephemera*, 2
1'. Wings with purplish markings; basal C-Sc crossveins of forewings not reduced (Fig. 18). Penis either greatly furcate (Fig. 23) or widely separated beyond subgenital plate (Figs. 22, 24); forceps rudimentary, 2 or 3-segmented (Figs. 22–24). *Potamanthellus*, 6
2. Terminal filament of male and female rudimentary (<0.1× length of cerci). Abdominal tergum 7–10 with broad dark median marking. Compound eyes of male relatively apart (distance between compound eyes ca. 1.0× diameter of a eye). *N. maxima*
2'. Terminal filament of male and female as long as cerci. Abdominal tergum 7–10 without broad dark median marking. Compound eyes of male close (distance between compound eyes <0.5× diameter of a compound eye). 3
3. Longitudinal veins of forewings purplish black. Mature body >13 mm. *N. purpurea*
3'. Longitudinal veins of forewings pale. Mature body 7–10 mm. 4
4. Caudal filaments annulated. *N. youngi*
4'. Caudal filaments not annulated. 5
5. Forefemora colored. Tarsi annulated. *N. compressa*
5'. Forefemora pale. Tarsi not annulated. *N. bicolor*
6. A_1 of forewings with 1 veinlet; angle between A_1 and veinlet almost 90°. Penes greatly furcate (Fig. 23). *P. caenoides*
6'. A_1 of forewings with 2 veinlets; angle between A_1 and veinlet 70–80° (Fig. 18). Penes widely separated beyond subgenital plate (Figs. 22, 24). 7
7. Mature body relatively large (>10.0 mm). *P. chinensis*
7'. Mature body relatively small (6–9 mm). *P. amabilis*

PHYLOGENY

The standard cladistic methodology we use was thoroughly discussed by Bae and McCafferty (1991) and McCafferty and Wang (1994). The outgroup for determining character state polarity is generally other Rectracheata and particularly pannote groups (i.e., Caenidae, Ephemerellidae, Leptohyphidae, Tricorythidae, etc.). Although McCafferty (1991) indicated that Baetiscidae could be the sister group of Neoephemeridae, based on internal anatomical data from Landa (1969, 1973) and Landa and Soldán (1985), there are more compelling morphological data showing that Caenidae, not Baetiscidae, is the sister group of Neoephemeri-

Table 1. Cladistic characters and character states (0 = plesiomorphy; 1 = apomorphy; 2, 3 = phenoclinal apomorphies).

Character	Character State
1. Labrum margin	0. Slightly to moderately emarginate 1. Deeply emarginate
2. Terminal segment of maxillary palp	0. >0.6× length of segment 2 1. <0.4× length of segment 2
3. Maxillary palp setation	0. Dense on segment 3 1. Sparse on segment 3
4. Terminal segment of labial palp	0. >0.6× length of segment 2 1. <0.4× length of segment 2
5. Labial palp setation	0. Dense on segment 3 1. Sparse on segment 3
6. Pronotum lateral expansion	0. Absent 1. Present
7. Mesonotum anterolateral expanision	0. Absent 1. Present
8. Pronotum anterosubmedian tubercles	0. Absent 1. Present
9. Mesonotum anterosubmedian tubercles	0. Absent 1. Present
10. Hindtibiae	0. <1.0× length of hindfemora 1. 1.2× length of hindfemora
11. Operculate gill	0. With distinct diagonal ridge 1. With reduced diagonal ridge 2. With vestigial diagonal ridge 3. Without diagonal ridge
12. Larval caudal filaments	0. Without rows of long setae 1. With rows of long setae
13. Wing markings	0. Without markings 1. With purplish brown markings
14. Veins of wings	0. Colored 1. Hyaline
15. Basal crossveins between C and Sc, forewings	0. Present 1. Absent
16. Larval caudal filaments	0. <1.0× length of body 1. 1.4× length of body
17. Adult terminal filament	0. Subequal to cerci 1. <0.1 length of cerci
18. Forceps	0. 4-segmented 1. 3-segmented
19. Penes	0. Not separated beyond subgenital plate 1. Separated beyond subgenital plate

dae (Wang et al., 1997). We therefore consider Caenidae the most closely related family.

With respect to interfamilial relationships, certain synapomorphies define Neoephemeridae as a monophyletic group. Larval synapomorphies are related to gill structure (Figs. 3, 8, 9). One synapomorphy is the single diagonal ridge found on the dorsum of the operculate gills of abdominal segment 2. In Caenidae and *Teloganella* complex (McCafferty and Wang, 1995), the dorsal ridge is Y-shaped. This ridge is secondarily lost in two most apotypic sister species of *Potamanthellus*. The second synapomorphy is the presence of well-developed setae on the inner margins of the operculate gills. In Caenidae, setae are well developed on the outer margin of the operculate gills. The third synapomorphy is the presence of broadly based, highly branched fibrillae on the outer margins of gills on abdominal segments 3–6. When fibrillae are present in Caenidae, they are narrow basally and undivided or forked.

Within the Pannota, Neoephemeridae also has a possible defining adult synapomorphy. This is the presence in the forewings of one or two veinlets attached to A_1 at almost right angles (Figs. 18, 20). The "forked A_1" of the forewings is unique among Pannota, but may be symplesiomorphic with that of Potamanthidae. The basally arched MP_2 and CuA of the forewings is also unique among Pannota, but may be symplesiomorphic with Ephemeroidea.

The cladistic characters used for hypothesizing intrafamilial relationships are given in Table 1. Figure 34 represents the cladogram deduced from our cladistic data; numbers in Fig. 34 are defining synapomorphies that correspond to apomorphies listed in Table 1. The most basal branch in the cladogram is strongly evidenced by five larval and five adult synapomorphies. The first of these branches is recognized as the genus *Potamanthellus* containing five extant species, whose branching sequence is evidenced by one phenoclinal character. The second of the two basal branches (Fig. 34) is relatively strongly branched (evidenced by five larval and one adult synapomorphies) into one lineage containing one species and another containing five species. By using a sequencing convention (Nelson, 1972, 1973), we recognize these distinctive lineages as the genera *Ochernova* and *Neoephemera*.

BIOGEOGRAPHY

Our methods for hypothesizing historical biogeography include the application of distributional patterns to cladistics data, and they were explained in detail by Bae and McCafferty (1991). We essentially employ a vicariance model with the understanding that mayflies are capable diffusion dispersers (Edmunds, 1972, 1982), and that dispersal models for intra-regional studies can be appropriate [e.g., Mesoamerican biogeography shown by McCafferty et al. (1992)].

Neoephemeridae shows a typical Laurasian distributional pattern (Fig. 1) involving the European Palearctic [P(EU)], central Asia [P(CA)], east Asia [P(EA)],

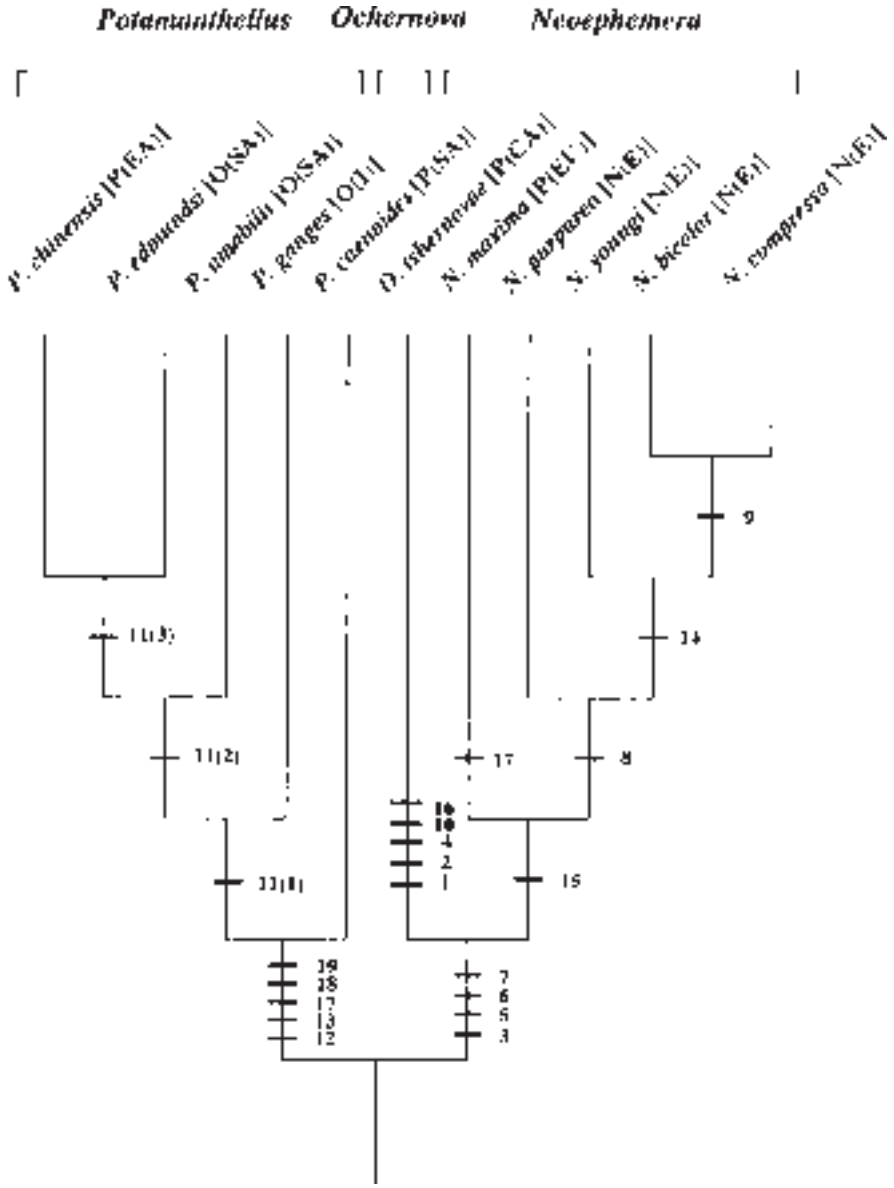


Fig. 34. Cladogram of extant Neoephemeridae [numbers are synapomorphies (see Table 1), bracketed letters refer to distribution, (see Biogeography)].

eastern Nearctic [N(E)], and Oriental (southeast Asia) [O(SA)] and India [O(I)]. The Oligocene fossil *P. rubiensis* is from the western Nearctic [N(W)].

Potamanthellus occurs in northeast Asia (far eastern Russia, Korea, northeastern China) and southeast Asia (southeastern China, Indochina, Malay peninsula, Indonesia, Philippines), and northern India. A comprehensive faunistic survey conducted in southeast Asia by Edmunds and Polhemus (1992) showed that Neoephemeridae (*Potamanthellus*) are restricted by Wallace's Line, as evidenced by their absence in the Celebes. *Neoephemera* occurs in the eastern Nearctic and European Palearctic. *Ochernova* occurs in central Asia (Tadzhikistan, Uzbekistan).

The distributional pattern of the Neoephemeridae appears to be most similar to that of the Potamanthidae [see Fig. 1 of Bae and McCafferty (1991)]. The reduced area cladogram (Fig. 35) of the Neoephemeridae that is generated from the species cladogram (Fig. 34) shows that the affinity between Palearctic east Asia and the Orient is strongest. Neoephemeridae, unlike Potamanthidae, however, shows closer affinities between eastern North America, Europe, and central Asia than between any of these and Palearctic east Asia. Based on the fossil *P. rubiensis*, western North America is more closely related to Palearctic east Asia than to eastern North America. This idea is in agreement with the "Asiamerica-Euramerica hypothesis" that was also exemplified in the Potamanthidae (Bae and McCafferty, 1991) and amply evidenced in other biota (e.g., Cox, 1974) .

It is probable that the ancestor of the hypothesized Neoephemeridae + Caenidae lineage was widespread throughout Pangaea (Caenidae is essentially cosmopolitan). A subsequent Neoephemeridae ancestor possibly either became isolated in Laurasia or originated there. Within the Neoephemeridae, after dispersal throughout most of the Northern Hemisphere, it is probable that the bifurcation of the *Potamanthellus* clade and the *Neoephemera* + *Ochernova* clade coincided with a Cretaceous vicariant event isolating Asiamerica from Euramerica. Within the

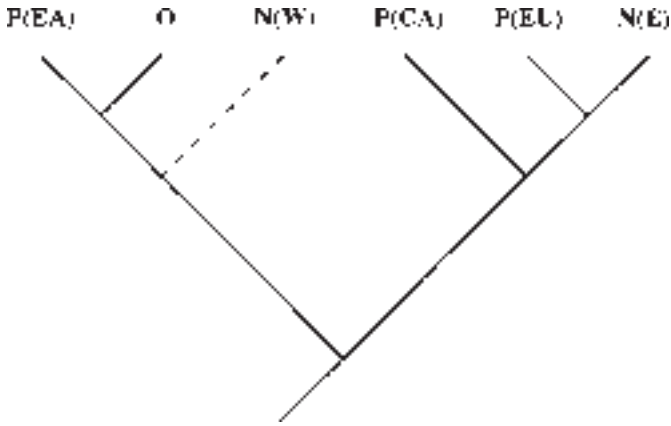


Fig. 35. Reduced area cladogram of Neoephemeridae (dashed branch represents fossil).

Neoephemera + *Ochernova* clade, the dichotomy between the generic lineages may coincide with another vicariance between Euramerica and central Asia probably sometime from the Cretaceous to Eocene. The Eocene vicariance of Europe and eastern North America would account for the isolation of one extant species of *Neoephemera* in Europe. Within the *Potamanthellus* clade, *P. chinensis* is isolated in temperate east Asia. The presence of *P. ganges* in India would have to be explained by dispersal sometime after the connection of the Indian subcontinent with Asia in the Eocene.

ACKNOWLEDGMENTS

We wish to thank G. Edmunds (Salt Lake City), W. Peters (Tallahassee), and H. Strümpel (Hamburg) for allowing examination of their collections. The following provided additional materials: S. Brooks (London), K. Günther (Berlin), T. Jazdzewska (Lodz), N. Kluge (St. Petersburg), K. Methven (Champaign, Illinois), and T. Tiunova (Vladivostok); and S. Andrikovics (Eszterházy), U. Aspöck (Vienna), C. Belfiore (Naples), L. Berner (Gainesville, Florida), D. Braasch (Potsdam), D. Chun (St. Petersburg), D. Dudgeon (Hong Kong), D. Goodger (London), H. Gui (Nanjing), S. Ishiwata (Kanagawa, Japan), S. Kang (Taichung, Taiwan), J. Legrand (Paris), S. Lewis (St. Cloud, Minnesota), M. Klonowska-Olejnik (Kraków), M. Sartori (Lausanne), F. Stehr (East Lansing, Michigan), A. Thomas (Toulouse), J. van Tol (Leiden), and N. Watanabe (Kagawa, Japan) provided useful information. Vietnamese translation was provided by staff at Hankuk University of Foreign Studies. Drawings were by S. Park (Seoul). The manuscript was critically read by C. Lugo-Ortiz and T. Wang (West Lafayette) and W. Peters (Tallahassee). Research was supported by Non-Directed Research Fund, Korea Research Foundation provided to the first author in 1994, and the paper has been assigned Purdue Agricultural Research Program Journal Number 15028.

REFERENCES

BAE, Y.J. and W.P. McCAFFERTY (1991): Phylogenetic systematics of the Potamanthidae (Ephemeroptera). – Trans. Am. Entomol. Soc. 117: 1–143.

BERNER, L. (1950): The mayflies of Florida. Univ. Florida Press, Gainesville, Florida.

— (1953): New mayfly records from Florida and a description of a new species. – Florida Entomol. 36: 145–149.

— (1956): The genus *Neoephemera* in North America (Ephemeroptera: Neoephemeridae). – Ann. Entomol. Soc. Am. 49: 33–42.

BERNER, L. and M.L. PESCADOR (1988): The mayflies of Florida, revised edition. Univ. Presses Florida, Tallahassee.

BURKS, B.D. (1953): The mayflies, or Ephemeroptera of Illinois. – Bull. Illinois Nat. Hist. Surv. 26: 1–216.

COX, C.B. (1974): Vertebrate paleodistributional patterns and continental drift. J. Biogeogr. 1: 75–94.

DANG, N.T. (1967): New genera, new species of the invertebrate fauna of fresh and brackish waters of North Vietnam. Tap San Sinh vat Dia Hoc 6: 155–165. (in Vietnamese).

DEMOULIN, G. (1958): Nouveau Schema de Classification des Archodonates et des Ephemeropteres. – Inst. royal Sci. nat. Belgique 34: 1–19.

— (1961): A propos des donnees recentes sur la *Caenis maxima* Joly (Ephemeroptera). – Bull. Ann. Soc. Roy. Entomol. Belg. 97: 63–68.

— (1962): A propos des donnees recentes sur *Leucorhoenanthus macedonicus* (Ulmer) (Ephemeroptera). – Bull. Ann. Soc. Roy. Entomol. Belg. 98: 368–370.

EATON, A.E. (1881): An announcement of new genera of the Ephemeridae. – Entomol. Mon. Mag. 17: 191–197.

— (1883–88): A revisional monograph of recent Ephemeridae or mayflies. – Trans. Linn. Soc., 2nd Ser. Zool., 3: 1–346.

— (1892): New species of Ephemeridae from the Tenasserium Valley. – Trans. Entomol. Soc. London. p. 185–190.
EDMUNDS, G.F., Jr. (1962): The principle applied in determining the hierarchic level of the higher categories of Ephemeroptera. – Syst. Zool. 11: 22–31.
— (1965): The classification of Ephemeroptera in relation to the evolutionary grade of nymphal and adult stages. – Proc. XII Internat. Congr. Entomol., London, 1964: 112.
— (1972): Biogeography and evolution of Ephemeroptera. – Ann. Rev. Entomol. 17: 21–42.
— (1982): Historical and life history factors in the biogeography of mayflies. – Am. Zool. 22: 371–374.
EDMUNDS, G.F., Jr. and D.A. POLHEMUS (1992): Zoogeographical patterns among mayflies (Ephemeroptera) in the Malay Archipelago, with special reference to Celebes. – p. 49–56 In: KNIGHT, W.J. and J.D. HOLLOWAY (Eds.) Insects and Rain forests of south east Asia. Royal Entomol. Soc. London.
EDMUNDS, G.F., Jr. and J.R. TRAVER (1954): An outline of a reclassification of the Ephemeroptera. – Proc. Entomol. Soc. Wash. 56: 236–240.
HANDLIRSCH, A. (1925): Überordnung: Ephemeroidea. – p. 414–424 In: C. SCHRÖDER (Ed.) Handbuch der Entomologie. Vol. 3. Gustav Fischer Verlag, Jena.
HSU, Y.C. (1935–36): New Chinese mayflies from Kiangsi Province (Ephemeroptera). – Peking Nat. Hist. Bull. 10: 319–326.
— (1936–37): The mayflies of China. – Peking Nat. Hist. Bull. 2(2): 129–148.
IKONOMOV, P. (1960): Die Verbreitung der Ephemeropteren in Makedonien. – Acta Muz. Mac. Sci., Natur. 7: 41–74.
ILLIES, J. (1967): Ephemeroptera. – p. 212–219 In: J. ILLIES (Ed.) Limnofauna Europaea. Gustav Fischer Verlag, Stuttgart.
JACOBSEN, G.G. and V.L. BIANCHI (1905): VIII. Mayflies. – p. 847–890 In: Orthoptera and Pseudoneuroptera of the Russian–Empire. Petrograd. (in Russian).
JAZDZEWSKA, T. (1975): *Neoephemera maxima* (Joly, 1870) (Ephemeroptera, Neoephemeridae) in Poland. – Bull. Entomol. Pologne (Wroclaw). 45: 227–238.
JOLY, E. (1870): Contributions pour servir à l'histoire naturelle des Ephémérines. – Bull. Soc. Hist. Nat. Toulouse. 4: 142–151, pl. 3.
JONES, J. (1977): The ecology, life cycle, and seasonal distribution of *Neoephemera* (s.s.) *youngi* Berner (Ephemeroptera: Neoephemeridae). – Unpubl. Masters Thesis, Fla. St. Univ., Tallahassee.
KAZLAUSKAS, R. (1959): Material about the mayflies (Ephemeroptera) in Lithuanian SSR with description of new species *Eurylophlebia lithuanica* Kazlauskas and imago *Neoephemera maxima* (Joly). – Vilniaus Valstybinio v. Kapsuko Vardo Universiteto Mokslo Darbai 23: 157–174.
— (1963): New and little-known mayflies (Ephemeroptera) from the USSR. – Entomol. Obozr. 42: 582–593.
KIMMINS, D.E. (1960): A list of the type-specimens of Ephemeroptera in the British Museum (Natural History). – Bull. Br. Mus. nat. Hist. (Ent.). 25: 307–324.
KLAPÁLEK, F. (1909): I. Ephemerida, Eintagsfliegen. – p. 1–32 In: BRAUER, A. (Ed.) Die Süsswasserfauna Deutschlands 8.
KOSS, R.W. and G.F. EDMUNDS, Jr. (1974): Ephemeroptera eggs and their contribution to phylogenetic studies of the order. – Zool. J. Linn. Soc. 55: 267–349.
LANDA, V. (1969): Comparative anatomy of mayfly larvae (Ephemeroptera). – Acta Entomol. Bohemosl. 66: 289–316.
— (1973): A contribution to the evolution of the order Ephemeroptera based on comparative anatomy. – p. 155–159 In: W.L. PETERS and J.G. PETERS (Eds.) Proc. 1st Intern. Conf. Ephem. Brill, Leiden.
LANDA, V. and T. SOLDÁN. (1985): Phylogeny and higher classification of the order Ephemeroptera: a discussion from the comparative anatomical point of view. – Academia, Prague.
LESTAGE, J.A. (1917): Contribution a l'étude des larves des Ephémères Paléarctiques. – Ann. Biol. 8: 213–457.
— (1930): Contribution a l'étude des larves des Ephémèroptéres. VII. Le groupe Potamanthidien. – Mém. Soc. Entomol. Belg. 23: 73–146.
LEWIS, S.E. (1977): Two new species of fossil mayflies (Ephemeroptera: Neoephemeridae and Siphlonuridae) from the Ruby River Basin (Oligocene) of southwestern Montana. – Proc. Entomol. Soc. Wash. 79: 583–587.

McCAFFERTY, W.P. (1991): Toward a phylogenetic classification of the Ephemeroptera: a commentary on systematics. – Ann. Entomol. Soc. Am. 84: 343–360.
McCAFFERTY, W.P. and G.F. EDMUNDS, Jr. (1979): The higher classification of the Ephemeroptera and its evolutionary basis. – Ann. Entomol. Soc. Am. 72: 5–12.
McCAFFERTY, W.P., R.W. FLOWERS, and R.D. WALTZ. (1992): The biogeography of Mesoamerican mayflies. – Tulane Studies in Zool. Bot., Suppl. Publ. 1: 173–193.
McCAFFERTY, W.P. and T.-Q. WANG. (1994). Phylogenetics and the classification of the *Timpanoga* complex (Ephemeroptera: Ephemerellidae). – J. N. Am. Benthol. Soc. 13:569–579.
— (1995): A new genus and species of Tricorythidae (Ephemeroptera) from Madagascar. – Ann Limnol. 31: 179–183.
McDUNNOUGH, J. (1925): New Canadian Ephemeridae with Notes III. – Canadian Entomol. 57: 168–176.
NELSON, G.J. (1972): Phylogenetic relationships and classification. – Syst. Zool. 21: 227–231.
— (1973): Classification as an expression of phylogenetic relationships. – Syst. Zool. 22: 344–359.
TIUNOVA, T.M. (1991): Description of imago *Potamanthellus rarus* (Ephemeroptera, Neoephemeridae) from Primorye. – Zool. Zh. (Moskba) 7: 136–138. (in Russian).
TIUNOVA, T.M. and I.M. LEVANIDOVA. (1989): Description of a new mayfly species (Ephemeroptera) from the Soviet Far East. – Aquatic Insects 4: 241–245.
TRAVER, J.R. (1931): A new mayfly genus from North Carolina. – Canadian Entomol. 63: 103–109.
— (1935): Part II. Systematics. – p. 239–739 In: J.G. NEEDHAM, J.R. TRAVER, and Y.C. HSU. The biology of mayflies. Comstock Publ. Co., Ithaca, New York.
— (1937): Notes on mayflies of the southeastern states. – J. Elisha Mitchell Sci. Soc. 53: 27–86.
TSHERNOVA, O.A. (1960): Position of the family Neoephemeridae in a system of mayfly order (Ephemeroptera). –Nauk. Dokl. V. Shkol., Biol. Nauk. 4: 52–58. (in Russian).
— (1970): On the classification of fossil and recent Ephemeroptera. – Entomol. Obozr. 49: 124–145. (in Russian).
TSHERNOVA, O.A., N. KLUGE, N.D. SINITSHENKOVA, and V.V. BELOV. (1986): 5. Order Ephemeroptera. p. 99–142 In: Identification of Insects of Far East USSR. LER, P.A. (Ed.) Vol. 1. Leningrad Press, Leningrad. (in Russian).
ULMER, G. (1919): Neue Ephemeropteren. – Arch. Naturgsch. 85: 1–80.
— (1920): Übersicht über die Gattungen der Ephemeropteren, nebst Bemerkungen über einzelne Arten. – Stett. Entomol. Zeit. 81: 97–144.
— (1932): Bemerkungen über die seit 1920 neu aufgestellten Gattungen der Ephemeropteren. – Stett. Entomol. Zeitg. 93: 204–219.
— (1939): Eintagsfliegen (Ephemeropteren) von den Sunda–Inselin. – Arch. Hydrobiol. Suppl. 16:443–692.
YOON, I.B. and Y.J. BAE. (1988): I. Order Ephemeroptera. p. 95–184 In: Illustrated encyclopedia of fauna & flora of Korea. Vol. 30 Aquatic insects. – Ministry of Education, Seoul.
WANG, T.-Q., W.P. McCAFFERTY, and Y.J. BAE. (1997): Sister relationships of the Neoephemeridae and Caenidae (Ephemeroptera: Pannota). – Entomol. News. in press.